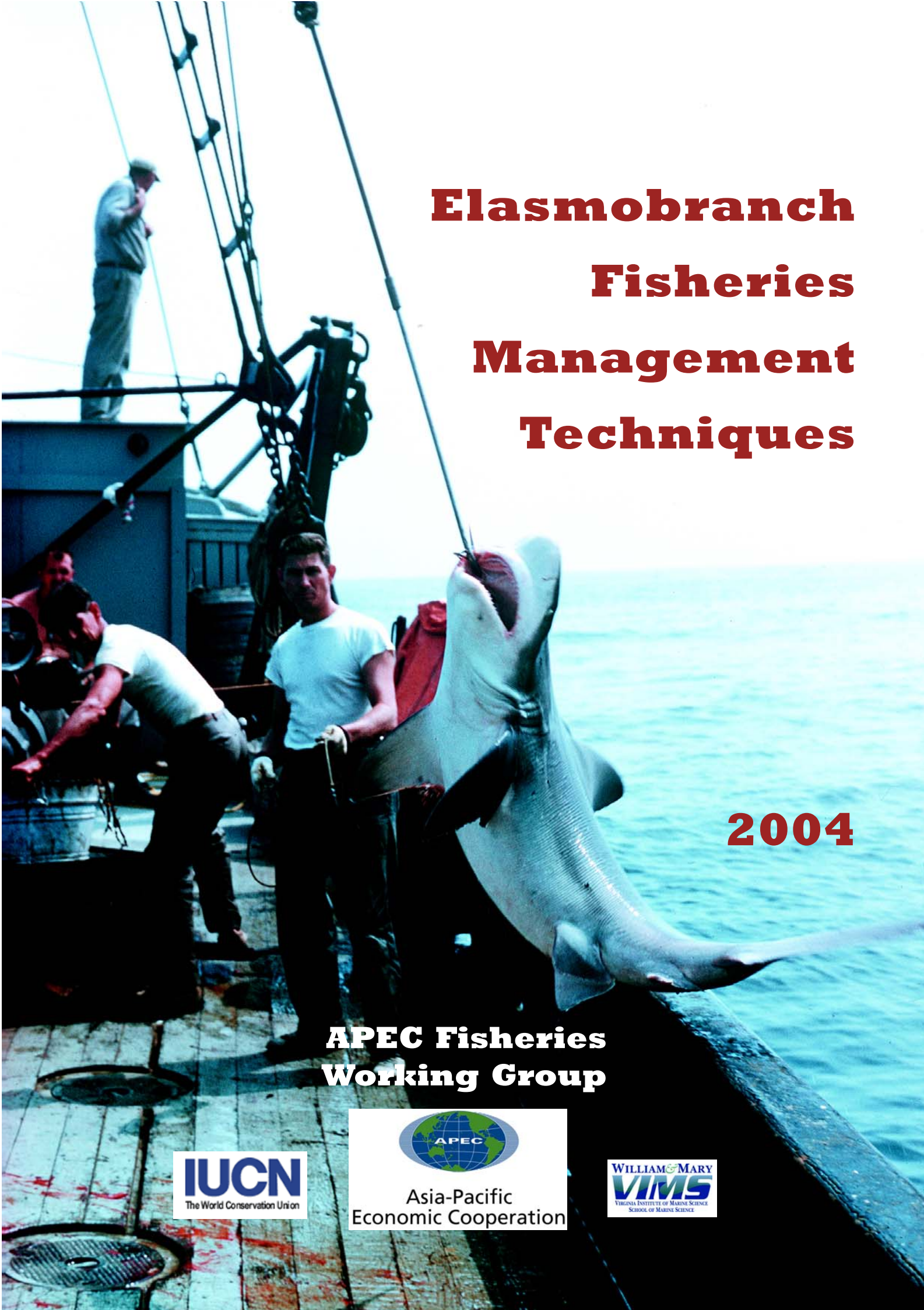

Elasmobranch Fisheries Management Techniques

2004

APEC Fisheries Working Group

IUCN The World Conservation Union

Asia-Pacific Economic Cooperation

William & Mary VIMS Virginia Institute of Marine Science School of Marine Science

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Edited by
John A. Musick
Ramón Bonfil

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DEDICATION

This book is dedicated to the shark fishers and fishery managers. May they have the wisdom and will to achieve and maintain sustainable shark fisheries.

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CHAPTER 1. INTRODUCTION: MANAGEMENT OF SHARKS AND THEIR RELATIVES (ELASMOBRANCHII)

John A. Musick, Virginia Institute of Marine Science, College of William and Mary, PO Box 1346, Gloucester Point, VA 23062 USA

Sharks and their relatives, the rays (subclass Elasmobranchii) are a group of about 1,100 species of mostly marine fishes (Compagno, 2001). Most sharks and rays that have been studied have slow growth, late maturity and very low fecundity compared to bony fishes (Camhi et al., 1998). These attributes result in very low intrinsic rates of increase (Smith et al., 1998) and very low resilience to fishing mortality (Hoenig and Gruber, 1990). Thus, most shark and ray populations can withstand only modest levels of fishing without depletion and stock collapse (Camhi et al., 1998; Musick, 1999; Cortes, 2000), and decline more rapidly and are not able rebound as quickly as other fishes to population reductions (Sminkey and Musick, 1995; 1996). Consequently, management must be implemented at the inception of shark fisheries (Musick, 1999). However, this has not been the case for the vast majority of shark fisheries that have developed around the world (Bonfil, 1994). Rather, the overwhelming pattern has been one of no management, rapid stock decline and collapse, with decades to recovery if recovery occurs at all (Anderson, 1990; Hoff and Musick, 1990).

Successful sustainable fisheries for sharks are possible, particularly for smaller species that mature early and have a relatively large number of young. The fishery for gummy sharks (*Mustelus antarcticus*) in Australia stands as a good example. Success in this fishery has come through knowledge of the biology of the species and active management measures (mostly through regulation of mesh size in the gillnet fishery) (Walker, 1998; Stevens, 1999). Even sharks with very low intrinsic rates of increase may be harvested sustainably if sufficient information exists on their demography and an effective management strategy can be enforced. Simpfendorfer (1999) reported on the sustainable dusky shark (*Carcharhinus obscurus*) fishery in Western Australia, which is focused on a limited catch (500-700 mt/yr) of young-of-the-year fish, with protection of all other age classes.

Although many sharks and rays have been of lower economic value in fisheries, the economic impact of stock collapse may be similar to more productive species because the population recovery time and economic loss last much longer (Musick, 1999). Well-documented cases of collapsed shark fisheries are the porbeagle (*Lamna nasus*) fishery in the North Atlantic (Anderson, 1990; Campana et al., 2001), the tope or soupfin shark (*Galeorhinus galeus*) fishery off California and Australia (Ripley, 1946; Olsen, 1959), various basking shark (*Cetorhinus maximus*) fisheries (Parker and Stott, 1965), the spiny dogfish (*Squalus acanthias*) fisheries both in the North Sea and off British Columbia (Holden, 1968; Ketchen, 1986; Hoff and Musick, 1990), and most recently the large coastal shark fishery off the east coast of the U.S. (Musick et al., 1993; NMFS, 1999). While the reasons behind the collapse of some of these fisheries

range from stock depletion to economic constraints or market changes (Ketchen, 1986; Myklevoll, 1989; Bonfil, 1994; 1999), the pattern of long periods for stock recovery prevails, and at least the stock of California soupfin shark has not recovered to its former level after more than 50 years despite the lack of fishing.

Although directed fisheries have been the cause of stock collapse in many species of elasmobranchs, a more important threat to long-lived sharks and rays is mortality in mixed-species fisheries and bycatch in fisheries targeted at other species (Bonfil, 1994; Musick, 1999). In those fisheries, species with higher production rates continue to support the fishery while species with lower rebound potential are driven to stock collapse or extirpation (Musick, 1999; Stevens et al., 2000). Thus the sand tiger (*Carcharias taurus*) and dusky shark (*Carcharhinus obscurus*) populations, which have very low intrinsic rates of increase, collapsed in the western North Atlantic shark fin fisheries in the late 1980s and show only modest signs of recovery (after ten years of fishery regulation), while the more productive sandbar shark (*Carcharhinus plumbeus*), although depleted, continues to drive the fisheries (Musick et al., 1993; Musick, 1999). Similarly, the barndoor skate (*Dipturus laevis*) is taken as bycatch in the New England and Canadian Atlantic ground fisheries and its decline and local extinction would have been unnoticed were it not for the fishery-independent data sets (where individual species are recorded) that were analyzed by Casey and Myers (1998). Several other large species of skates may be threatened with extinction (Dulvy and Reynolds, 2002). Imprecise reporting of fishery statistics where several species are lumped together as one category (i.e., "sharks" or "skates") can mask basic changes in community structure and profound reduction in populations of the larger, slower growing species (Dulvy et al., 2000). Thus the traditional paradigm that fisheries will become commercially extinct before the targets of those fisheries become biologically extirpated does not apply in many cases.

Several species of elasmobranchs depleted by fisheries have recently come under protection of national regulations. The barndoor skate, two species of sawfishes (*Pristis pectinata, P. perotteti*) and the sand tiger (*Carcharias taurus*), dusky (*Carcharhinus obscurus*), and night (*Carcharhinus signatus*) sharks were added in 1999 to the U.S. National Marine Fisheries Service (NMFS) Candidate List for Threatened and Endangered Species because of large documented declines caused by overfishing (Diaz-Soltera, 1999). *Pristis pectinata* has since been listed as Endangered. The sand tiger, dusky and several other species of sharks became protected under the NMFS Fishery Management Plan (FMP) for Sharks of the Atlantic Ocean (NMFS, 1999). The sand tiger and great white sharks are also protected by regulations in South Africa and Australia (Camhi et al., 1998). In recent years the status of elasmobranch species has come under closer scrutiny worldwide by the World Conservation Union (IUCN) Shark Specialist Group (SSG), and 62 shark species out of 226 species assessed are currently recognized as threatened with extinction (IUCN, 2003). The number of threatened species will certainly increase as all the sharks and batoids are assessed (>1100 species).

In addition to the obvious concern over possible extinction of some elasmobranch species and the ensuing economic hardship due to the collapse of the fisheries, a further problem is the negative effects that strong declines in apex predators can have on ecosystems. The removal of sharks occupying the role of top predators in their ecosystems can have not only the expected effect of releasing control over their main prey, but sometimes unexpected second and third degree effects on non-prey species through trophic linkages (Stevens et al., 2000; Schindler et al., 2002).

International concern over the sustainability of shark fisheries started to build in the late 1980s and early 1990s as shark fisheries expanded globally in response to lucrative shark fin markets in southeast Asia (Bonfil, 1994; Rose, 1996). In 1994 the 9th Conference of Parties (CoP) to the Convention on International Trade of Endangered Species (CITES) adopted a resolution on "The Status of International Trade in Shark Species." The resolution called upon the United Nations Food and Agriculture Organization (FAO) to review information on the global status of shark stocks and the effects of international trade on them. The FAO with appropriate international expert consultation developed an International Plan of Action for the Conservation and Management of Sharks (IPOA-Sharks) which was adopted in 1999. For the purpose of the IPOA-Sharks, the term "shark" includes all chondrichthyans (sharks, batoids, and chimaeras). The guidelines (FAO, 2000) for the IPOA-Sharks state that nations contributing to fishing mortality of shark stocks should participate in their conservation and management, that shark resources be used sustainably, and that waste and discards be minimized. Shark fishing nations were called upon in the IPOA-Sharks to prepare National Shark Assessment Reports (Appendix 1) and to implement National Shark Plans (Appendix 2). Unfortunately, when progress on the IPOA-Sharks was reviewed by the FAO Committee on Fisheries (COFI) in February 2001 and by CITES in 2002 it was found that only a small number of shark fishing nations had submitted Shark Assessment Reports or Plans. Many of the countries that had submitted these documents had not adequately addressed the issues raised in the IPOA nor did they propose sufficient action to begin precautionary sustainable shark fisheries management (IUCN, 2002 a;b).

The objectives of the present manual are to provide the information necessary for fisheries managers to effectively address the IPOA Sharks, thus leading to sustainable shark fisheries. We attempt to provide a step-by-step approach to collecting the information necessary for proper stock assessment and sustainable shark management. Each chapter progresses from simple to more complex techniques. We begin in Chapter 2 by explaining the objectives of fisheries management and the methods that may be used to achieve those objectives. Then, in Chapter 3 we describe how to identify sharks and rays. In Chapter 4 we describe the value and methodology of tagging studies in shark management and in Chapter 5 we provide similar treatment for genetic techniques. Chapter 6 explains how to determine age and growth and Chapter 7 describes techniques to study reproductive biology. Chapter 8 describes how to estimate mortality. In Chapter 9 we review demographic population models and in Chapter 10 stock

assessment and population dynamics models are explained. Chapters 11 and 12 describe, respectively, fisheries-dependent and fisheries-independent sampling procedures. Chapter 13 reviews options that may be available for managing elasmobranch stocks. Lastly, in Chapter 14 we provide a brief overview of elasmobranch utilization.

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CHAPTER 2. THE PURPOSE OF STOCK ASSESSMENT AND THE OBJECTIVES OF FISHERIES MANAGEMENT

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2.1 BASIC CONCEPTS AND THE IMPORTANCE OF MANAGEMENT AS THE ULTIMATE GOAL OF FISHERIES SCIENCE

The intention of this chapter is to briefly introduce some important concepts that will be needed throughout the rest of the manual and whose understanding is essential for the correct practice of fisheries work and the successful management of fisheries. The chapter also provides a general framework for the rest of the manual and gives context to the different and interlaced roles of stock assessment and management, which are sometimes mixed and confused. Given the importance and scarcity of good management in present-day fisheries, it is never redundant to clarify and emphasize these basic concepts and put the different components of fisheries work into perspective. The overall feeling and some of the sections of this chapter are inspired by the book of Hilborn and Walters (1992) and readers are encouraged to give a thorough read to this excellent source for more in-depth information.

Fisheries Science is the multidisciplinary study of fisheries. Which disciplines are part of Fisheries Science is to a point a matter of opinion, but a preliminary list would include fisheries biology, marine ecology, stock assessment, natural resource economics, social sciences, fishing technology, oceanography, statistics, and computer modeling.

A ***fishery*** is defined as the set composed of a particular stock (for a definition of stock see Chapters 4 and 5) plus the fishing activities related to its harvest, inclusive of fishermen, vessels, gears and even associated facilities. Often the word stock refers to a population or part of the population of a ***single species*** but in the frequent case of ***multispecific*** fisheries it includes a group of at least two similar or diverse species.

Stock assessment is the part of Fisheries Science that studies the status of a fish stock as well as the possible outcomes of different management alternatives. It tells us if the abundance of a stock is below or above a given target point and by doing so lets us know whether the stock is overexploited or not; it also tells us if a catch level will maintain or change the abundance of the stock. But stock assessment is not the goal of Fisheries Science.

The ultimate objective of Fisheries Science is to inform management. This statement embodies the real meaning of the work of fisheries scientists and technicians, whose fundamental objective is neither to learn how fish grow, where they go or how fast they reproduce, nor to investigate how much fishermen catch, how or where they catch it, or how much money they make. The real and ultimate goal of fisheries science is to provide the information needed for the adequate management of fisheries. Ultimately, if the collective work of all those working in Fisheries Science does not translate into management decisions and their implementation, then we are wasting time and money.

This does not mean that fish biology, stock assessment and other disciplines are not extremely important; in fact they are, but it is essential to keep in mind that they are a very important ***means to an end***. The relevance of all the knowledge we can obtain about the biology of the resources and the dynamics of capture fisheries is that this information is needed to underpin the proper management of the fishery, including target and non-target species, detrimental effects of fishing on ecosystems, and also the human communities depending on fishery resources. It follows from the above that it is worthwhile for governmental agencies charged with fisheries research and management to prioritize and invest resources in fisheries biology and stock assessment of resources for which this work is going to be actually used to do fisheries management. This is a very important fact often ignored in many parts of the world. On the other hand, basic monitoring of unexploited or less important resources can be invaluable several years down the line when fisheries exploitation expands or its associated effects are felt. In this case, it is usually academic and independent research institutions that can carry out the basic monitoring that might be unaffordable to government agencies. It is also often overlooked that a prerequisite to successful management is the existence of the proper institutional and legal structures. Without ***management institutions***, management ***plans*** with clearly stated ***objectives*** and management ***rules*** there can be no effective decision making and implementation for fisheries management.

2.2 THE PURPOSE OF STOCK ASSESSMENT IN FISHERIES SCIENCE

Stock assessment makes use of diverse types of information to give managers advice about the status of a fishery and the possible outcomes of management actions. This includes aspects not only related to the resource abundance such as whether the stock is depleted or close to its maximum biomass, but also in regards to other important aspects of fish population dynamics such as the current levels of mortality and expected levels of future recruitment, or even economically relevant features such as likely changes in catch per unit effort.

Stock assessment has been defined in many ways, often in terms of its objectives. Sparre and Venema (1992) proposed that the basic purpose of stock assessment is "to provide advice on the optimum exploitation of aquatic living resources". Probably the best modern definition comes from Hilborn and Walters (1992): "Stock assessment involves the use of various statistical and mathematical calculations to make quantitative predictions about the reactions of fish populations to alternative management choices." The last definition is especially relevant because it explicitly says two important things, that ***quantitative predictions*** are needed in the process and that the objective is to provide ***advice*** to management ***about choices***.

2.2.1 Quantitative predictions, dynamics, and uncertainty

In order to be of practical use, modern fisheries stock assessment must be able to make quantitative predictions. To state that a fishery resource is "abundant" or "overfished" without further

detail is of limited use for shaping management decisions if the level of abundance or depletion is not expressed as a quantity such as "the fishable stock is at 30% of its original virgin biomass". Equally important, stock assessment should be able to make ***quantitative predictions*** of the outcomes of different management regulations, such as how likely it is that an overexploited stock will recover to a target level in a specified time-frame under different catch or effort quotas. This is why modern stock assessment work is by necessity a ***quantitative*** discipline. While decades ago it was difficult to make these types of quantitative predictions, computers now allow us to do calculations we would hardly be capable of doing 20 years ago, and as time passes numerical methods are becoming more rigorous and powerful for stock assessment.

One of the most important roles of stock assessment is to understand the ***dynamics*** of fisheries. This follows because biological resources, fishermen and the environment are changing entities; they are dynamic not static. Furthermore, fisheries will necessarily respond dynamically over time to management actions as well as to external factors such as environmental forces. Understanding all of these dynamics in order to make good predictions is the ultimate role of stock assessment.

Uncertainty is an intrinsic characteristic of stock assessment. First, natural systems have a lot of random variability that translates into uncertainty and which can be due to variations in fish growth (Fargo and Kronlund, 2000) and reproductive output, as well as to environmental effects (abiotic and biotic) on biological and ecological processes (Parsons et al., 1998). Other sources of uncertainty are the variations in the behavior of fishing fleets and gear, the errors and biases in data collection, and the often incomplete or less than ideal quality of the data sets available for performing stock assessment. Uncertainty also arises from the choice of model used for stock assessment; some models are better suited to capture the underlying dynamics of a given resource than others but it is often impossible to determine which model is more correct for a particular stock. Considering all of the above, it is not surprising to find that the results of fisheries stock assessment are never precise estimates of biomass or mortality, but are in reality estimates that contain a certain degree of uncertainty and doubt. Dealing with uncertainty, acknowledging it and incorporating it into the decision-making process is something extremely important but that only recently has begun to be put into practice. Further reading on the need to embrace uncertainty and new methods to achieve this can be found in Punt and Hilborn (1997), Hilborn and Lierman (1998), McAllister et al. (1999), and Patterson et al. (2001).

2.2.2 The concept of MSY and its evolution from an objective to a reference point

The traditional concept of the dynamics of fishery resources is that there is an underlying model according to which as fishing effort increases, catch will increase up to a maximum, and if effort continues to grow then catches (also known as yield) will decrease. This leads directly to the

concept of maximum sustainable yield (MSY) which has been the holy grail of fisheries (Larkin, 1977).

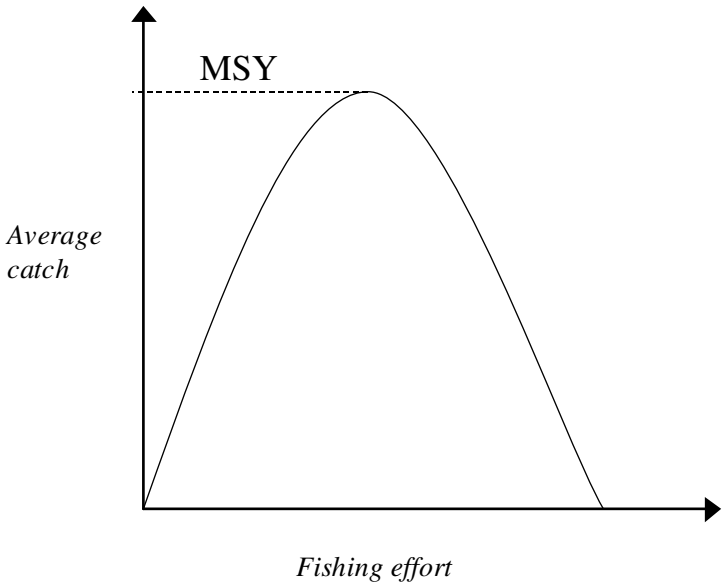

Figure 2.01 A graphical representation of the Maximum Sustainable Yield (MSY) concept.

The specific shape of the yield curve shown in Figure 2.01 does not matter. The important principle always holds: zero effort means zero catch; too much effort leads to small or almost zero catch. Also, in theory there should be a point at which catch has a maximum—at least on average—and supposedly once the curve reaches the top, the MSY level has been found. For decades, finding MSY and keeping fisheries at this prescribed level of catch and effort became the sole objective and obsession of fisheries science, as eloquently put by Larkin (1977).

There are several problems with this concept, the first practical problem being that natural systems have a lot of random variability. In practice, real data will always reflect this variability as "noise." The great danger of focusing stock assessment work solely in finding MSY and its associated optimum effort (f_{opt} defined as the effort level that produces MSY) is that we can seldom be totally sure that we have witnessed the MSY level. Even if managers try to be very careful and cautious by developing a fishery at a very slow pace it will never be guaranteed that the stock will not be overexploited or that opportunities will not be wasted. An excellent example of the difficulties in finding MSY comes from work on Atlantic yellowfin tuna (*Thunnus albacares*) published by FAO and cited by Hilborn and Walters (1992). When scientists performed the first assessment of this resource in the mid-1970s, they thought they had already arrived at the MSY level and calculated this at about 50,000 t. However, due to lack of effective management the fishery continued to grow and a second analysis 10 years later suggested a different MSY level of more than 100,000 t, clearly indicating that the first assessment lead to a "false" MSY. The question remaining was if the second assessment was also an underestimate.

The real problem in the above example and most real fisheries is that in all cases and especially in situations of noisy data we would have to go beyond MSY to make sure that we have actually

found it. In other words until yield does not substantially decrease for a good period of time at increased effort levels we cannot be sure that MSY has been observed. This effectively means that we can never prevent overexploitation, at least not a small amount of it in the best case. This is an important principle identified by Hilborn and Walters (1992): *"You cannot determine the potential yield from fish stocks without overexploiting them."* The secret is not to overexploit the stock beyond recovery in our effort to find MSY. An additional practical problem is that once fisheries have actually passed the MSY point and gone into the overexploitation phase, more problems arise. In such cases, the fishery is already in the overcapacity side of the curve. This leads to another sad but important principle stressed by Hilborn and Walters (1992): *"The hardest thing to do in fisheries management is to reduce fishing pressure."*

In an ideal situation a new fishery should start with all the mechanisms in place to assure, a) detection of MSY quickly after passing this point (i.e., a good monitoring and data acquisition system should be in place), and b) there should be mechanisms in place from the onset of exploitation , to reduce effort effectively without detrimental effects (high taxes that can be later used to buy back boats or compensate for the lost catches and revenue of each boat).

Nowadays, MSY is a theoretical concept that should hold on average, but it is mostly useful as a *general concept* that helps us to guide our work; it is *not the aim* of fisheries assessment. In present times the MSY concept is used to derive management targets and limits or biological reference points (BRPs). Biological reference points are levels of total biomass, spawning stock biomass, fishing mortality rate or other measurable characteristics of a fish population and a fishery, which are either the target of management or a limit beyond which the fishery will not be permitted to go. Two common BRPs are the biomass at which the population can produce the maximum sustainable yield (B_{MSY}) and the fishing mortality needed to achieve MSY (F_{MSY}). For additional reading about these and related concepts readers should refer to Clark (1991), Jacobsen (1992), Smith et al. (1993), Caddy and Mahon (1995), and Hayes (2000). A further important consideration is that MSY and the reference points based on it assume that environmental conditions are constant. However, human-induced (habitat destruction, species depletion) and environmentally driven phenomena (climatic "regime shifts"), can all produce changes in MSY. This issue has commonly been either ignored or mishandled in fisheries science.

2.2.3 Model complexity and the importance of cross-comparison in stock assessment

Predictions are always based on the use of a model, whether the model is explicit or implicit. Even the simplest prediction about what will happen to a stock if effort is increased implies a set of assumptions or conceptual model. Formally, a model is just a representation or abstraction of a given

system or process, which in the case of quantitative disciplines such as fisheries stock assessment takes the form of equations or sets of equations. The type and complexity of models depends on the field of research and the particular problem to be analyzed. In terms of Holling's (1978) classification, problems in population modeling generally lie in the area of low quality/quantity of relevant data. However, it is important to emphasize that the complexity of a model (understood as the number of variables included) is not always directly related to its performance and usefulness.

Models available for stock assessment (see Chapters 9 and 10 for more details) range from the simple holistic models that intend to capture all biological processes in a simple equation such as surplus production models, to the detailed and elaborate age-structured, spatially-structured, multi-stock or even multi-species models that include several sets of equations and which intend to give a more realistic representation of fish population dynamics. But while intuition tells us that complicated and detailed models should be better than simple ones because they more accurately represent "reality," research has shown that simple models can often perform better because they require fewer parameters to be estimated, and very frequently the uncertainty surrounding the estimation of some of these parameters only reduces the ability of models to produce useful information (Ludwig and Walters, 1985; 1989; Ludwig et al., 1988). Readers are encouraged to investigate this topic in more detail by referring to chapter 3 of Hilborn and Walters (1992) for an excellent discussion and further references on this topic. Starfield and Bleloch (1986) give an excellent accessible introduction to model building.

Perhaps the most important message that readers should take home is that while analyzing a fishery, it is imperative to avoid using a single "best" method; the idea that any given model is the best and only model to be used for fisheries stock assessment is dangerously wrong. Instead, it is best to employ a carefully chosen suite of methods—considering the available data—and if possible including both simple and complex models. This will allow the cross-comparison of alternative results that helps detect coincidences and patterns as well as inconsistencies, often highlighting errors in data or guiding the acquisition of additional key information through additional research. In a similar fashion, conflicting results using the same model with different data sets should be carefully analyzed for possible biases in the data. Stock-assessment scientists should ask themselves why there might be differences in predictions about the status of the stock or about the outcomes of different management alternatives across models. An objective picture of the situation can only be obtained when we question the conclusions from one analysis with those of a different one and critically use the different results to gauge our conclusions and to identify which pieces of the puzzle are missing. Only this complete process will allow us to improve the data and methods, and therefore increase the capacity to perform better assessments in the future. The same principle applies also to different data sets that could be available to perform a particular stock assessment. Sound stock assessment is achieved only through healthy cross-comparison and exhaustive questioning of the results of alternative models and data sets.

Finally, it should be mentioned that the complex and often politically charged topic of model choice in stock assessment can nowadays be dealt with through the use of Bayesian approaches (Hammond and O'Brien, 2001) and decision analysis techniques (Punt and Hilborn, 1997; McAllister and Kirkwood, 1998). These methods offer quantitative ways to choose between different models and management options taking into account the uncertainty involved, and are the best way to make management decisions based both on the outcomes of the stock assessment and the probabilities of success of the proposed management options.

2.3 THE DIFFERENT OBJECTIVES OF FISHERIES MANAGEMENT AND THEIR INTERPLAY

What is the purpose of fisheries management? While early fisheries management had implicitly or explicitly MSY as it most important objective (Gulland, 1968) presently MSY is considered only a biological concept and benchmark to guide management. Although MSY still plays an important role as a guiding light for fisheries management, often specific and multiple objectives of fisheries management may be more important than obtaining maximum yield in the long term (Alverson and Paulik, 1973). According to Hilborn and Walters (1992), the most widely accepted fundamental purpose of fisheries management is "to ensure the sustainable production over time from fish stocks, preferably through regulatory and enhancement options that promote economic and social well-being of the fishermen and industries that use the production".

In the modern world of fisheries, management tries to balance multiple objectives that span beyond biological concerns. Oftentimes these multiple objectives are in opposition to each other, such that it is not possible to achieve all of them simultaneously. Managers have to make quantitative decisions about how many fish can be caught, what is the number of boats that will be allowed to enter a fishery, or what is the minimum size of a fish or a gillnet mesh that should be allowed. They also have to make decisions about how much should be spent on research, enforcement of regulations, administration, etc. Within this context, fisheries assessment is about giving advice on the status of the resource and the likely results of alternative measures. Once this is done, the choice of which action to take remains (usually a given amount of fish or quota that can be caught by many different combinations of effort and number and size of boats), and this is where choices have to be made by managers, usually on economic and social grounds. More precisely, fisheries management objectives can be broken down into at least the four categories presented below.

2.3.1 Biological and conservation objectives

By default the biological objective of fisheries management is obtaining MSY, or in other words achieving biological yield maximization. This concept has already been explained above. The standard indicator of biological yield is the annual weight or number of fish caught.

Resource conservation, as well as biological and genetic diversity, are also important biological objectives with an increasingly important role in fisheries management. Explicit directives to avoid putting stocks of target ***and*** non-target species at risk of extinction, and to develop plans for their recovery in case they are already endangered, play a very important role in fisheries legislation in many parts of the world. This is exemplified in the 1996 Magnuson-Stevens Fishery Conservation and Management Act of the USA. Even more recently, ecosystem-health objectives are beginning to take a very important role in fisheries management (Sainsbury et al. 2000; Stevens et al. 2000). Several fishery management plans already incorporate ecosystem objectives and it is just a matter of time until ecosystem-based objectives replace some of the more traditional biological objectives such as obtaining single-species MSY levels. However, that topic is beyond the scope of the present manual.

2.3.2 Economic objectives

In economic terms, to obtain the maximum amount of fish (MSY) is not the main objective. Fisheries are an economic activity and thus should aim for economic rent and more specifically for ***profit maximization***; that is the maximization of total revenue minus the total costs. Thus, the concept of maximum economic rent (MER) is an economic analogue to MSY. The MER level is defined as the point on the revenue curve (simply the yield curve times the unit value of fish landed) where the difference between the total costs of fishing (typically a straight inclined line) and revenues is greatest. However, as shown in figure 2.02 the point of the curve where we find MER will be by definition always at an effort level that is lower than MSY. It is clear from this that it is impossible to attain MSY and MER at the same time and this is a typical example of a likely conflict between multiple objectives in fisheries management (Figure 2.02). Further reading on economics and fisheries management can start with Crutchfield (1965) and MacKenzie (1992).

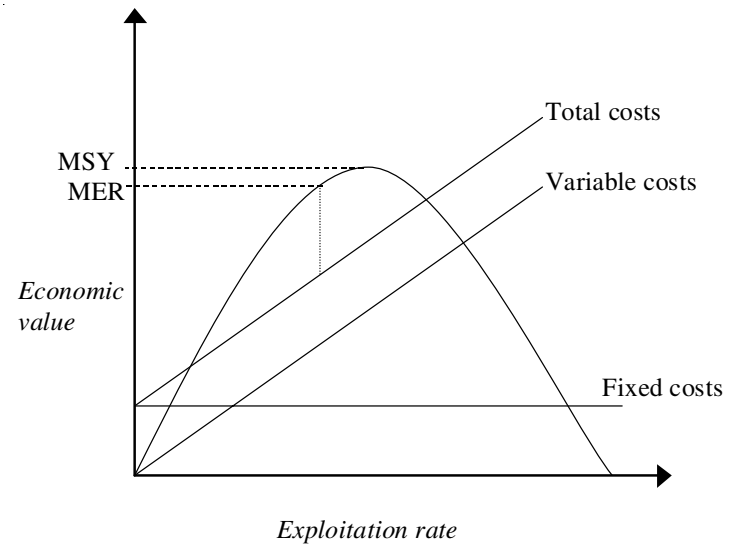

Figure 2.02 A graphical representation of the Maximum Economic Rent (MER) concept and a comparison with MSY.

2.3.3 Social objectives

Social objectives are concerned with employment and equity. Fisheries are not only about landing fish and making money out of it, but also about employing people and making sure that those involved in the fishery make a living that is adequate and sustainable. In many coastal communities of the world it is common that fishing is the most important source of employment. In such situations, having a large number of not-so rich fishermen might be more desirable than having a few very rich ones. Also, it is often important to preserve community structure and traditional lifestyles. Communities that have been fishing for a few hundred years and hold traditional fishing rights, such as the case with many indigenous groups, must be taken into consideration as part of management. From the social point of view, the total number of jobs related to the fishing activity is often the standard indicator, as well as the distribution of income among fishers and the maintenance of traditional lifestyles. Excellent further reading in topics related to economic and social issues in modern fisheries can be found in Fairlie (1995).

2.3.4 Recreational objectives

In some parts of the world, fish stocks have to be shared between commercial fisheries and recreational fisheries. Although both sectors are pursuing fish, their objectives are often very different. For recreational purposes, both the catch and the effort (number of successful fishing trips) might be important objectives. The total number of fish available to be fished is usually more important to a sport fishery than the total biomass of fish available, and in the specific case of trophy fish (such as marlins, swordfish or tunas), the size of the fish will be of outmost importance. In such a case it might be an objective for the fishery to have a few large fish rather than many small ones. The standard indicators for recreational fisheries include the estimated total value of recreational effort (dollars per day times days fished), and the number and size of the recreational catch.

2.3.5 Fisheries management as a balancing act and the importance of explicit objectives

Fisheries management is about making difficult decisions among multiple choices. The decisions go beyond choosing between multiple stock assessment model/data results with different degrees of uncertainty, but also include choosing or balancing between conflicting objectives. While the obvious dilemma between whether to aim for MSY or MER has already been mentioned above, perhaps the major and most difficult dilemma faced today by fishery managers throughout the world is the conflict between economic performance and social issues. Fisheries throughout the world are grossly over-capitalized; massive subsidies are responsible for the persistence of a situation in which too many vessels and too many fishermen chase fish stocks that could be fished by fewer vessels and crews in a much more economic efficient way (Greboval and Munro, 1999). However, should hundreds of

thousands or perhaps even millions of jobs across the coastal areas of the world be lost in the name of economic efficiency? And where are resources going to come from to give alternative jobs or pensions to those displaced? Balancing these opposing objectives is a major challenge for fishery managers. It is precisely for this reason that the explicit statement of the objectives for fisheries management is an extremely important step, but one that is unfortunately often overlooked in fisheries science. The major risk of not having explicit objectives is that management then faces getting lost in a sea of political waves driven by which interest group flexes more power at any point in time. This will probably lead only to disaster in the long term. On the other hand, Hilborn and Walters (1992) have pointed out correctly that it might not be desirable to set very rigid and detailed objectives that might be impossible to reach, thereby leaving management at an impasse when legislation does not allow for frequent and efficient review of management objectives. Given the likelihood that objectives will eventually collide with each other even if the have not been explicitly stated, it is more important that a healthy and open discussion of the overall general objectives of management for each fishery is held as early as possible. However, it is important to clarify at this point that it is not the job of biologists and sometimes not even managers to define what the objectives of fisheries management will be. This should ideally be a collective decision by a management advisory body that includes all stakeholders and interested groups, from fishers and local communities, to government agencies and non-governmental organizations.

2.4 ACKNOWLEDGMENTS

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CHAPTER 3. TAXONOMY AND FIELD TECHNIQUES FOR IDENTIFICATION: WITH LISTING OF AVAILABLE REGIONAL GUIDES.

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3.1 SHARKS, RAYS AND CHIMAERIDS: WHAT ARE THEY, AND HOW ARE THEY CLASSIFIED?

Sharks, rays and chimaerids comprise the class Chondrichthyes that are separated from the other major class of living fishes, the Osteichthyes (comprising about 95% of the modern fish fauna), in having a skeleton made entirely of cartilage (the Osteichthyes have a bony skeleton). All chondrichthyans also have small tooth-like denticles on their skin and internal fertilization mitigated by male claspers (modified pelvic fins). About 57% of them give birth to live young; the remainder lay large eggs contained in a horny capsule.

The chondrichthyans are divided into elasmobranchs, the sharks, skates and rays, and holocephalans or chimaeras. The elasmobranchs have 5-7 gill openings on each side of the head, a body largely covered by dermal denticles and teeth that are continuously replaced and embedded in the gums. Chimaeras have a single gill opening, a largely naked skin and teeth that are fused into plates that grow with the animal. They have a large head, large pectoral fins, two dorsal fins (the first preceded by a long spine), a weak caudal fin that may have a long terminal filament and they may have an anal fin that is barely separated from the caudal fin. Adult male chimaerids have extra claspers on their head and in front of the pelvic fins. Currently, there is no uniform agreement on the higher classification of the chondrichthyans, and there are many alternate schemes. This chapter follows Compagno (1999a, b) and McEachran et al. (1996), although with some differences, in separating the elasmobranchs into two superorders of sharks (Selachei), the Squalomorphii and Galeomorphii that together contain the eight orders of living sharks, and one superorder of batoids (Rajimorphii) with six living orders. Sharks are mostly fusiform in shape (a few are ray-like), have one or two dorsal fins, (sometimes with a spine at their origin), usually have an anal fin, and most have a well-developed caudal fin. Rays are derived from sharks and have become dorso-ventrally flattened, mostly for life on the bottom (although a few are shark-like in shape). Rays have their gills on the underside of the head and their enlarged pectoral fins are joined to the head in front of the gill slits. They have one or two dorsal fins (occasionally none) without fin-spines, no anal fin and a thin, often whip-like, tail.

3.1.1 Diversity

Compagno (2001) lists 60 families within the living orders of chondrichthyans. There are nearly 500 species of living sharks, over 600 species of batoids and 50 species of chimaeras, with new species constantly being described.

Chondrichthyan fishes exhibit great diversity inhabiting most of the seas on earth (although only a few species live in cold polar waters) from the intertidal zone to the deep abyss, and a few also inhabit freshwater lakes and rivers and hypersaline habitats. Diversity is greatest in shallow, tropical

regions, particularly in the Indo-Australian area. In the northwest Australian region, which has about 178 species, some 23% of known species are ubiquitous, about 15% are endemic and the remainder have more regional distributions (Last and Seret, 1999). Endemism is almost entirely of demersal species, and in the tropical eastern Indonesian-Australian region it is most pronounced on the continental slope, except in northwest Australia where more than 60% of the endemics are demersal shelf species (Last and Seret, 1999). The distributional status of a number of problematic taxonomic genera such as *Squalus, Centrophorus, Mustelus* and *Himantura*, as well as several deep-water groups, may change when thorough systematic studies are carried out on a regional or global basis. Chondrichthyans vary greatly in maximum size with sharks ranging from 20-1200 cm total length, rays from 25-880 cm long and up to 670 cm disc width and chimaerids from 50-200 cm long. Sharks vary in shape from the "typical" carcharhinids to the bizarre hammerheads and threshers. Some sharks are ray-like and some rays are shark-like in shape. They vary in color from drab browns and greys to the highly ornate patterning of some of the wobbegongs and stingrays. Most are predators, but there is a diversity of feeding mechanisms from giant planktivores to the semi-parasitic cookie-cutter sharks.

3.2 GLOSSARY/TERMINOLOGY

anal fin: the unpaired fin on the underside of the body behind the anus in sharks (Figs. 3.1a, 3.3)

anterior: the front or head end (Fig. 3.1a)

barbel: a slender, fleshy, tentacle-like sensory structure on the underside of the snout of some sharks (Fig. 3.1a)

caudal: pertaining to the tail region

caudal fin: the tail fin (Figs. 3.1a, 3.2, 3.3)

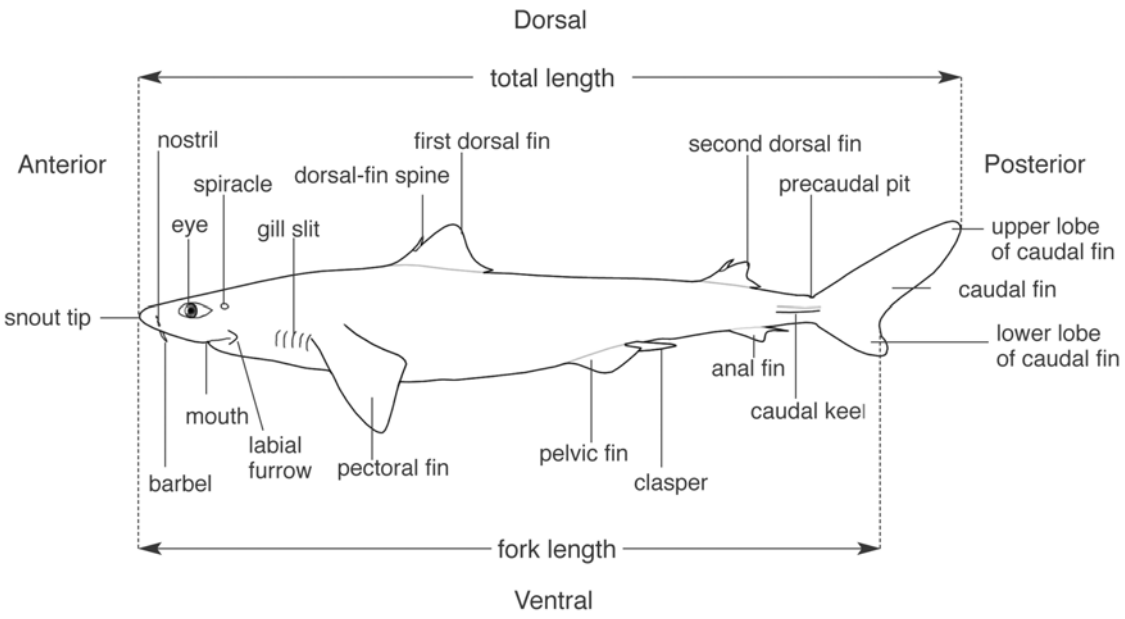

Figure 3.1a Terminology for a generalized shark.

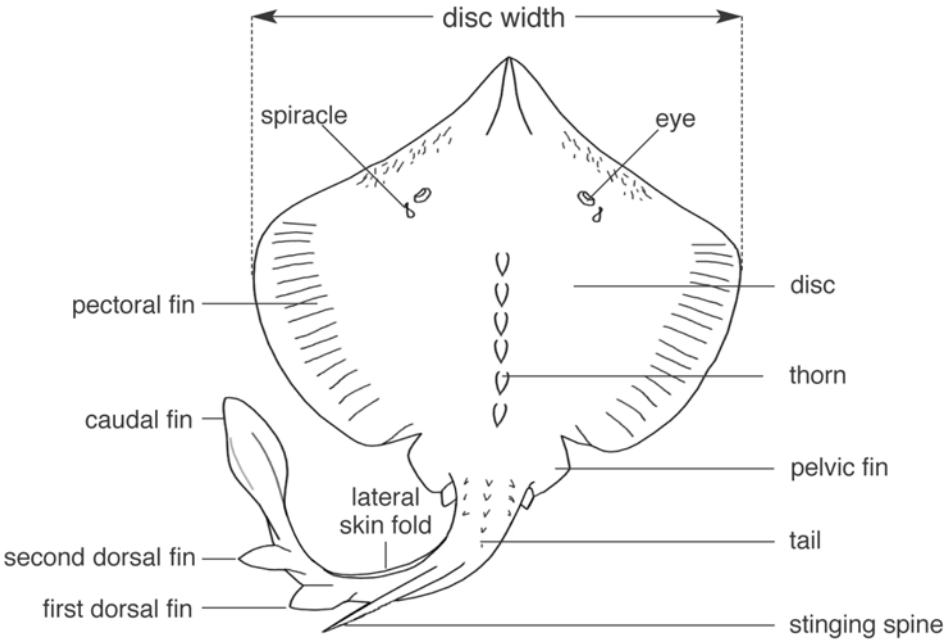

Figure 3.2 Terminology for a generalized ray.

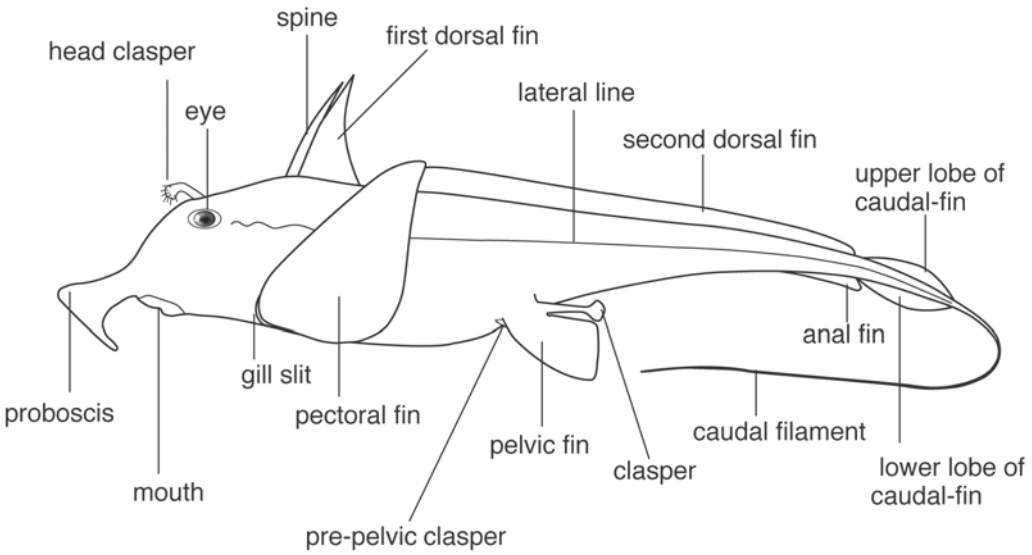

Figure 3.3 Terminology for a generalized chimaera.

caudal keel: a longitudinal, fleshy ridge along the side of the caudal peduncle (Fig. 3.1a)

caudal peduncle: the posterior part of the body supporting the caudal fin (from the insertions of the second dorsal and anal fins to the anterior of the caudal fin)

chondrocranium: the cartilaginous skeleton enclosing the brain and inner ear

clasper: paired cylindrical extensions of the pelvic fins of males used in mating (Figs. 3.1a, 3.2, 3.3)

cusp: a projection (point) on a tooth; many teeth have just one large cusp but some have additional side cusps

dermal denticles: the tooth-like scales of sharks, rays and chimaeras

diplospondylous: elasmobranchs have two types of vertebrae; diplospondylous vertebrae extend posteriorly from the back of the body cavity, and have two centra per myotome. In most shark species, the transition from monospondylous to shorter diplospondylous vertebrae begins above the pelvic fins

disc: the combined head, trunk and enlarged pectoral fins of some sharks and rays with dorsoventrally flattened bodies (Fig. 3.2)

dorsal: the upper surface of the body or head (Fig. 3.1a)

dorsal fin: the unpaired fin or fins along the upper surface of the back (Figs. 3.1a, 3.2, 3.3)

endemic: confined to a localized area (e.g., a species endemic to southern Australia is not found anywhere else)

fusiform: shaped like a spindle or cigar; tapered at both ends

gill slit: a long, narrow gill opening in sharks and rays (Figs. 3.1a, 3.2, 3.3)

head length: distance from the tip of the snout to the most posterior gill slit

insertion: (of a fish's fin) the most posterior point of a fin base

interdorsal ridge: ridge running along the mid-dorsal surface between the dorsal fins

keel: a fleshy or bony ridge (Fig. 3.1a)

labial furrows: the fold behind the corners of the mouth which provide slack in the skin for protrusion of the jaws (Fig. 3.1a)

lateral: refers to the sides

lunate: crescent-shaped; refers to the caudal fin when the upper and lower lobes are about the same size

meristics: pertaining to serially repeated structures such as vertebrae, teeth and other structures that can be counted (like spiral valve turns)

monospondylous: elasmobranchs have two types of vertebrae; monospondylous vertebrae extend posteriorly from the chondrocranium, and have one centrum per myotome. In most shark species, the transition from longer monospondylous to shorter diplospondylous vertebrae begins above the pelvic fins

morphometrics: a character based on measurement. In fish, measurements are taken as a straight line, not around the curve of the body

nasal flaps: skin flaps extending from the nostrils

nictitating eyelid: an eyelid which can be pulled up or down (varies between families) over the whole eye (Fig. 3.1b)

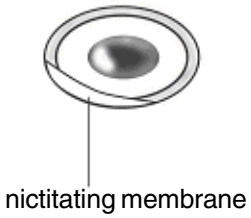

Figure 3.1b Shark eye showing lower eyelid.

nostril: external opening of the nasal organs, usually pore-like in fishes (Fig. 3.1a)

origin: of a fish's fin, the most anterior point of a fin base

pectoral fins: paired fins just behind or just below the gill opening of sharks and chimaeras (Fig. 3.1a, 3.3), part of the disc in rays (Fig. 3.2)

pelvic fins: paired fins on the underside of the body (at the posterior of the body cavity) of sharks and chimaeras (Fig. 3.1a, 3.3), and near the tail in rays (Fig. 3.2)

posterior: the hind or tail end (Fig. 3.1a)

precaudal pit: a notch on the dorsal or ventral surface of the caudal peduncle just in front of the caudal fin of some sharks (Fig. 3.1a)

proboscis: elongated, flexible extension of the snout (Fig. 3.3)

rostrum: a rigid projection of the snout

skin fold: an area where skin is bent over upon itself, forming a fleshy ridge (Fig. 3.2)

snout: the part of the head in front of the eyes of fishes (Figs 3.1a, 3.2)

spiracle: a respiratory opening behind the eye in sharks and rays (Figs. 3.1a, 3.2)

spiral valve: section of the intestine arranged with tight spiral turns, or broad turns like a scroll of paper, to increase the surface area for absorbtion

stinging spine: the large, serrated, sword-like bony structure on the tail of some rays (Fig. 3.2)

symphysials: small teeth at the center of the jaws that are noticeably different in size and shape from the adjacent laterals

terminal filament: filamentous section at the end of the caudal fin in some chimaerids (Fig. 3.3)

thorn: a sharp, tooth-like structure on the skin of a skate or ray (Fig. 3.2)

tooth row: the line of functional and replacement teeth derived from a single germinal area that is usually at approximately right angles to the jaw cartilage.

tooth plate: fused (often beak-like) teeth of chimaerids

tooth series: the line of teeth parallel to the jaw axis, all of them in different rows

total length: longest length of a fish, measured as a straight line from the snout tip to the tip of the upper caudal fin (excluding the terminal filament of chimaerids) (Fig. 3.1a)

vent: anus/urogenital opening

ventral: refers to the lower surface or underside of the body (or head) (Fig. 3.1a)

3.3 CHARACTERS USED FOR IDENTIFICATION

3.3.1 Field identification

When in the field, whether it is at sea or sampling fish markets, there is some basic equipment that should be carried for identifying sharks and rays. This should comprise a camera, notebook, forms, vernier calipers, tape measure, calculator, sharp knife and selected identification sheets from regional guides. A digital camera can be particularly useful, as can be a tape recorder, and all these items can easily be carried in a backpack. Where possible, it is easiest to operate in pairs; this means someone can keep clean hands for taking notes, photographs, etc. For any regional identification study it is important, where possible, to build up both a photographic and specimen collection (see later sections). The collection of material will vary on the individual situation. Trips onboard research or commercial fishing vessels offer the best chance for getting fresh material. Local fish markets also provide excellent opportunities for good quality material and in undeveloped countries with poor data collection systems can also provide information on the fishing methods and gear being employed (particularly where vessels land directly to the market). It is important to set up a protocol (particularly in tropical locations where specimens dry out and deteriorate rapidly) for photographing, measuring and retaining specimens in a quick and efficient manner. Identification forms, tailored for the individual, should be designed to make the recording of measurements and meristics easier.

Characters used for identification vary with the group, but generally color and markings, fin positions and shape, presence of an anal fin, number of gill slits, possession of dorsal fin spines, proportional body measurements, vertebral counts, tooth shape and counts are important in the sharks. In batoids, tooth characters are less useful while disc and tail shape, color and markings, position of the dorsal fins, structure of the mouth and nostril region, and distribution and shape of dermal thorns and denticles are important. In the chimaerids, color, head shape, fin position and shape, relative heights of the dorsal fin and spine, tooth plate structure and presence of an anal fin are important diagnostic characters. Some characters vary between the sexes, and so it is important to record the sex of the individual. Males can be distinguished by their claspers, paired cylindrical extensions of the pelvic fins used in mating. In mature individuals the claspers are elongated and rigid. Immature males have short soft claspers that are sometimes overlooked.

Color varies with life stage and many species (particularly triakids, carcharhinids and sphyrnids), which have a metallic bronzy sheen in life, become a drab grey after death. Photographs

(see later) are particularly important in documenting color, fin positions and body proportions. Proportional body measurements are expressed as percentages of total length (TL) in sharks, most batoids and chimaerids (although the long caudal filament is excluded) and disc width in rays. Total length is measured as a straight line (not over the body curve) from the tip of the snout to the tip of the upper caudal fin lobe (Fig. 3.1a). Total length can vary depending on how the upper caudal lobe is positioned; usually it is pulled back parallel to the body axis in species with a weak lower caudal lobe. In sharks with more equally lobed caudal fins, the upper lobe is pulled back while still maintaining a "normal" tail position. Other length measurements frequently used for sharks are fork length, tip of the snout to the fork in the tail (Fig. 3.1a) and precaudal length, tip of the snout to the origin of the upper caudal fin. Total length is used for most rays, but in the dasyatids, gymnurids, myliobatids, rhinopterids and mobulids disc width, the maximum width across the body (Fig. 3.2), is measured as the tail is often damaged. Fin and body measurements should follow schemes proposed by Compagno (2001) and should include both longitudinal (parallel to the body axis) and point to point measurements. Measurements on most small species can be made with a combination of vernier calipers, a measuring board and possibly a standard 40 cm ruler. For large species, a combination of vernier calipers, large spring calipers, a 1 m wooden or steel rule and tape measure or folding measuring board can be used. Usually it is only necessary to make a few measurements to check diagnostic characters, but for unusual or possibly new species a full set of measurements should be taken (see Compagno, 1984). Pre-designed forms should be used for recording this information. Waterproof paper, although expensive, can be useful.

Vertebral counts can be made easily in the field, even on relatively large specimens, with the aid of a large, sharp, wide-bladed butchers knife. Protocol for precaudal (mono and diplosondylous) and caudal counts should follow Compagno (1984) and Garrick (1982). Precaudal counts are taken to the anterior edge of the precaudal pit. To make a count the tail should first be severed at the precaudal pit. The precaudal count can then be made by placing the specimen on its side and, starting at the tail, filleting it by running the knife along the vertebral column continuing forward right into (or through) the chondrocranium. Usually only minimal scraping of flesh from the column is required before counting is possible. Counts should not include the half vertebra fused to the back of the chondrocranium. When making the caudal count it is important not to damage the delicate terminal vertebrae. It is best to run the knife about half way along the column from the cut end, and then firmly grasp the flap of cut skin and flesh and strip off the remainder by pulling on it. In small specimens, the count may have to be completed in the laboratory using a microscope. Tooth counts and tooth shape are most important in the carcharhinids. Counts should follow the protocol in Garrick (1982) essentially being expressed as the number of laterals (left and right side) and symphysials in the upper jaw over those in the lower jaw.

For example: 13-1-13 for *Carcharhinus leucas*
12-1-12

Teeth counts for carcharhinds can usually be made *in situ*; sometimes slitting the mouth corners can help in accessing the extreme lateral teeth. Where there is any uncertainty, jaws can be removed, cleaned and examined in the laboratory. It is a good idea to compile a reference collection of jaws (see section 5). In the carcharhinids the shape of the upper laterals can be diagnostic, although differences between species are often subtle. Garrick (1982) and the series of papers by Bass, D'Aubrey and Kistnasamy (1973-76) on South African sharks provide excellent drawings and photographs of carcharhinid teeth. Compagno (1984, 2001) includes useful drawings of teeth for most species for which they are diagnostic.

3.3.2 Laboratory identification

Some characters and techniques are more practically carried out in the laboratory. Where it is possible to retain and transport specimens for measuring, electronic calipers linked to a pre-designed spreadsheet can greatly facilitate time-consuming proportional measurements. Where specimens need to be retained for a collection vertebral counts can be made by X-ray. Pins can be used to mark the position of the precaudal pit. Exposure rates and film will vary depending on the type of machine available. Tooth counts on newly-born carcharhinids, or species with many tooth rows such as the scyliorhinids (mainly required for new species descriptions) are best carried out in the laboratory using a microscope. If several duplicate specimens are available it is easiest to remove and dry the jaws before counting (although some distortion of tooth rows can occur). If specimens must be retained intact, removal of all mucous, blotting dry, the use of water-soluble dyes and pins as reference marks can aid examination under the microscope. Spiral valve counts (number of turns or flaps in the intestine, which is immediately posterior to the stomach) can be useful in some groups. This is most easily carried out by removing it from the specimen, opening lengthways with scissors, washing out all the contents and mucous, and then counting (this can also be done in the field). In some cases, characters such as dermal denticles, clasper structure and occasionally chondrocranium structure may be required. Preparation techniques for these can be found in Compagno (1988).

3.4 TAKING PHOTOGRAPHS

The left side of sharks and chimaerids should be photographed; dorsal and ventral views of batoids should be taken. A shot of the underside of the head back to the level of the pectoral-fin origins should be taken for sharks, and for some families a dorsal view; more detailed shots of teeth, fin markings, mouth regions etc., can be taken as necessary. Specimens should be washed clean and layed out on a plain matte white background so that their fin origins and inner margins are clearly visible. For ventral shots, where white is a common skin color, a darker matte background may be required. Thick plastic material is relatively easy to carry and clean in the field. Plasticine, small

stones, pieces of paper, wood, etc., can be used to prop-up the fins or stabilize the head. Bright sunlight can cause problems with reflection and shadows, and a shady area is preferable. With very large specimens, fitting them into the field of view can be a challenge and may call for innovative solutions such as climbing onto the roof of a truck or taking shots from a balcony or ladder. Always include a scale, preferably a colored rule. It is a good idea to also include a label with the species name or a field code, this can be cropped out later if necessary. Maintain a register of all photographs taken. Where available, digital cameras are an advantage as results can be checked immediately. It is very helpful to compile a photographic collection to accompany a regional collection of specimens.

3.5 SPECIMEN COLLECTION, PRESERVATION AND CATALOGUING

Any serious attempt to document regional chondrichthyan faunas should involve compiling and maintaining a reference collection of specimens. Specimens should be collected as fresh as possible, washed, photographed, measured, labeled and fixed in 10% formalin made up with seawater (40-44% concentrated formaldehyde = 4% formalin). All specimens over about 15 cm TL should be injected in the body cavity with concentrated formalin using a large gauge hypodermic needle. Waterproof paper labels recording the species identification along with a field number in pencil (entered in a register with date, collection location, identifier, length and sex of the specimen) should be attached to the specimen. (Plastic waterproof paper, such as Phase 3, tends to split but can be used if encased in a self-sealing plastic bag; we use Nalgene polypaper, which doesn't tear.) Labels are best attached through the upper caudal-fin lobe of sharks, close to the caudal fin of chimaerids and towards the margin of the "wings" of batoids using plastic T tags fired from a tagging gun (type used by clothing companies such as Monarch 3020 from Canada). Specimens should be fixed in containers that allow them sufficient space to prevent them being bent or distorted. For smaller specimens, 30 litre polythene drums with large diameter screw-on (or snap-on) lids are ideal; for larger sharks fiberglass or polyethylene tanks (approximate dimensions 1.5 m long, 0.5 m wide and 0.8 m deep) with sealing lids are required (these may have to be specially manufactured). After fixation in formalin for four weeks, specimens should preferably be transferred to 70% ethanol after first washing in water. A layer of muslin covering the specimens in the tank will help to prevent those at the top from drying out. Fluid levels should be monitored periodically, every month if tanks are stored outside in tropical areas. For large specimens, it may not be possible to retain the whole animal in which case the head, and possibly fins of sharks should be kept. For large rays, the wings can be removed. Particularly for carcharhinids, jaw collections can be valuable. Jaws should be cut out of the shark and all flesh removed by paring away the muscle and skin with a sharp knife or scalpel. When clean, the jaw should be held open (two pieces of wood across the jaws work well) and dried in the shade (if placed straight into the sun they may distort).

3.6 DISSECTION

Dissections for vertebral and spiral valve counts, and preparation of jaws have been covered in previous sections. Those interested in more complicated dissections and preparations such as those for clasper elements and chondrocrania should consult Compagno (1988).

3.7 FAMILY KEY

The illustrated family key provided here is taken from Daley et al. (2002). It should be noted that there are some minor differences between the systematic scheme followed in the key, and that in section 3.8 which follows Compagno (1999b) and McEachran et al. (1996). In particular, the Squalidae have been separated into several families (section 3.8) that have not been recognized as such in many of the regional guides cited herein and used for identification by fisheries workers.

KEY TO FAMILIES

Step 1 Five to seven gill openings on each side of head (figs 1, 4), last two openings sometimes very close together and appearing as one. **Go to Step 2**

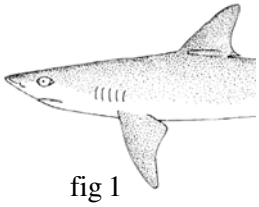

fig 1

head of shark

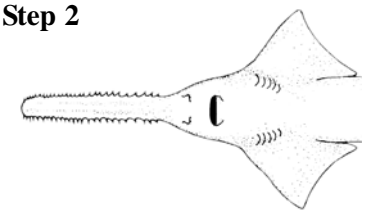

fig 4

undersurface of head

One external gill opening on each side of head (fig 2). **Go to Step 43**

fig 2

head of chimaera

Step 2 Snout saw-like, flattened and armed with lateral teeth (figs 3, 5). **Go to Step 3**

Snout not saw-like, no lateral teeth. **Go to Step 4**

Step 3 Gill slits on undersurface of head (fig 4); no barbels on snout (fig 3)

sawfishes (Pristidae) fig 3

fig 3

fig 5

Gill slits on sides of head (fig 5); barbels present on snout (fig 5).

sawsharks (Pristiophoridae) fig 5

Step 4 Body dorsoventrally flattened, ray-like (fig 6); eyes on top of head, except in devilrays (fig 29), eagle rays (fig 30) and cownose rays (fig 31). **Go to Step 5**

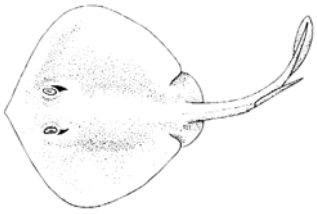

fig 6

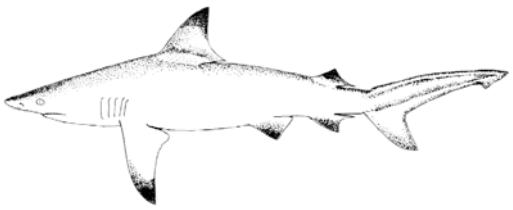

fig 7

Body more or less streamlined, shark-like (fig 7); eyes on sides of head (fig 7).
Go to Step 19

Step 5 Gill openings partly on sides of head (fig 8); pectoral fins clearly detached from head (front part of fin extending forward of fin origin) (fig 8). angel sharks (Squatinidae) fig 9

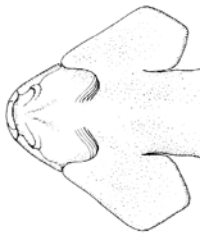

fig 8
undersurface of head

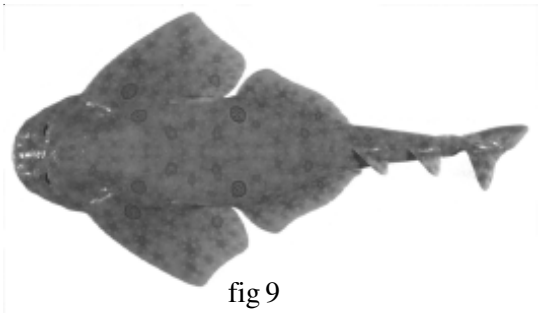

fig 9

Gill openings entirely on undersurface of head (fig 10); pectoral fins wholly or partly joined to head (fig 10). **Go to Step 6**

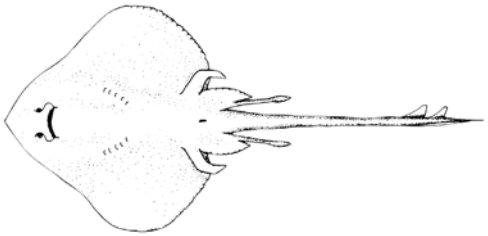

fig 10
undersurface

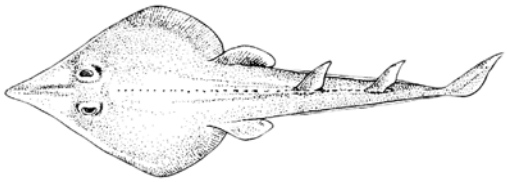

fig 11

Step 6 Two distinct dorsal fins (fig 11); first dorsal fin originating closer to insertion of pelvic fins than to tip of tail (fig 11). **Go to Step 7**

Dorsal fins 0–2; origin of first dorsal fin closer to tail tip than to insertion of pelvic fins when two fins are present (fig 10). **Go to Step 11**

Step 7 Disc large relative to tail, its maximum width more than twice tail length behind pelvic-fin tips (fig 13); dorsal fins close together (fig 14). **Go to Step 8**

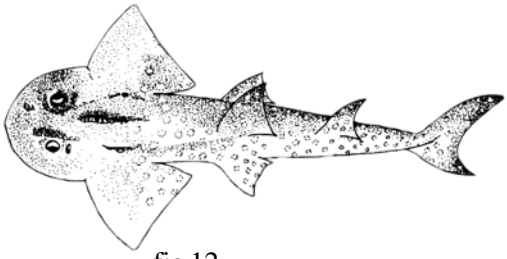

fig 12

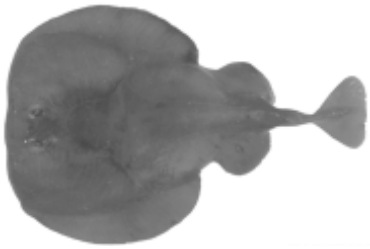

fig 13

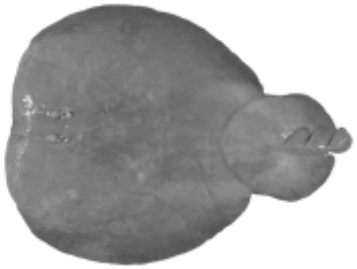

fig 14

fig 15

Disc smaller relative to tail, its maximum width about equal to or less than tail length behind pelvic-fin tips (fig 12); dorsal fins widely separated (fig 11). **Go to Step 9**

Step 8 Caudal fin much larger than dorsal fins, about the same size as pelvic fins (fig 13). torpedo rays (Torpedinidae) fig 13

Caudal fin barely larger than dorsal fins, much shorter than pelvic fins (fig 14). coffin rays (Hypnidae) fig 14

Step 9 Caudal fin with a well-developed, angular lower lobe (fig 15); pectoral and pelvic fins not overlapping (fig 15). sharkfin guitarfishes (Rhynchobatidae) fig 15

Lower lobe of caudal fin not well defined (fig 16); pectoral and pelvic fins touching or over lapping (fig 16). **Go to Step 10**

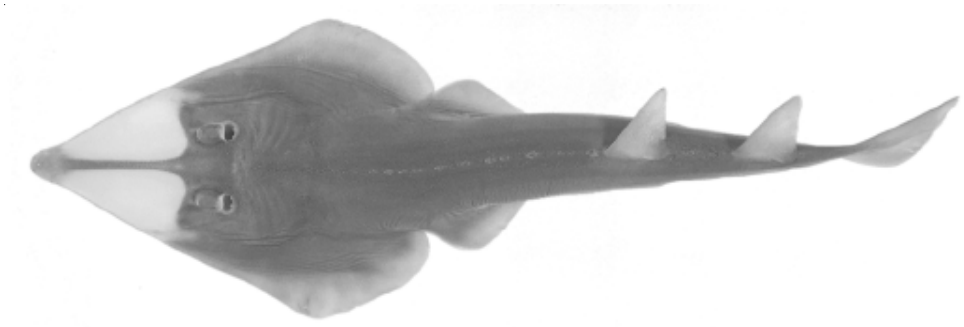

fig 16

Step 10 Snout wedge-shaped, forming a sharp angle at tip (fig 16) or snout broadly rounded; thorns or fine denticles present on body or tail (surface rough); no electric organs. shovel nose rays (Rhinobatidae) fig 16

Snout broadly rounded; body surface entirely smooth; electric organs present fig 17. numbfishes (Narcinidae) fig 17

fig 17

Step 11 Pelvic fin divided into two distinct lobes (fig 18); no enlarged stinging spine on tail (fig 18). **Go to Step 12**

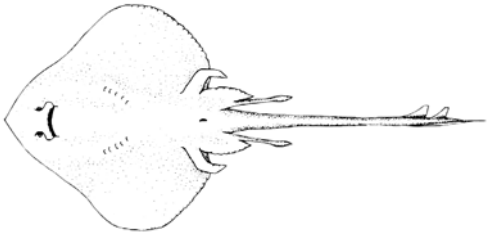

fig 18

undersurface

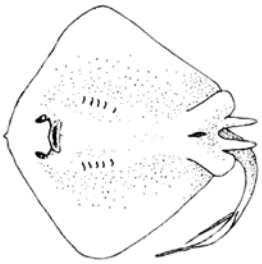

fig 19

undersurface

Pelvic fin with one lobe (fig 19); 1–2 enlarged, serrated stinging spines usually present on tail (deep scar visible when spine absent) (fig 19). **Go to Step 13**

Step 12 Thorns or fine denticles (rough to touch) present on at least part of dorsal surface (fig 20); snout in front of eyes less than 8 times eye diameter; tail slender but not thread-like (fig 20). skates (Rajidae, in part) fig 20

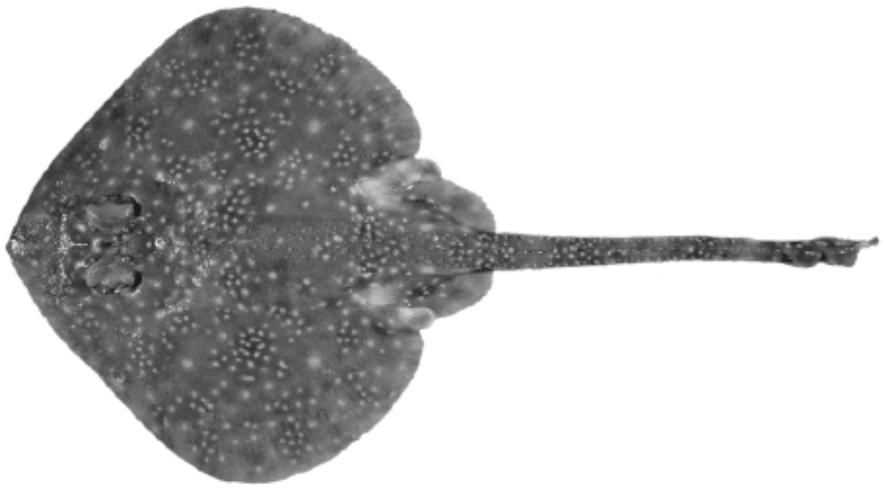

fig 20

Entire dorsal surface smooth (except for outer disc thorns of male) (fig 21); snout in front of eyes more than 8 times eye diameter; tail very short, thin and thread-like (fig 21). leg skates (Rajidae, in part)

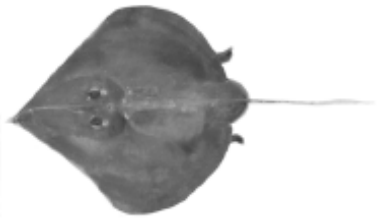

fig 21

Step 13 Six pairs of gill slits (fig 22). sixgill stingrays (Hexatrygonidae) fig 23

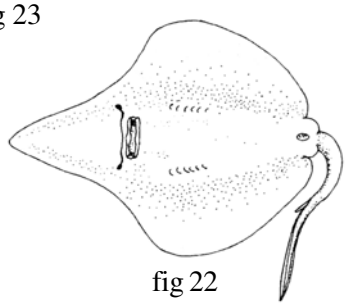

fig 22

undersurface

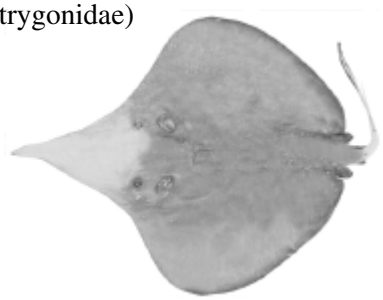

fig 23

Five pairs of gill slits (fig 19). **Go to Step 14**

Step 14 Anterior part of head not extended beyond disc (fig 24); eyes located on top of head and well inward from disc edge (fig 24). **Go to Step 15**

fig 24

fig 25

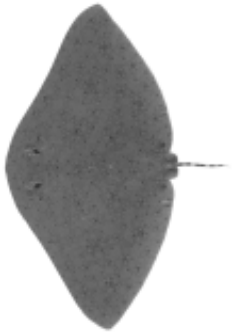

fig 26

Anterior part of head extended beyond disc (fig 25); eyes located on side of head (fig 25). **Go to Step 17**

Step 15 Disc very broad, width more than 15 times length (fig 26); tail extremely short and thread-like (fig 26). butterfly rays (Gymnuridae) fig 26

Disc width less than 15 times length (fig 27); tail moderately (fig 28) to very (fig 27) long. **Go to Step 16**

Step 16 No caudal fin (fig 27); central disc and dorsal surface of tail normally with some thorns or small rounded projections (fig 27). stingrays (Dasyatidae) fig 27

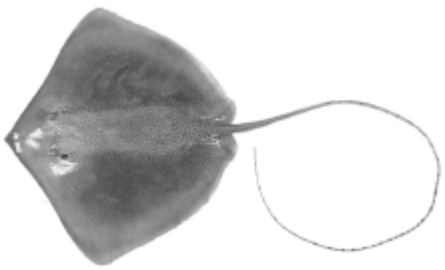

fig 27

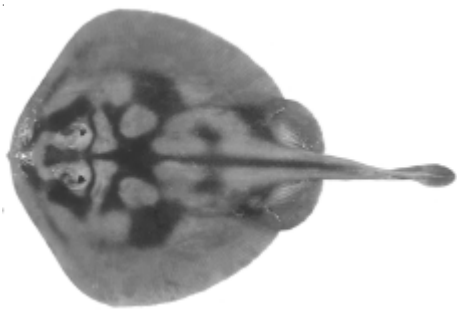

fig 28

Caudal fin present (fig 28); no thorns or small rounded projections on disc or tail (completely smooth). stingarees (Urolophidae) fig 28

Step 17 A long, paddle-like flap projecting forward from each side of head (fig 29); teeth minute, in many rows, more than 10 rows in each jaw. devilrays (Mobulidae) fig 29

No long, paddle-like flap projecting forward from each side of head, instead with a single, fleshy, lobe (fig 30) or pair of broadly rounded lobes forming the snout (fig 31); teeth large, plate-like, less than 10 rows in each jaw. **Go to Step 18**

fig 29

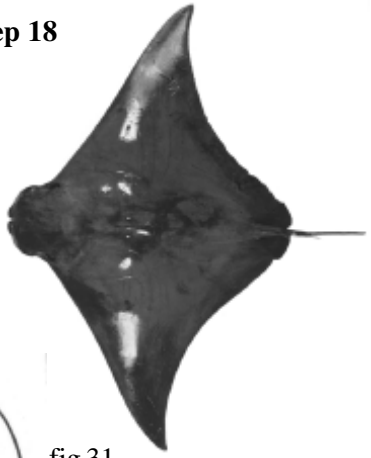

fig 31

fig 30

Step 18 Undersurface of snout uniformly rounded (fig 30); floor of mouth with small fleshy projections. eagle rays (Myliobatidae) fig 30

Undersurface of snout with two lobes separated by a deep central notch (fig 31); floor of mouth without small fleshy projections. cownose rays (Rhinopteridae) fig 31

Step 19 A single dorsal fin (fig 32); 6–7 pairs of gill openings (fig 32). **Go to Step 20**

Two dorsal fins (fig 33); 5 pairs of gill openings (fig 33). **Go to Step 21**

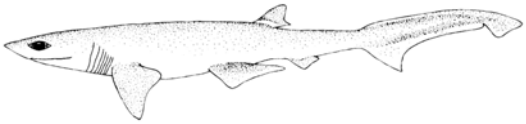

fig 32

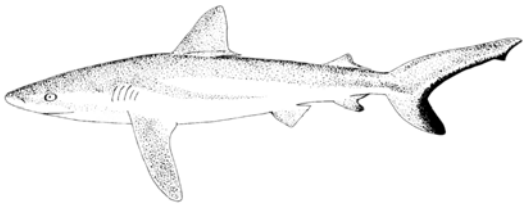

fig 33

Step 20 Mouth at tip of snout (fig 34); first gill openings connected around throat (fig 35); no notch on underside of upper caudal-fin lobe (fig 34). frilled sharks (Chlamydoselachidae) fig 34

fig 34

Mouth on undersurface of head (fig 37); first gill openings not connected around throat (fig 36); notch on underside of upper caudal-fin lobe (fig 37). sixgill and sevengill sharks (Hexanchidae) fig 37

fig 35

fig 36

undersurface of head

fig 37

fig 38

Step 21 Anal fin absent (figs 38–40). **Go to Step 22**

fig 39

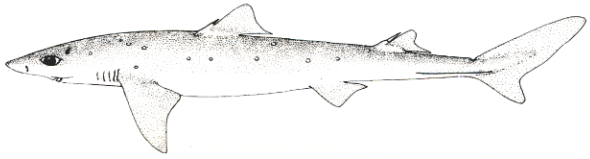

fig 40

Anal fin present (fig 41), sometimes small (fig 42). **Go to Step 24**

Step 22 First dorsal fin originating behind pelvic-fin origins (fig 38); dorsal fins located near caudal fin and almost touching each other (fig 38); denticles extremely large. bramble sharks (Echinorhinidae) fig 38

First dorsal fin originating in advance of pelvic fins (fig 40); dorsal fins well separated and located well forward of caudal fin (fig 39); denticles not greatly enlarged. **Go to Step 23**

Step 23 Trunk laterally compressed, almost triangular in cross-section; fins tall, height of first dorsal fin more than or about equal to head length (fig 39). prickly dogfishes (Oxynotidae) fig 39

Trunk rounded or oval in cross-section; fins much lower, height of first dorsal fin much less than head length (fig 40) dogfishes (family Squalidae) fig 40

Step 24 Head hammer-shaped (fig 41); eyes located on outer edge of head (fig 41) hammerhead sharks (Sphyrnidae) fig 41

Head not hammer-shaped. **Go to Step 25**

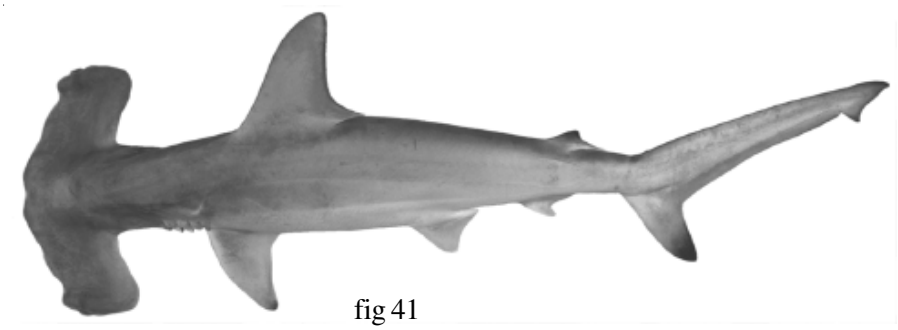

fig 41

Step 25 Length of caudal fin equal to or more than half total length (fig 42); body not spotted or banded. thresher sharks (Alopiidae) fig 42

fig 42

fig 43

Caudal fin much less than half total length (fig 43) (caudal fin also long in *Stegostoma* but body spotted and/or banded, see fig 52). **Go to Step 26**

Step 26 Dorsal-fin spines present (fig 43) horn sharks (Heterodontidae) fig 43

Dorsal-fin spines absent. **Go to Step 27**

Step 27 Snout extending above mouth as long, flattened, blade-like shelf (fig 44); nostrils close to mouth (fig 45). goblin sharks (Mitsukurinidae) fig 44

fig 44

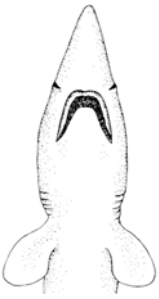

fig 45

undersurface of head

Snout not as above (extended slightly in some catsharks, family Scyliorhinidae, fig 71), but nostrils well forward of mouth). **Go to Step 28**

Step 28 Whole mouth forward of front edge of eye (fig 46). **Go to Step 29**

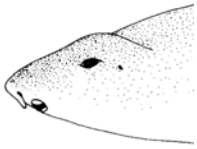

fig 46

head

fig 47

head

Mouth partly beneath or behind front edge of eye (fig 47). **Go to Step 35**

Step 29 Mouth at snout tip and very broad (fig 48); caudal fin forked, upper and lower lobes tall (fig 48); no notch on underside of upper caudal-fin lobe (fig 48). whale sharks (Rhincodontidae) fig 48

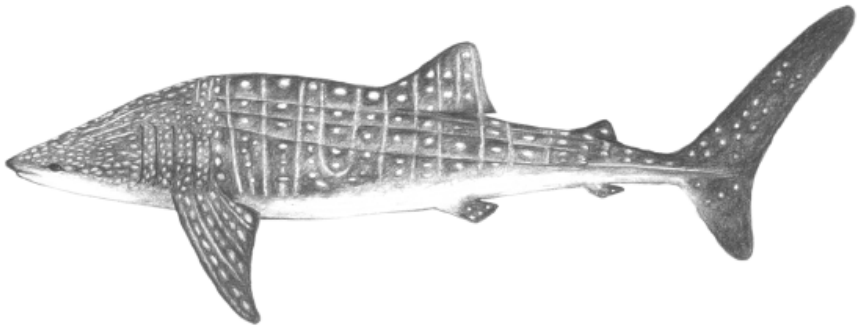

fig 48

Mouth smaller, not right at snout tip (fig 49); upper and lower lobes of caudal fin low (fig 49); a notch on underside of upper caudal-fin lobe (fig 49). **Go to Step 30**

fig 49

Step 30 No fleshy lobe or groove on outer edge of nostril (fig 50). **Go to Step 31**

Fleshy lobe and groove present on outer edge of nostril (fig 51). **Go to Step 32**

fig 50
undersurface of head

fig 51
undersurface of head

Step 31 Caudal fin very long, almost as long as body (fig 52); ridges present on side of body (fig 52). zebra sharks (Stegostomatidae) fig 52

fig 52

fig 53

Caudal fin shorter, much less than half length of body (fig 53); no ridges on side of body. nurse sharks (Ginglymostomatidae) fig 53

Step 32 Origin of anal fin forward of origin of second dorsal fin (fig 54); anal fin more than its base length from caudal fin (fig 54). collared carpet sharks (Parascylliidae) fig 54

fig 54

Origin of anal fin well behind origin of second dorsal fin (fig 55); anal fin next to caudal fin (fig 55) and sometimes barely distinguishable from it (fig 59). **Go to Step 33**

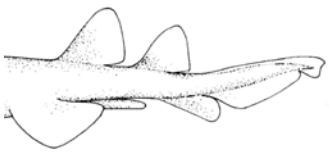

fig 55
tail

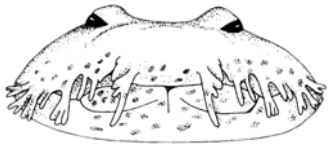

fig 56
front view of head

Step 33 Body strongly flattened (top to bottom) anteriorly (fig 56); skin flaps present along side of head behind nostrils (fig 56); enlarged canine teeth at tip of both jaws. wobbegongs (Orectolobidae) fig 58

Body more or less cylindrical anteriorly (fig 57); no skin flaps along side of head behind nostrils (fig 57); teeth small, those at tip of jaws not distinctly larger than those next to them. **Go to Step 34**

fig 57

front view of head

fig 58

Step 34 Tail long, distance from anus to lower caudal-fin origin greater than distance from snout to anus (fig 59); insertion of second dorsal fin well in front of anal-fin origin (fig 59). longtail carpet sharks (Hemiscylliidae) fig 59

fig 59

Tail shorter, distance from anus to lower caudal-fin origin less than distance from snout to anus (fig 60); insertion of second dorsal fin over or slightly behind origin of anal fin (fig 60). blind sharks (Brachaeluridae) fig 60

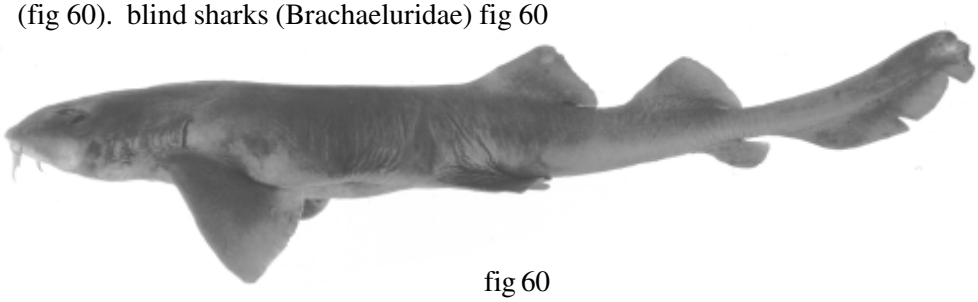

fig 60

Step 35 Caudal-fin lobes almost the same size, upper lobe less than 15 times longer than lower lobe (fig 61). **Go to Step 36**

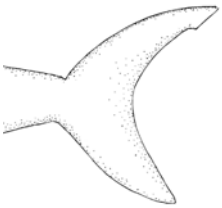

fig 61

caudal fin

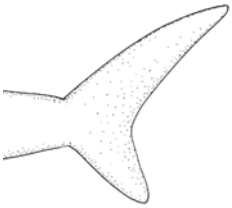

fig 62

caudal fin

Caudal-fin lobes of unequal length, upper lobe more than 15 times longer than lower lobe (fig 62). **Go to Step 37**

Step 36 Gill openings very long, extending on to both dorsal and ventral surfaces (fig 63); first gill openings almost continuous on throat; more than 150 rows of small hook-like teeth in both jaws (fig 65). basking sharks (Cetorhinidae) fig 63

fig 63

fig 64

Gill openings shorter, confined to sides (fig 64); first gill openings widely separated on throat; less than 40 rows of sharp blade-like teeth in each jaw (fig 66). mackerel sharks (Lamnidae) fig 64

fig 65

teeth of upper jaw

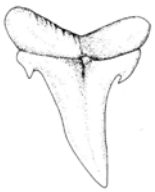

fig 66

Step 37 Mouth huge and at tip of snout, lower jaw extending to snout tip (fig 67); very large sharks. megamouth sharks (Megachasmidae) fig 67, not featured

Mouth located on undersurface of head, distance from snout to mouth distinctly longer than eye diameter (fig 68). **Go to Step 38**

fig 68

head

fig 69

Step 38 Eyes very large, more than half greatest height of snout (fig 69); gill openings extending onto dorsal surface of head (fig 69); caudal keels present (fig 69). crocodile sharks (Pseudocarchariidae) fig 69

Eyes smaller, less than half greatest height of snout (fig 70); gill openings not extending onto dorsal surface of head (fig 70); caudal keels absent in most species. **Go to Step 39**

fig 70

Step 39 Eyelid fixed, not capable of closing over eye. grey nurse sharks (Odontaspididae) fig 70

Eyelid capable of closing over eye (nictitating). **Go to Step 40**

Step 40 First dorsal-fin origin well behind pelvic-fin origin (fig 71). catsharks (Scyliorhinidae) fig 71

fig 71

First dorsal-fin origin well in front of pelvic-fin origin (fig 72). **Go to Step 41**

fig 72

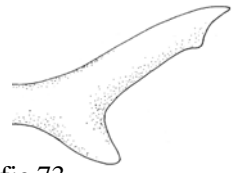

fig 73

caudal fin

Step 41 No precaudal pit (fig 73); leading edge of upper lobe of caudal fin smooth (fig 73). hound sharks (Triakidae) fig 72

Precaudal pit present (fig 74); leading edge of upper lobe of caudal fin usually rippled (fig 74). **Go to Step 42**

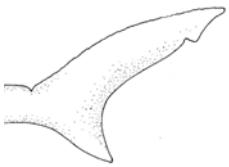

fig 74

caudal fin

fig 75

Step 42 Posterior edge of second dorsal fin deeply concave (fig 75); spiracles present (fig 75). weasel sharks (Hemigaleidae) fig 75

Posterior edge of second dorsal fin not deeply concave (fig 76); spiracles mostly absent. whaler sharks (Carcharhinidae) fig 76

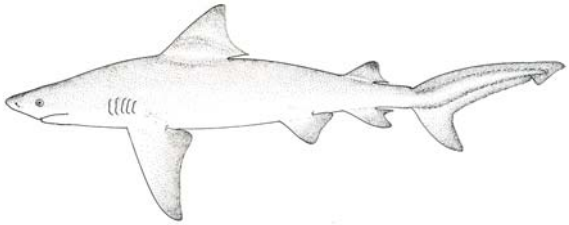

fig 76

fig 77

Step 43 Snout long and flexible with a hoe-shaped tip (fig 77); caudal fin arched upward (fig 77). elephant fishes (Callorhinchidae) fig 77

Snout straight, bluntly rounded or pointed (figs 78, 79); caudal-fin axis straight (figs 78, 79). **Go to Step 44**

fig 78

Step 44 Snout relatively short, tip bluntly rounded (fig 78). shortnose chimaeras (Chimaeridae) fig 78

Snout very long, tip pointed (fig 79). spookfishes (Rhinochimaeridae) fig 79

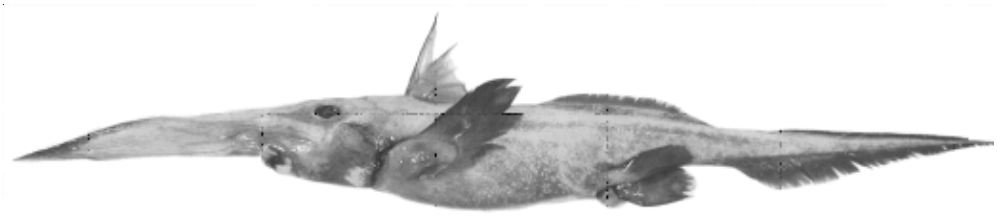

fig 79

3.8 ORDERS AND FAMILIES

3.8.1 Order Hexanchiformes (frilled, sixgill and sevengill sharks)

These sharks are easily identified by the combination of six or seven pairs of gill slits on each side, a single dorsal fin and an anal fin. The order contains two families. The Chlamydoselachidae (frilled sharks) includes one living species, which has an elongate, eel-like body, six pairs of gill slits and a reptilian-like head with terminal mouth and long tricuspid teeth. The family Hexanchidae (sixgill and sevengill sharks) have a fusiform body, ventral mouth with comb-like lower teeth and six or seven pairs of gill slits. The family contains four medium to large (14-48 m) sharks that mainly live near the bottom in deep water in temperate and tropical regions (one species inhabits shallow bays and estuaries).

3.8.2 Order Squaliformes (dogfish sharks)

Squaliform sharks are identified by the combination of a fusiform body, short snout (not saw-like), five gill slits, no anal fin and usually spines in front of the dorsal fins (minute or absent in a few species). There are seven (Compagno, 1999b) living families; the Echinorhinidae, Squalidae, Centrophoridae, Etmopteridae, Somniosidae, Oxynotidae and Dalatiidae. The echinorhinids (bramble sharks) contain two relatively rare species (2.6-4.0 m) of deep water, bottom-living, temperate and tropical sharks which have two small, posterior-placed, spineless dorsal fins (origin of first behind pelvic-fin origins) that are close together, and enlarged, thorny denticles on the body. There are four species of small (mostly < 1 m) oxynotids (prickly dogfishes) that live near the bottom in deep water of temperate and tropical regions. These bizarre shaped sharks have a hump-backed body almost triangular in cross section, ridges between the pectoral and pelvic fins, two high, sail-like dorsal fins with spines, and very rough skin. The squalids (dogfishes) contain two genera (*Cirrhigaleus* and *Squalus*) and about 12 mostly small (< 1.2 m) species. Squalids have two relatively low dorsal fins usually preceded by spines, the origin of the first anterior to the pelvic-fin origins. The centrophorids (gulper sharks) comprise about 14 species within two genera of small to medium sized (up to 1.6 m) sharks, the etmopterids (lantern sharks) contain five genera and about 38 small (mostly < 1 m) species and the dalatiids (kitefin sharks) contain seven genera and about 10 mostly very small (with the exception of *Dalatias* which attains about 1.8 m) species. The somniosids (sleeper sharks) comprise four genera and about 16 species and include *Somniosus* spp. some of which attain about 7 m in length and are among the largest of sharks. The genera *Centrophorus, Etmopterus* and *Squalus* contain many species that are very difficult to identify, with many new forms being reported as new areas are sampled. Snout length, dorsal fin shape, color markings (particularly of juveniles), denticle patterns, spine thickness and height of the spine relative to the dorsal fin are important characters. Revision on a global (or at least large regional) scale is required to fully resolve their taxonomy at the species level.

3.8.3 Order Pristiophoriformes (sawsharks)

This order contains one living family the Pristiophoridae (sawsharks) comprised of two genera and about seven relatively small (< 1.5 m) species. Sawsharks are unmistakable among the sharks because of their blade-like snout armed with rostral teeth (resembling a saw); they also have barbels on the underside of the saw, sub-cylindrical to slightly flattened (but not ray-like) bodies, two dorsal fins without spines, five or six pairs of gill slits and no anal fin. Sawsharks should not be confused with the batoid family Pristidae (sawfish) that have the pectoral fins joined to the head in front of the ventrally placed gill slits, no barbels on the saw, and which grow much larger (up to 7 m).

3.8.4 Order Squatiniformes (angel sharks)

Squatiniform sharks are easily identified by the combination of no anal fin and a dorso-ventrally flattened, ray-like body with broad pectoral fins and a terminal mouth. However, unlike batoids

the gill slits are on the sides of the head and the pectoral fins join the head behind the gill slits (although they project forward of them as a lobe). The order contains the single living family Squatinidae (angel sharks) that is comprised of about 14 globally distributed species.

3.8.5 Order Heterodontiformes (bullhead or horn sharks)

Heterodontiform sharks are identified by the combination of an anal fin and two dorsal fins preceded by spines. The order contains a single living family Heterodontidae (bullhead or horn sharks) comprising eight species of warm temperate and tropical, medium-sized (up to 1.6 m) sharks from the Pacific and western Indian Ocean. Other distinctive characters are a large, blunt head with a prominent ridge above each eye, a small, nearly terminal mouth, rough skin and molar-like rear teeth.

3.8.6 Order Orectolobiformes (carpet sharks)

Orectolobiform sharks are identified by the combination of an anal fin, two dorsal fins without spines, five gill slits on each side of the head and a mouth that is well in front of the eyes. They comprise a diverse group of mainly Indo-Pacific, benthic sharks including the small, shallow-water epaulette shark found on coral reefs, the flattened and ornately colored wobbegongs and the giant, planktivorous whale shark. The order contains seven living families, the Parascylliidae (collared carpet sharks), Brachaeluridae (blind sharks), Orectolobidae (wobbegongs), Hemiscylliidae (longtail carpet sharks), Stegostomatidae (zebra sharks), Ginglymostomatidae (nurse sharks) and Rhincodontidae (whale sharks).

The Rhincodontidae contains a single, huge (reaching 12 m), circum-tropical, plankton-feeding species that has a very wide, almost terminal mouth, minute teeth, long gill slits with internal filter screens, longitudinal ridges on the body, a semi-lunate caudal fin (except in very small juveniles) and a color pattern of light spots and stripes on a dark background. The Stegostomatidae also contains a single distinctive species that has a long, blade-like upper caudal lobe (about as long as the rest of the shark), rough skin with a color pattern of dark spots on a yellow background (juveniles with yellow stripes on a dark background), small mouth connected to the nostrils by grooves, barbels, longitudinal ridges on the body and two dorsal fins close together. The Ginglymostomatidae contains three species of medium to large sharks that have small mouths connected to the nostrils by grooves (but no lobes or grooves on the outer margin of the nostrils), barbels, two relatively large, posteriorly placed dorsal fins and a caudal fin with a weak ventral lobe. The orectolobids are distinctive, dorso-ventrally flattened (in front of the dorsal fins) sharks with skin flaps along the sides of the head, enlarged canine teeth and ornate color patterns. There are three genera and seven recognized species. However, the group is more complex and requires more detailed work with several probable new species taken recently in the Indo-Pacific region. The remaining three families contain small, often superficially similar species that can also be confused with some of the catsharks (family Scyliorhinidae). However, in the

catsharks the mouth is located partly beneath the eyes. In the parascylliids (two genera, seven species), the anal-fin origin is in advance of the second dorsal-fin origin, and the anal fin is separated from the caudal fin by a distance greater than the anal base length. The anal and caudal fins are almost touching in the brachaelurids (one genus, two species) and hemiscylliids (two genera, 12 or 13 species) and the anal-fin origin is well behind the second dorsal-fin origin. The brachaelurids have a short tail (distance from vent to lower caudal-fin origin less than distance from snout to vent) while the hemiscyllids have a long tail (distance from vent to lower caudal-fin origin greater than distance from snout to vent).

3.8.7 Order Lamniformes (mackerel sharks)

This order of mainly large (1.1-6.0 m) sharks is comprised of five families and can be identified from the following combination of characters: an anal fin, two spineless dorsal fins, a mouth located partly beneath the eyes, relatively large teeth, no barbels or grooves connecting the nostrils and mouth, and no nictitating membrane over the eyes.

Of the six families, the Alopiidae (thresher sharks) are unmistakable having an enormously elongated, scythe-like upper caudal-fin lobe that is equal in length to the rest of the body (the zebra shark also has a long upper caudal lobe, but has barbels, and grooves connecting the nostrils and mouth). There is one genus and three species of thresher sharks. The Cetorhinidae (basking sharks), contains a single living species of huge (up to 10 m) plankton feeders. Basking sharks have a stout, fusiform body, conical snout (elongate and proboscis-like in juveniles < 4 m), huge gill slits that almost encircle the head (with internal filter screens), caudal keels and a lunate caudal fin. Basking sharks are grey-brown above and paler ventrally, and superficially resemble large white sharks (family Lamnidae), but have minute teeth.

The family Odontaspididae (sand tiger sharks) contains two genera and three species of large, stout-bodied sharks with conical snouts, long awl-like teeth with lateral cusplets, two large dorsal fins, a large anal fin, and an asymmetric caudal fin with a short ventral lobe. The families Pseudocarchariidae (crocodile sharks), Megachasmidae (megamouth sharks) and Mitsukurinidae (goblin sharks) each contain a single living species of readily identifiable sharks. The goblin shark (attaining 3.8 m) has a bizarre head with an elongated snout forming a flat, blade-like rostrum, and very protrusile jaws, and the filter-feeding megamouth (attaining 5 m) has a bulbous, blubbery whale-like head and a very wide, terminal mouth. The crocodile shark is smaller (up to 1.1 m), has a fusiform body, conical snout, very large eyes, long gill slits, a low first dorsal fin, asymmetric caudal fin, and is dark brown above and paler ventrally.

The family Lamnidae (mackerel sharks) consists of three genera and five species of high-profile sharks, the white, mako and porbeagle that are of considerable importance to fisheries. These

large (3-6 m) species have conical snouts, fusiform, spindle-shaped bodies, awl-shaped or triangular teeth, minute second dorsal and anal fins, caudal keels, and lunate caudal fins. The shape of the teeth, body coloration and number of caudal keels are important for identification at the species level.

3.8.8 Order Carcharhiniformes (ground sharks)

This diverse order of sharks contains many commercially important species within its eight families. They can be identified by the following combination of characters; an anal fin, two spineless dorsal fins, a mouth located partly beneath the eyes, five gill slits, relatively large teeth, no barbels or grooves connecting the nostrils and mouth, and a nictitating membrane over the eyes. The families Leptochariidae (barbeled houndsharks) and Pseudotriakidae (false catsharks) each contain a single living species, and together with the Proscylliidae (finback catsharks) comprising four genera and seven species, are relatively obscure groups. The Scyliorhinidae (catsharks) is by far the largest family of sharks with 15 genera and more than 110 mostly small, bottom-living species. The Carcharhinidae (requiem sharks) comprise 12 genera and about 50 species of small to large "typical looking" sharks. The Triakidae (houndsharks) are also relatively speciose with nine genera and about 40 species, while the Hemigaleidae (weasel sharks) have four genera and five species and the Sphyrnidae (hammerheads) have two genera and nine species.

The Sphyrnidae are easily recognized by their bizarre, hammer-shaped heads. Variations in head size and shape are important for species identification. The Pseudotriakidae are also very distinctive with a very long, low first dorsal fin and over 200 rows of teeth in each jaw. The Scyliorhinidae are best separated from the other families by the position of their first dorsal-fin base, which is opposite or behind the pelvic-fin base. The Hemigaleidae and Carcharhinidae have precaudal pits and an undulating or rippled dorsal margin to the upper caudal fin, while the other families have no precaudal pits and a smooth dorsal caudal margin. These two families are difficult to tell apart and while hemigaleids have a small spiracle, usually absent in carcharhinids, reliable diagnosis mainly relies on the structure of the intestinal valve. The carcharhinids have a scroll-type valve and the hemigalids a spiral one. The Proscylliidae have labial furrows that are very short (confined to mouth corners) or absent, and comb-like posterior teeth. Triakids and leptochariids have much longer labial furrows and posterior teeth that are not comb-like. In the leptochariids, the upper labial furrows are very long (length more than half the mouth width) and there are barbels on the nasal flaps. The traikids have no nasal barbels (except in *Furgaleus*) and the upper labial furrows are shorter (length less than half the mouth width).

The genus *Carcharhinus* (Carcharhinidae) contains about 30 species that are difficult to identify for those not experienced with the group. Important characters are fin shape and positions, color markings on the fins, the presence of an interdorsal ridge, tooth and vertebral counts and the

shape of the upper teeth in the middle of the jaw. Species in the genus *Mustelus* (Triakidae) are also notoriously difficult to identify with partial overlap of many of the morphological, morphometric and meristic characters used to separate them. An increasing number of "regional forms" have been discovered recently.

3.8.9 Order Torpediniformes (electric rays)

The four families Torpedinidae (torpedo rays), Hypnidae (coffin rays), Narcinidae (numbfishes) and Narkidae (sleeper rays) are small to medium-sized (0.15-1.8 m) rays with large, oval, rounded or shovel-shaped discs, naked skin without denticles, short stout tails with usually two (occasionally one or none) dorsal fins and a broad caudal fin. The thick pectoral disc has two kidney-shaped electric organs on its ventral surface. In the numbfishes (four genera and at least 17 species), the tail length from behind the pelvic-fin tips is about equal to, or a little longer than the maximum disc width while in the other three families the disc is wider than the tail length. The coffin rays, that comprise one species endemic to Australia, have a pear-shaped disc, pelvic fins joined together to form a smaller second disc and a very short tail only extending slightly beyond the pelvic fins. The caudal fin is about the same size as each of the two dorsal fins, and much smaller than the pelvic fins. In the torpedo rays (one genus, at least 15 species) the caudal fin is much larger than either of the two dorsal fins and about the same size as the pelvic fins. The sleeper rays (four genera, nine species) have a large round pectoral disc and a strong tail with only a single or no dorsal fin.

3.8.10 Order Pristiformes (sawfishes)

The family Pristidae (sawfishes) consists of two genera and about six species of mostly large (up to 7 m) tropical marine and freshwater species. These are unmistakable batoids with the snout highly modified into a "saw" bearing large lateral rostral teeth. Unlike the superficially similar sawsharks (family Pristiophoridae), sawfish have their gill slits situated ventrally (rather than laterally) on the head, have no barbels on the saw and their relatively small pectoral fins join the head in front of the gill slits. The number of rostral teeth, shape of the caudal fin and position of the first dorsal fin relative to the pelvic fins are important characters for identification at the species level.

3.8.11 Order Rhiniformes (sharkrays)

McEachran et al. (1996) consider this order to comprise one family (Rhinidae) containing a single species of large ray (*Rhina ancylostoma*) attaining a length of at least 2.7 m. It has a broadly rounded head distinctly demarcated from its pectoral fins, falcate shark-like fins, almost lunate caudal fin and horny ridges on its back bearing thorns and spines. Other authors have placed *Rhina* together with *Rhynchobatus* in the Rhinidae (Compagno, 1999b) or in the Rhynchobatidae (Last and Stevens, 1994).

3.8.12 Order Rhynchobatiformes (wedgefishes or sharkfin guitarfishes)

The single family Rhynchobatidae (sharkfin guitarfishes) contains mainly inshore rays with a flattened body, a mostly wedge-shaped or oval disc and a broad, shark-like tail with two large dorsal fins and a large caudal fin. In the shovelnose rays (*Rhinobatos* spp.), the first dorsal-fin origin is behind the pelvic fin, the caudal fin has a weak ventral lobe and a well-developed dorsal lobe with a straight posterior margin. Diversity is highest in the Indo-West Pacific region with four genera and about 40 species, but more are likely to be discovered as these rays are not well known in many areas. The sharkfin guitarfishes have the first dorsal-fin origin in front of the pelvic-fin insertions, both caudal lobes are well developed and the posterior margin of the dorsal lobe is concave. There are two genera and more than five species which mostly occur in the Indo-West Pacific; however, the taxonomy of the genus *Rhynchobatus* requires more study.

3.8.13 Order Rajiformes (skates)

The taxonomy of the skates is very complex with two subfamilies, some 26 genera and around 200 species. These bottom living rays have enlarged pectoral fins forming a disc that varies in shape from nearly circular to rhomboidal. Their pelvic fins are deeply notched forming two lobes, and they have a fairly narrow tail with two (rarely one or none) small dorsal fins near the tiny caudal fin. Most species have enlarged thorns around the eyes, along the dorsal midline or on other parts of the body. The shape of the disc and snout, the presence and shape of the cartilage supporting the snout, relative lengths of the pelvic-fin lobes and the pattern of thorns are important characters at the species level. The genus *Anacanthobatus* (leg skates) consists of about 18 species that have their pelvic fins separated into a mobile leg-like front lobe, and normally have smooth skin.

3.8.14 Order Myliobatiformes (stingrays)

This is a complex grouping which McEachran et al. (1996) consider contains three suborders (Platyrhinoidei, Zanobatoidei and Myliobatoidei) and two superfamilies (Hexatrygonoidea and Dasyatoidea); in the interests of simplicity this account differs slightly from their classification. The families Urolophidae (stingarees), Hexatrygonidae (sixgill stingrays), Dasyatidae (stingrays), Gymnuridae (butterfly rays), Myliobatidae (eagle rays), Rhinopteridae (cownose rays) and Mobulidae (devilrays) usually have one or more stinging spines on the dorsal surface of the tail, a large pectoral disc and a stout to very slender tail with a caudal fin and single dorsal fin variably present or absent. The hexatrygonids are unique among the batoids in having six pairs of gill slits; there is a single genus and about seven species most of which are known only from a single specimen. More work is required to resolve the validity of these species. The gymnurids (two genera and at least 12 species) have a very wide (width more than 1.5 times its length), butterfly-shaped disc and a very short filamentous tail. Mobulids are the largest of all rays (attaining at least 7 m width). The two genera and about 10

species are easily recognized by their wide, angular, wing-like discs, prominent fleshy lobes projecting forward like scoops on each side of the head, terminal (or nearly so) mouth with minute teeth (they are plankton feeders) and filamentous tails. Myliobatids (four genera and about 22 species) and rhinopterids (one genus and about 10 species) also have wing-like disc shapes and filamentous tails, but a single bulbous fleshy lobe extends around the snout in myliobatids; in rhinopterids this is indented to give it a distinctive bilobed forehead. Dasyatids have a circular to rhomboidal disc with a whip-like tail that usually has stinging spines but lacks dorsal, anal or caudal fins. However, they may have membranous skin folds on the dorsal and or ventral midlines of the tail; the central disc and dorsal tail surface usually has thorns or tubercles. Dasyatids are represented by at least five genera and more than 60 species that occur in marine and freshwater habitats; their often large size (some species > 2 m disc width) makes them difficult to study and more taxonomic work is required on the group. Disc and snout shape, color patterns (which may change subtly with size), the presence of membranous skin folds on the tail, and the pattern of denticles on the disc and tail are important characters for identification at the species level. Urolophids resemble dasyatids in body shape, but have shorter tails with a well developed caudal fin, and usually no thorns or tubercles on the disc or tail. There are three genera and about 40 species of urolophids. Disc and tail shape, structure of the nostrils, presence of a dorsal fin and color pattern are important for identifying species. However, some species are difficult to identify on external characters alone.

The family Platyrhinidae (thornback rays) comprise two genera and two species of inshore batoids that have round or heart-shaped discs, long, stout, shark-like tails, two large dorsal fins (situated anteriorly on the tail), no stinging spines, and large thorns on the disc and tail. Compagno (1999b) placed the family Platyrhinidae within the order Rhinobatiformes.

3.8.15 Order Chimaeriformes (chimaeras)

Diagnostic features of the chimaeras were given in section 3.1; the order contains three families, the Callorhinchidae (elephant fishes), Chimaeridae (shortnose chimaeras) and Rhinochimaeridae (longnose chimaeras). There is one genus and three species of silvery colored elephantfishes that are easily recognized by their long snouts terminating in a flexible hoe-shaped structure, relatively short-based second dorsal fin, large anal fin and well-developed caudal fin that has no caudal filament and is arched upwards from the body axis. Shortnosed chimaeras (two genera and at least 22 species) have a relatively short snout with a bluntly rounded tip and a caudal-fin axis that is straight. Most species occur in deep water and are dark brown to purply-black in color; the systematics of the group needs more attention with several new forms reported recently. Longnose chimaeras (three genera, at least seven species) also have a straight caudal-fin axis, but they have a very long snout with a pointed tip; they range in color from pinkish-white to black.

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CHAPTER 4. TAGGING METHODS AND ASSOCIATED DATA ANALYSIS

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4.1 INTRODUCTION

Tagging methods have a long history of use as tools to study animal populations. Although the first attempts to mark an animal occurred sometime between 218 and 201 B.C. (a Roman officer tied a note describing plans for military action to the leg of a swallow, and when the bird was released, it returned to its nest which was in close proximity to the military outpost in need of the information), it is uncertain when fish were first marked (McFarlane et al., 1990). An early report published in *The Compleat Angler* in 1653 by Isaak Walton described how private individuals tied ribbons to the tails of juvenile Atlantic salmon (*Salmo salar*) and ultimately determined that Atlantic salmon returned from the sea to their natal river (Walton and Cotton, 1898; McFarlane et al., 1990). Since the late 1800s, numerous fish tagging experiments have been conducted, with an initial emphasis on salmonids, followed soon after by successful attempts at tagging flatfish and cod. Pelagic species, namely Pacific herring (*Clupea harengus pallasi*) and bluefin tuna (*Thunnus thynnus*), were successfully tagged in the early 1900s, while elasmobranch tagging studies did not commence until the 1930s. Since 1945, large-scale tagging programs have been initiated all over the world in an effort to study the biology and ecology of fish populations.

Modern tagging studies can be separated into two general categories. Tag-recovery studies are those in which individuals of the target population(s) are tagged, released, and subsequently killed upon recapture, as in a commercial fishery; while capture-recapture studies are designed to systematically tag, release, and recapture individuals on multiple sampling occasions. The former study-type often facilitates the establishment of a cooperative tagging program in which fish are tagged by both scientists and volunteer fishermen. The primary advantage of a cooperative program is the sheer volume of fish that can be tagged each year, since it is possible to combine the efforts of scientists and a large number of volunteer recreational and commercial fishermen. The latter study-type typically leads to the creation of agency- or institution-based tagging program in which only those scientists directly involved with the study tag fish.

When starting a tagging program, the choice of whether to design a tag-recovery study (that may or may not be cooperative) or a capture-recapture study largely depends on the objectives of the tagging program. For example, although tag-recovery studies tend to be much less labor intensive than capture-recapture studies, the analysis of tag-recovery data does not easily yield estimates of population size, which is often of interest to fisheries managers. Similarly, the quality of the data associated with a cooperative tag-recovery study can sometimes be suspect, since the level of tagging experience and overall commitment to the tagging program in terms of the precision of the data being collected at the time of tagging can vary significantly among fishermen. However, in some situations, it may not be possible to develop a tagging program without the help of volunteer fishermen, since a single agency may not be able to assume the cost associated with capturing and tagging hundreds or possibly thousands of fish each year.

The intent of this chapter is to serve as an overview of tagging studies and their use as tools for increasing our biological understanding of elasmobranch populations and ultimately the information from which we base management decisions. In a practical sense, however, it is virtually impossible in a single

chapter to adequately discuss all of the various aspects of tagging studies and the analysis of tagging data. As such, this chapter will focus on issues related to tag-recovery programs and the analysis of tag-recovery data, primarily because the cost effectiveness of these types of studies has rendered them a very common approach for inferring life history characteristics of aquatic populations. The chapter begins with a discussion of the various tag types that can be used to mark individuals, followed by a treatment of the various types of analysis methods that can be used to derive information from tag-recovery data. Not included in the chapter is a stand-alone section on the design of tag-recovery studies, largely because it is difficult to accommodate all types of data collection and subsequent analyses using a single study design. That said, however, it is extremely important to base the development of a tag-recovery program on a clearly and rigorously defined study design. I have chosen to address the details associated with sampling and data collection procedures periodically throughout the text, and in accordance with the type of data and analysis being discussed. For more information on the design of capture-recapture studies and the associated methods for data analysis, efforts should be made to consult the comprehensive monographs developed by Burnham et al. (1987) and Pollock et al. (1990).

4.2 TAG TYPE AND PLACEMENT

No single tag type (and therefore tagging technique) is appropriate for all species of sharks, or in some instances, all life stages within a particular species. As such, great consideration should be given to the choice of tag type when developing a tagging program. Factors that can be used to assist with the selection of a tag include but need not be limited to (Wydoski and Emery, 1983; McFarlane et al., 1990; Kohler and Turner, 2001):

- The objectives of the tagging study or program.
- The effect of the tag on the life history characteristics of the species under study, namely, reproduction, survival, and growth.
- The durability, longevity, and stability of the tag.
- The stress associated with the capture, handling, and tagging process.
- The size and number of individuals to be tagged.
- Ease (or lack thereof) of tag application.
- Cost of purchasing the tags and conducting the tagging experiment.
- The amount and type of cooperation required among agencies, states, or countries for the tagging study to be successful.

For studies involving teleost species, the number of different tag types that have been used to mark individuals is fairly extensive (McFarlane et al., 1990). Although a similar diversity among tag types can be documented for studies involving shark populations, the Petersen disc, internal anchor tag, Rototag, and dart tag tend to be the most widely used (Kohler and Turner, 2001).

4.2.1 Petersen disc tag

The Petersen disc tag, which was developed by Petersen (1896), is one of the first tags ever used to study fish populations. Although the Petersen disc tag has undergone several modifications over the years, in essence, the tag is comprised of two plastic discs that are placed on each side of the individual and connected by either a wire or a pin running through either the dorsal fin or the musculature at the base of the dorsal fin (Figure 4.01). The tag information is generally printed on the discs. Petersen disc tags were used in many of the early shark tagging studies, which studied the growth and movement of a variety of shark species in the Pacific (Holland, 1957; Kato and Carvallo, 1967; Bane, 1968).

There are two key drawbacks associated with the use of Petersen disc tags. Specifically, they are

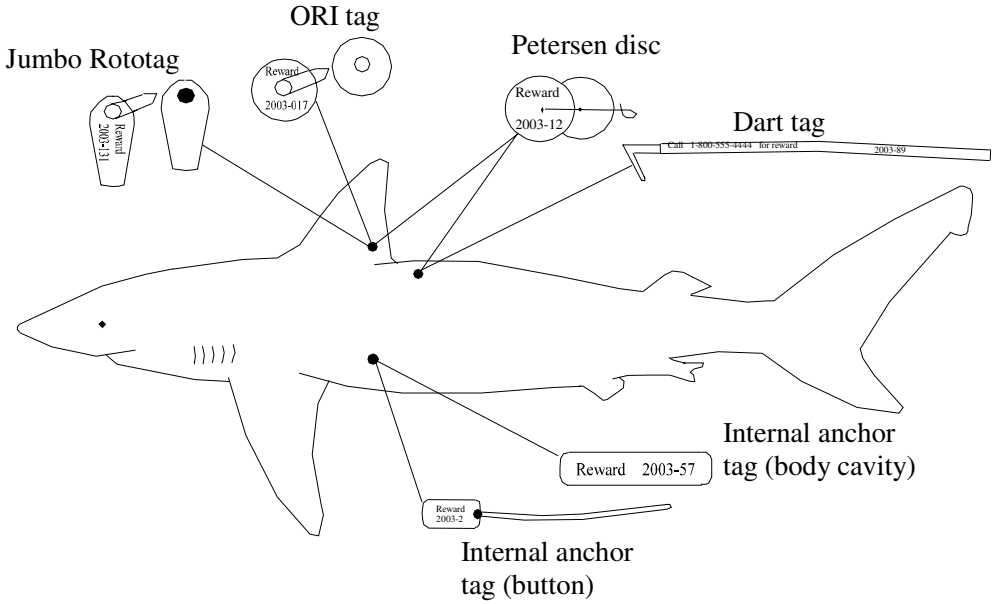


Figure 4.01 Types of internal and external tags typically used to tag sharks. The appropriate anatomical location for attachment is indicated for each tag-type.

prone to fouling by barnacles and algae and they can severely limit body and fin thickness by restricting growth, especially when used for long-term tagging studies. This restriction of growth can lead to splitting and deterioration of the dorsal fin, particularly with immature sharks since their cartilaginous dorsal rays tend to be softer than those of mature sharks, and also because they will experience a more dramatic growth rate over time when compared to mature individuals (Kohler and Turner, 2001).

4.2.2 Internal anchor tag

Rounsefell and Kask (1943) discuss the development of the internal anchor tag, which was designed to overcome some of the problems associated with the use of Petersen disc tags, particularly the restriction of growth. There are two types of internal anchor tags. The first tag, which is sometimes referred to as a “body cavity tag”, is small and rectangular in shape, and is inserted completely into the body cavity through a small incision in the lower half of the body wall (Figure 4.01). All pertinent informa-

tion is printed on the tag, which is typically made of plastic. The second tag is sometimes referred to as a "button" tag and is comprised of a vinyl streamer attached to an elongated plastic disc (Figure 4.02). The disc serves as the anchor and again it is inserted into the body cavity through a small incision in the body wall, with the streamer protruding external to the individual. The tag information is usually printed on both the plastic disc and the streamer (Figure 4.01).

Each type of internal anchor tag has been used for a variety of shark tagging studies (Olsen, 1953; Grant et al., 1979; Hurst et al., 1999). An advantage of internal anchor tags is that they can be retained for many years, which is desirable given the longevity of many shark species. In terms of tag recovery, however, body cavity tags are only detectable once an individual is gutted. This characteristic renders it impossible to conduct a capture-recapture study using this tag type. Button tags are more visible than body cavity tags, despite the fact that the streamers are susceptible to fouling and abrasion. The application of some type of antibiotic salve or antiseptic solution to the tagging wound is recommended when using either type of internal anchor tag.

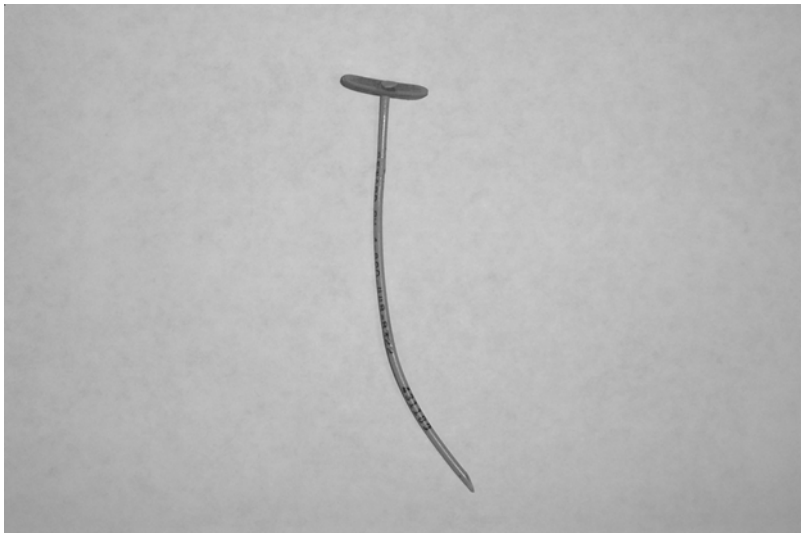


Figure 4.02 A "button" internal anchor tag. The tag is comprised of a vinyl streamer attached to an elongated plastic disc. The disc serves as the anchor and it is inserted into the body cavity through a small incision in the body wall, with the streamer protruding external to the individual.

4.2.3 Rototag

Davies and Joubert (1967) describe the early use of Rototags, which were originally manufactured by Daltons of Henley-on-Thames, UK for livestock tagging but have been adapted for marine and wildlife tagging studies. The Jumbo Rototag (Figure 4.03) and the ORI tag (which is a modified Jumbo Rototag) are typically applied with an applicator through a hole in the leading edge of the first dorsal fin created by a leather punch (Figure 4.01). Both tag types are made from a high-grade nylon, with the Jumbo Rototag being semirectangular in shape and the ORI tag more circular in shape. Early experiments with the Jumbo Rototag indicated that the tag was susceptible to vertical movement due to the hydrodynamics of swimming (Davies and Joubert, 1967). The suspicion that this vertical movement caused swelling and irritation prompted the design of the ORI tag.

As with the Petersen disc tag, the Jumbo Rototag and ORI tag are susceptible to fouling and can negatively influence growth. Nevertheless, these tags have been used in numerous tagging studies of shark species (Kato and Carvallo, 1967; Thorson and Lacy, 1982; Stevens, 1990; Kohler et al., 1998).

Until 1988, they were the primary tag used in the common skate (*Dipturus batis*) tagging program conducted off the west coast of Scotland by the Science Department of Glasgow Museums, and are also used by the Central Fisheries Board of Ireland for their blue shark tagging program.

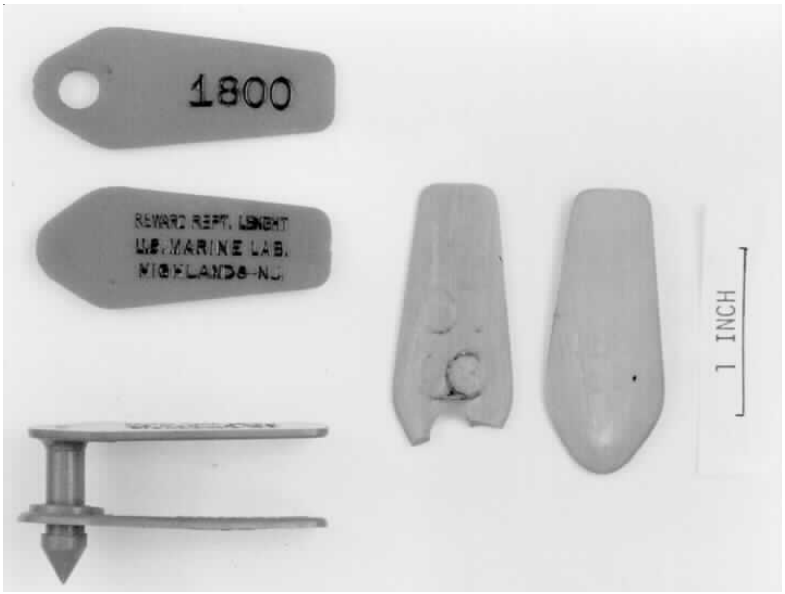


Figure 4.03 Jumbo rototag showing tag number and mailing address [from the NMFS Cooperative Shark Tagging Program website (http://na.nefsc.noaa.gov/sharks/intro.html)].

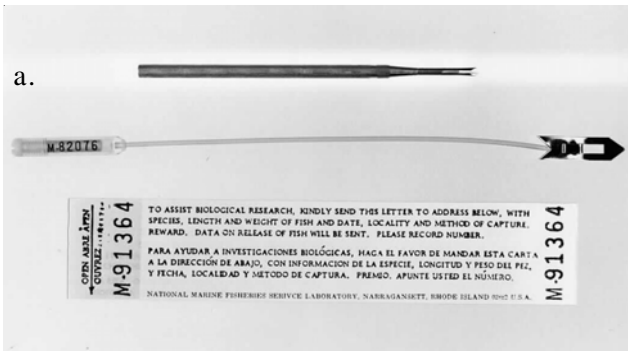
4.2.4 Dart tag

The origin of the dart tag can be traced back to early tagging studies of marine pelagic fish, particularly tunas (McFarlane et al., 1990). The dart tag was developed primarily to facilitate the safe and effective tagging of individuals in the water, since many pelagic species attain sizes that are too large to be handled onboard a vessel. Relative to the original design, the dart tag was modified for use on sharks (Casey, 1985) and a variety of types of dart tags have been used by numerous tagging programs over the years (Kohler and Turner, 2001). Fundamentally, a dart tag is comprised of a streamer, which can be made of monofilament line, vinyl, or nylon line that is attached to either a stainless steel, plastic, or nylon pointed head (Figure 4.01, Figure 4.04a). All pertinent tag information is either printed on the streamer itself or on a legend that is enclosed by a capsule and attached to the streamer. Application of a dart tag is usually accomplished using a stainless steel tagging needle, which is used to drive the pointed head of the tag into the dorsal musculature of the individual (Figure 4.04b). Efforts are generally made to apply the tag at an angle so that streamer lies alongside the individual while it swims. For sharks, the optimal location for a dart tag is next to the base of the first dorsal fin.

The main advantage of using a dart tag is its ease of application. Relative to the Petersen disc tag, Rototag, and internal anchor tag, very little time is needed to successfully mark an individual with a dart tag. This characteristic combined with the fact that minimal training is necessary to become proficient at applying a dart tag has rendered it the most commonly used tag type in shark tagging studies (Kohler and Turner, 2001). Specific large-scale and longstanding tagging studies that utilize the dart tag include the NMFS Cooperative Shark Tagging Program (Kohler et al., 1998; Kohler and Turner, 2001) and the Australian Cooperative Game-Fish Tagging Program (Pepperell, 1990).

4.3 DATA COLLECTION AND ANALYSIS

Tag-recovery studies facilitate the collection of a variety of types of information on the species under study. These data can be used to infer delineation of nursery areas, habitat utilization, stock identification, length/weight relationships, growth rates, gear selectivity, patterns of movement, survival/mortality,



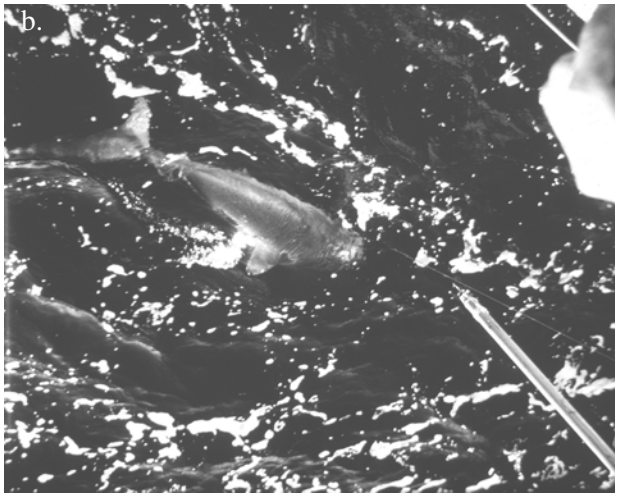


Figure 4.04 (a) An "M" type dart tag displaying tagging needle and legend [from the NMFS Cooperative Shark Tagging Program website (http://na.nefsc.noaa.gov sharks/intro.html)]; (b) application of a dart tag to an individual along side a vessel [photo by J. A. Musick].

spatial and temporal distribution, relative abundance, species and size composition and sex ratio (Kohler and Turner, 2001). The following subsections contain a more detailed presentation of these data types and their associated methods of analysis. With respect to deriving survival/mortality information from tag-recovery data, my discussion is brief since a more complete treatment of the topic is provided in section 8.3.2 of Chapter 8.

While many of the aforementioned types of data are fairly simple and straightforward, it is still important that they be collected under a rigorously defined sampling design. A commonly applied design is a stratified random sampling design where the strata are defined according to variations in water depth, salinity, water temperature or latitude/longitude. Although data collected haphazardly can provide anecdotal information about a particular species, subsequent analyses of those data will not yield accurate inferences about the population as a whole. The choice of a sampling design and the subsequent sampling gear often depend on a variety of factors, most notably the objective(s) of the study, the topography and size of the study area, and the general life history characteristics of the species under study. Despite these factors, a concept that is essential for deriving population level inferences is that the data collected are representative of the target species in the study area. Hence, sampling should take place during all seasons (unless the target species are not year-round residents) and over all spatial locations or habitat types that the target species occupies within the study area. Clearly, temporal and spatial information may not be available for species and areas that are not well studied, which implies that a very non-tailored and systematic sampling design must be adopted. Also, efforts should be made to sample with a gear-type that is relatively non-selective; that is, one that will capture a wide variety of species and that will capture males and females of all sizes with approximately equal probability. In practice, this need may render a longline more appropriate than a gillnet.

4.3.1 Delineation of nursery areas, habitat utilization, stock identification

It is possible but often very difficult to use data reflecting the location of tag recoveries to effectively delineate the nursery area of a species. Provided that an adequate number of young-of-the-year (YOY) could be tagged and, of those, an adequate number of tag recoveries are tabulated, information on the location of tag recoveries can be used to determine the habitat utilization and extent of the nursery area for YOY individuals. In addition, if a representative sample of a species in a particular location is tagged (i.e., individuals of varying sizes from both sexes in the area), it may be possible to determine the habitat range of the whole population. Moreover, if several population level ranges have been delineated, inferences about the degree to which various stocks mix and ultimately stock identification can be inferred. However, the generally low tag-recovery rates observed with most elasmobranch species combined with inaccurate reporting of recapture location from fishers can render it difficult to accurately characterize habitat ranges.

An alternative approach to using the locations of tag recoveries to delineate the range of a population is to infer about habitat utilization from the spatially explicit catch data obtained from sampling efforts designed to capture individuals for tagging. Note that data resulting from supplemental sampling efforts that are designed to "canvas" the suspected range or study area will likely be needed. This approach was used by Grubbs (2001) to characterize the nursery ground of YOY sandbar sharks (*Carcharhinus plumbeus*) in Chesapeake Bay. Although it was known that the Bay served as a nursery area for YOY sandbar sharks, the exact geographical area within the Bay utilized by YOY sandbar sharks was not known. Hence, Grubbs (2001) added stations to the sampling protocol of an existing longline survey in such a manner as to systematically sample for the presence of YOY sharks from the Bay mouth northward. The northernmost latitude of the nursery area was determined by noting the location where the catches of YOY sandbar sharks became zero.

A second alternative approach that can be used to delineate habitat utilization and discern degrees of site fidelity involves the use of acoustic telemetry (see section 8.3.3 of Chapter 8 for more information on telemetry). To conduct a telemetry study, high-power, ultrasonic transmitters must be surgically or externally implanted in a representative sample of the target species. Receivers are then used to monitor transmitter output for the purpose of intermittently tracking the movements and space utilization of tagged individuals. Prior to conducting the study, a tracking protocol that specifies the length of the tracking session, the number of fish tracked each session, and frequency at which position information is obtained should be developed. If previous telemetry studies have been conducted for the species under study, it is recommended to adopt the same tracking protocol so that the data are comparable. Morrissey and Gruber (1993) used acoustic telemetry to examine the spatial and temporal patterns of activity of juvenile lemon sharks (*Negaprion brevirostris*) in the Bahamas. The study was the first to utilize nonarbitrary sampling and successfully characterized patterns of movement and degree of site fixity in any elasmobranch species. The study also examined the correlation between size of habitat range and body size.

4.3.2 Length/weight relationship

The observed length and weight measurements taken at the time of first capture can be used to establish a number of predictive relationships. For example, it is often useful to develop conversions among the various length measurements, which can usually be accomplished using simple linear regression:

$$L_1 = \alpha + \beta L_2, \qquad (4.1)$$

where L_1 and L_2 are the two length measurements (e.g., fork and total length (FL, TL), or FL and precaudal length (PCL), etc.) for which a predictive relationship is desired, and α and β are the standard simple linear regression parameters that are to be estimated. Prior to applying equation 4.1, it is recommended to plot the length measurements against each other to ensure that a linear trend is present. Efforts should also be made to develop length conversion relationships for males and females separately, as well as for the sexes combined. As an example, see the FL/TL relationship derived by Natanson et al. (1999) for tiger sharks (*Galeocerdo cuvier*) in the western North Atlantic.

In addition to predictive relationships among various types of length measurements, it is also possible to use the size data collected at the time of first capture to establish a length/weight predictive relationship. This type of relationship is typically derived using the following power function (Figure 4.05).

$$W = \alpha L^{\beta}, \qquad (4.2)$$

where W and L represent weight and length, respectively, and α and β are regression parameters (not to be confused with those of equation 4.1). Nonlinear regression techniques (Bates and Watts, 1988) can be used to estimate α and β, and it is generally recommended to fit equation 4.2 to sex-specific as well as combined length/weight data. Stevens (1990) applied equation 4.1 to length/weight data obtained at the time of tagging for tope sharks (*Galeorhinus galeus*), blue sharks (*Prionace glauca*), and porbeagle sharks (*Lamna nasus*) off the coast of England.

Despite the fact that equation 4.2 is frequently used to relate length and weight data, it should be noted that it might not always be the most appropriate model. When attempting to derive a predictive relationship between any variables, it is reasonable to fit several models to the data. Alternative models for length/weight relationships might include a linear, quadratic, or change-point model, which is a piecewise function that is designed to fit two or more models each to separate portions of the data (Chappell, 1989). By fitting a suite of models to the data, it is then possible to use model selection techniques, notably likelihood ratio tests and/or Akaike's Information Criterion (AIC) and related measures (Burnham and Anderson, 1998) to assess model performance and ultimately identify the model that best fits the data.

4.3.3 Growth rates

If fishers record the date and length when tagged fish are recaptured, then information on growth increments can be obtained and ultimately used to estimate the parameters of the von Bertalanaffy (1938) growth function (VBGF). An obvious advantage to this approach is that a VBGF can be defined in the absence of age data. The VBGF takes the form (Figure 4.06):

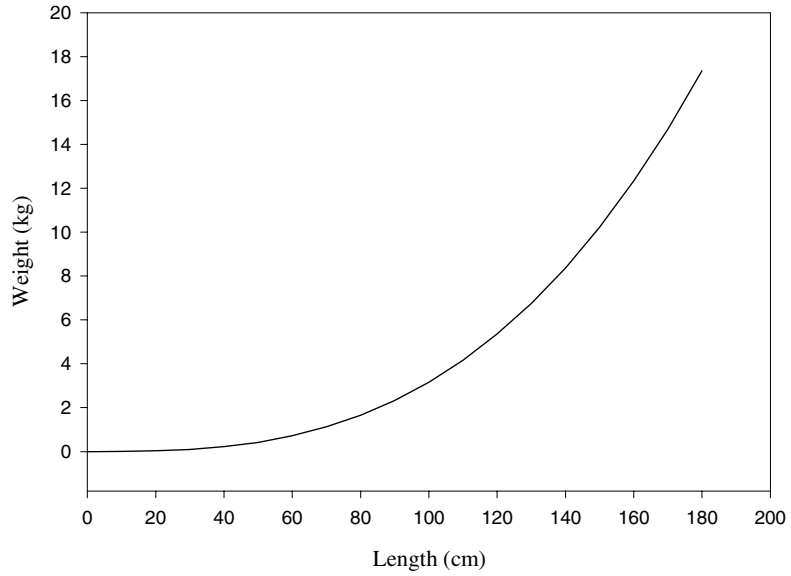


Figure 4.05 General shape of the power function typically used to relate length and weight under the assumption that $\alpha = 0.000005$ and $\beta = 2.9$. Although these parameter values are not based on actual length/weight data, they closely resemble the estimates obtained by Stevens (1990) for tope in the eastern North Atlantic.

$$l_t = l_\infty (1 - e^{-k(t-t_0)}), \qquad (4.3)$$

where l_t is the length of an individual at age (or time) t, l_∞ is the theoretical maximum attained length, k is the growth coefficient, and t_0 is the hypothetical age (or time) that an individual is of length zero. Note that equation 4.3 can be developed for males and females as well as for the sexes combined (see Chapter 6 for more details on growth).

A significant body of literature exists on the procedures of estimating growth parameters from recovery data (Gulland and Holt, 1959; Fabens, 1965; Cailliet et al., 1992; Wang, 1998). What follows is a description of the method developed by Gulland and Holt (1959) primarily because it is fairly straightforward, however, efforts should be made to use several methodologies when analyzing growth increment data. Tests can then be performed to statistically compare the results from different methods.

Gulland and Holt (1959) noted that the length of an individual at time $t+a$ would be:

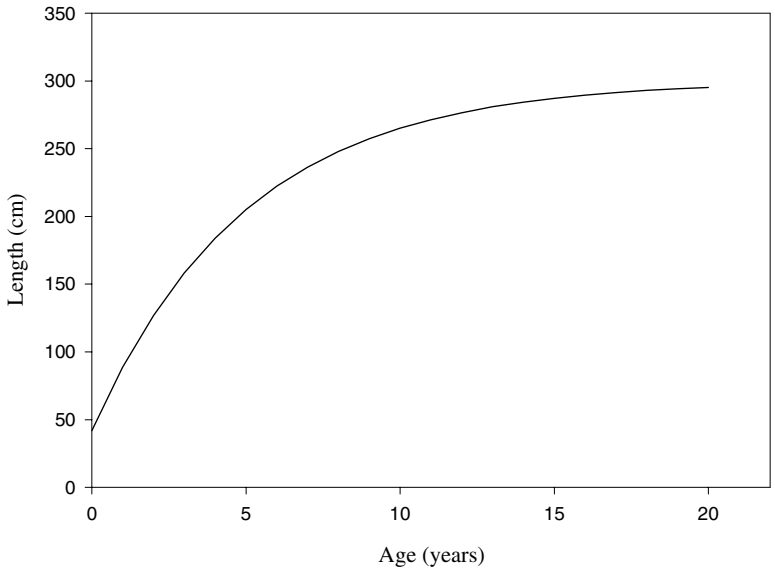


Figure 4.06 General shape of the von Bertanalffy growth curve under the assumption that $l_4 = 300$, $k = 0.20$, and $t_0 = -0.75$. Although these parameter values are not based on actual age/length or length increment data, they do not differ substantially from estimates derived by Natanson et al. (1999) for tiger sharks in the western North Atlantic.

$$l_{t+a} = l_\infty (1 - e^{-k(t-t_0+a)}). \qquad (4.4)$$

Therefore, the growth increment from time t to time $t+a$, denoted by δl, is given by:

$$\delta l = (l_{t+a} - l_t) = l_\infty e^{-k(t-t_0)}(1 - e^{-ka}), \qquad (4.5)$$

and the growth per unit time, denoted by g, is:

$$g = l_\infty e^{-k(t-t_0)} \frac{(1 - e^{-ka})}{a}. \qquad (4.6)$$

If x represents the midpoint of the length interval (l_t, l_{t+a}), then $x = ½(\ l_t + l_{t+a})$, and after some algebraic manipulations, the following equation holds:

$$l_\infty e^{-k(t-t_0)} = \frac{2(l_\infty - x)}{1 + e^{-ka}}. \qquad (4.7)$$

Substitution of equation (4.7) into equation (4.6) yields:

$$g = (l_\infty - x) \frac{2(1 - e^{-ka})}{a(1 + e^{-ka})}. \qquad (4.8)$$

Thus, equation 4.8 implies that the growth over a fixed time period and the midpoint of the corresponding length interval are linearly related. Hence, linear regression techniques can be used to derive estimates of k and l_∞. The parameter t_0 cannot be estimated from tag-recovery data alone, since it requires an estimate of absolute size at age (Natanson et al., 1999). Given an estimate of the average size at a particular age (or time), the VBGF can be rearranged to yield an estimate of t_0:

$$t_0 = t + \left(\frac{1}{k}\right)\left[\log_e\left(\frac{l_\infty - l_t}{l_\infty}\right)\right]. \qquad (4.9)$$

In practice, t_0 is usually estimated by letting $t = 0$ and l_t be the average size at birth (Natanson et al., 1999).

Depending on the number of tag-recoveries and, hence, the amount of length increment data available, it may be possible to derive growth parameter estimates for the males, female and sexes combined of a single species in a particular region, multiple species in a particular region, and/or for a single species in several geographically distinct parts of its range. If multiple growth curves are available, it is recommended to use statistical techniques to formally compare the derived growth information. In general, two types of comparisons are typically of interest (Wang and Milton, 2000):

1. Within-species comparisons of growth parameters when two sets of estimates are obtained from different time periods, areas or sexes.
2. Between-species comparisons of growth parameters.

A major problem when trying to statistically compare growth parameters from two groups of fish is that estimates of the VBGF parameters tend to be correlated. The presence of covariances among parameter estimates implies that traditional univariate statistical procedures cannot be used to perform the aforementioned within- or between-species comparisons of growth parameters. To overcome this problem, Wang and Milton (2000) suggested comparing growth parameter estimates using a generalized T^2-statistic. To test the hypothesis H_0: $G_1 = G_2$ versus the alternative H_A: $G_1 \neq G_2$, where G_1 and G_2 are column vectors of VBGF parameters estimates for two groups of fish and

$$G_1 - G_2 = \begin{bmatrix} l_{\infty(1)} - l_{\infty(2)} \\ k_{(1)} - k_{(2)} \\ t_{0(1)} - t_{0(2)} \end{bmatrix} , \qquad (4.10)$$

the T^2-statistic is calculated as

$$T^2 = [G_1 - G_2]' V^{-1} [G_1 - G_2] , \qquad (4.11)$$

where $[G_1 - G_2]'$ is the transpose of $[G_1 - G_2]$, and V is the variance-covariance matrix of $[G_1 - G_2]$. The distribution of the T^2-statistic is approximately chi-squared with 2 degrees of freedom. The corresponding critical value $\chi^2(\alpha)$, where α is the desired level of significance.

4.3.4 Gear selectivity

Selectivity can be defined as the probability of capture at a given age/size relative to the probability of capture at the age/size of maximum vulnerability. Determining the selectivity of a particular gear for different sized individuals is often a key component of fishery stock assessments. In the strictest sense, all fishing gears used to capture fish are selective to some degree. For example, individuals of varying sizes are generally not captured with equal probability by a gillnet, since the girth of some individuals may be substantially larger than the mesh size of the net. Longlines and hook-and-line gear are also selective, since mouth size relative to hook size influences the probability of capture.

In general, gear selectivity is very difficult to estimate largely because it is not easy to quantify how swimming speed influences the probability of capture. However, over the years several approaches have been used to estimate the selectivity of various gear types, particularly gillnets (Olsen, 1959; Regier and Robson, 1966; Kirkwood and Walker, 1986; Borgstrom and Plahte, 1992; Helser et al., 1998). With respect to tag-recovery data, Myers and Hoenig (1997) developed a method for estimating the selectivity of a variety of gear types from the tag recoveries associated with several separate tagging experiments (since a single tagging experiment often does not provide enough recoveries to estimate selectivities reliably). The method involves fitting a generalized linear model (McCullagh and Nelder, 1989) to the data to estimate the size, gear, and experiment effects from a collection of experiments. Specifically, if r_{igl} represents the observed number of tag recoveries from tagging experiment i captured with gear-type g of length l, then the expected number of tag recoveries is given by the following expression:

$$E[r_{i,g,l}] = N_{i,l} R_{i,g} U_{i,g} S_{g\,l}, \qquad (4.12)$$

where N is the number of individuals tagged, R is the product of the fraction of individuals that survive the tagging process, the proportion of tags not shed, and the proportion of recovered tags that are reported (which is assumed to be constant over length), U is the exploitation rate, and S is the selectivity (which is assumed to be constant over the experiments included in the analysis). If the probability of capturing a tagged individual is modeled as $p_{i,g,l} = R_{i,g}U_{i,g}S_{g\,l}$, the generalized linear model takes the form:

$$\log(\pi_{i,g,l}) = \log(R_{i,g}) + \log(U_{i,g}) + \log(S_{g,l}). \qquad (4.13)$$

Equation 4.13 possesses the three features of a generalized linear model: the function is linear, the expected value of the dependent variable is related to the linear combination of the explanatory variables via a link function (in this case the log link), and the error distribution is in the exponential family (in this case a binomial error since the probability of observing r_{igl} tag recoveries is a binomial random variable).

Inherent to the method are the assumptions that tag-induced mortality, natural mortality, tag loss, and tag-reporting rate are independent of fish length for each gear type and that growth and natural mortality are small enough to be ignored during the analysis. To avoid violation of the latter assumption, Myers and Hoenig (1997) recommend only considering tag-recoveries associated with individuals that were at liberty for only a short period of time. Although this method has never been applied to elasmobranch tag-recovery data, Myers and Hoenig (1997) applied it to 137 tagging experiments of Atlantic cod (*Gadus morhua*) and showed that the selectivity of otter trawls changed from the 1960s to the 1980s and that the selectivity pattern assumed in several of the cod stock assessments was incorrect.

4.3.5 Movement

One of the principal objectives of most elasmobranch tag-recovery studies is to derive information on movement. Over the years, there have been numerous studies documenting the patterns of movement and space utilization for shark species worldwide. For example, Francis (1988) described the inshore-offshore movements of rig (*Mustelus lenticulatus*) in New Zealand, Gruber et al. (1988) and Morrissey and Gruber (1993) collectively described patterns of movement and home range for lemon sharks in the Bahamas, and Casey and Kohler (1992) characterized the movement of shortfin mako sharks (*Isurus oxyrinchus*) in the western north Atlantic. Many more examples of studies that derived information on the movement of sharks from tag-recovery data can be found in the literature (see Kohler and Turner (2001) for comprehensive list of these studies).

Efforts aimed at documenting patterns of activity and space utilization from tag-recovery data typically begin by calculating the distance traveled and the time at liberty for each recaptured individual. From those calculations, population-level estimates of movement can be determined by calculating the mean and median distance traveled and the total range of distances (minimum and maximum) traveled. In general, data associated with individuals that were recaptured within a short time of tagging are typically

excluded from distance calculations, largely because it is important to allow newly tagged individuals enough time to become fully mixed into the overall tagged population (mixing ensures that tagged population is representative of the total population). However, the decision to exclude these "immediate" recaptures does often depend on the objectives of the study. Although there is no "official" amount of time to allow for mixing, Francis (1988) omitted all recaptures that were within 20 days of the time of tagging in the movement analysis of rig.

As with the growth increment data, if there is a sufficient number of tag recoveries, it may be possible to develop relationships between distance traveled and time at liberty for the males, female and sexes combined of a single species in a particular region, multiple species in a particular region, and/or for a single species in several geographically distinct parts of its range. If multiple characterizations of movement are available, it is recommended to use statistical techniques to formally compare the derived movement information. Two types of statistical analyses can be used to perform these comparisons:

1. A simple t-test, which tests for statistical differences between the mean distances traveled by two groups (e.g., males and females of a particular species; sexes combined for two species; a species in two regions of its geographic distribution, etc.).
2. Analysis of variance (ANOVA), which tests for statistical differences between the mean distances traveled by several groups (e.g., males and females of species in several locations of its geographical distribution).

A two sample t-test can be used to test the hypotheses H_0: $d_1 = d_2$ versus H_A: $d_1 \neq d_2$, where d_1 and d_2 represent the mean distance traveled for the two groups being compared, respectively. An equivalent form of the hypotheses is H_0: $d_1 - d_2 = 0$ versus H_A: $d_1 - d_2 \neq 0$, and the t-value for testing these hypotheses is:

$$t = \frac{d_1 - d_2}{S_p\sqrt{\frac{1}{n_1} + \frac{1}{n_2}}}, \qquad (4.14)$$

where n_1 and n_2 represent the sample sizes of the two groups, respectively, and s_p is the pooled standard deviation, which is calculated as a weighted average of the two sample variances S_1^2 and S_2^2:

$$S_p = \sqrt{\frac{(n_1-1)s_1^2 + (n_2-1)s_2^2}{n_1 + n_2 - 2}}, \qquad (4.15)$$

The test statistic calculated from equation 4.14 can be compared to the critical value and H_0 is rejected if $t \leq -t_{\alpha/2},v$ or if $t \leq t_{\alpha/2},v$, where α is the significance level and $v = n_1+n_2 -2$ is the degrees of freedom. The two-sample t-test assumes that both samples are randomly chosen from normal populations with equal variances (Zar, 1999). In practice, it is difficult to know if these assumptions will be met, however, several studies have shown that the t-test is robust enough to endure considerable departures from its theoretical assumptions, particularly when the sample sizes are equal or nearly equal (Zar, 1999).

As stated previously, the above t-test is appropriate for situations when two means are being compared, however, to test the hypotheses H_0: $d_1 = d_2 = \ldots = d_k$, where *k* is the number of groups being compared, versus H_A: not H_0, the procedure of ANOVA must be used. ANOVA is a large area of statistical methods and is not described in detail in this chapter. For more information on ANOVA, it is recommended to consult a statistical methods textbook (e.g., Zar (1999)). For an example of ANOVA being used to compare the mean distances traveled by several groups of a shark species, see Francis (1988).

4.3.6 Survival/mortality

Brownie et al. (1985) developed a series of models for multiyear tag recovery studies that can be used to estimate age- and year-specific finite rates of survival (*S*) and tag recovery (*f*). More recently, Pollock et al. (1991) and Hoenig et al. (1998) showed it is possible to convert tag-recovery rates to finite exploitation (*u*), when information on the short-term tag retention, tag-induced mortality, and tag-reporting rate is available. Estimates of year-specific total instantaneous mortality (*Z*) can be obtained from year-specific finite rates of survival, and if information on the instantaneous rate of natural mortality (*M*) is known, the year-specific estimates of *Z* can be used to recover year-specific estimates of instantaneous fishing mortality (*F*) rates. Also, if the timing of the fishery is known, year-specific estimates of finite exploitation can also be used to derive year-specific estimates of *F* (in the case of a continuous Type II fishery, information on *M* will again be needed). A detailed discussion of these analyses is presented in section 8.3.2 of Chapter 8.

4.3.7 Spatial and temporal distribution, relative abundance

Data reflecting the time and location of capture for tagging over the course of a year can be used to develop a rudimentary understanding of seasonal habitat utilization, and thus, the spatial and temporal distribution of the target species. In addition, the catch data derived from sampling efforts serves as a spatial and temporal index of relative abundance for each species. One approach that can be used to better understand the observed patterns of relative abundance involves correlating the spatially explicit relative abundances with data that delineates habitat type (if not already available, this type of information may need to be collected at the time of first capture). Although stand-alone correlations between catch and habitat type are informative, it is often difficult to fully understand the observed patterns of relative abundance without additional auxiliary data. Information on abiotic factors such as depth, water temperature, salinity and dissolved oxygen can also be used to help explain the observed patterns of distribution and ultimately form a more complete understanding of the ecological preferences of the target species.

4.3.8 Species composition, size composition, sex ratio

Information on the species composition in a specific location or region and the sex ratio of a particular species are two basic but important types of data that can be collected by simply processing the catch of the gear used to collect individuals for tagging. In addition, when individuals are tagged onboard a vessel, information on size composition can easily be obtained by taking sex-specific measurements of

length, which includes TL, FL, and PCL, and weight. Under circumstances when individuals are too large to be handled and tagging takes place in the water, it may only be possible to take length measurements. In areas where elasmobranchs are not well studied and information is lacking, collecting these types of data can be viewed as the first step toward developing an understanding of the life history characteristics of the species inhabiting a particular region.

4.4 ASSUMPTIONS OF TAG-RECOVERY STUDIES AND AUXILIARY STUDIES

When attempting to use tag-recovery data to infer about growth rates, gear selectivity, patterns of movement, and survival/mortality, it is generally necessary to make the following assumptions:

1. The tagged sample is representative of the target population.
2. There is no tag loss or, if tag loss occurs, a constant fraction of tags is lost from each cohort and all tag loss occurs immediately after tagging. Also, the probability of immediate tag loss is not sex- or size-dependent.
3. The time and location of tagging and tag recovery are correctly recorded.
4. The lengths and weights of individuals are measured without bias at the time of tagging.
5. The lengths of individuals are measured without bias at the time of tag recovery.
6. Survival rates are not affected by tagging process or, if they are, the effect is restricted to a constant fraction dying immediately after tagging. Also, the probability of immediate tag-induced mortality is not sex- or size-dependent.
7. The fate of each tagged individual is independent of the other tagged individuals.
8. Tagging does not affect growth.
9. There are no significant size-selection processes for individuals within similar age ranges.
10. All tagged individuals within a cohort experience the same annual survival and tag-recovery rates.
11. The decision made by a fisher on whether or not to return a tag does not depend on when or where the individual was tagged.

Although tag-recovery studies can be plagued by a variety of factors, it is possible to conduct auxiliary studies to assess the possibility of violating a few of the aforementioned assumptions. Specifically, to determine the rates of immediate tag loss and tag-induced mortality (assumptions 2 and 6), newly tagged individuals can be held in cages or holding pens for a short period of time (Gruber et al., 2001; Latour et al., 2001). Rates of chronic or long-term tag loss (assumption 2) are best assessed by double tagging individuals (Latour et al., 2001). Although estimates of the tag-reporting rates associated with commercial and recreational fishers are not needed for the types of analyses described herein, knowledge of these tag-reporting rates can be extremely useful, particularly when trying to derive survival/mortality information. Rates of tag reporting are best estimated by conducting a high reward study (Henny and Burnham, 1976; Pollock et al., 2001). Additional remedies to some more of the problems of tag-recovery studies as they pertain to survival/mortality estimation are discussed in section 8.3.2 of Chapter 8.

4.5 ARCHIVAL TAGS

Archival, or data storage tags are designed to intermittently record data on (among others) the depth of an individual, ambient temperature, and light intensity. The data from these tags is downloaded when the tagged fish is recaptured and the tag is recovered. These types of tags were first used on southern bluefin tuna (*Thunnus maccoyii*) in Australia in the early 1990s, and have recently been used to study elasmobranchs. Specifically, the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) Lowestoft Laboratory, which is located in the United Kingdom, has used archival tags to study the movements of thornback rays (*Raja clavata*) in both the Irish Sea and Thames Estuary (Arnold and Dewar, 2001). Similarly, Australia's Commonwealth Scientific and Industrial Research Organisation (CSIRO) has used archival tags to study the position of school sharks on the continential shelf off South Australia (West and Stevens, 2001). One problem associated with an archival tagging study is the expense, since for many species, tag-recovery rates are too low to justify the cost of the tags. However, the data from archival tags do have the potential to solve some important ecological questions (Arnold and Dewar, 2001).

Figure 4.07 Wildlife Computers Pop-up Archival Transmitting (PAT) tag.

Pop-up archival satellite tags were developed in part to alleviate some of the problems associated with low tag-recovery rates. In summary, these tags combine data storage tags with satellite transmitters and are designed to detach themselves from fish at a predetermined time (Figure 4.07). Ultimately they float to the sea surface and communicate their location via a satellite link. The first pop-up satellite tags were deployed in 1997 to further assist with ongoing efforts directed at studying long-term movements of Atlantic bluefin tuna (Block et al., 1998). Some of these tags were programmed to record temperature information on hourly time scales, while others were programmed to take measurements on daily time scales. Deployment time of these tags ranged from 3 to 90 days. Lutcavage et al. (1999) also used pop-up satellite tags to study bluefin tuna in the North Atlantic. Tags have also been successfully placed on other large pelagic species, including yellowfin tuna, albacore, blue and striped marlin, and white, basking, thresher and salmon sharks (Arnold and Dewar, 2001; Boustany et al., 2002).

There is a growing perception among researchers that some of the methods used to attach pop-up archival satellite tags to marine fishes are unreliable. This perception originated from documented case studies were tags detached from individuals prior to the predetermined time, thereby compromising the success of the tagging study. However, the exact cause of the early release of these tags is not known. Pop-up satellite tags are typically attached to pelagic teleosts via a dart that is inserted into the dorsal musculature of the individual. For sharks, tags can be attached using a dart or by attaching the tag to a rototag-like apparatus through a

hole in the first dorsal fin. To improve the retention and overall performance of pop-up satellite tags, a variety of darts have been developed, ranging in terms of both shape and material used for construction. At present, however, a universally accepted attachment method has not been identified, so for each tagging study, great care should be directed at evaluating the potential effectiveness of each attachment method as it pertains to the species under study.

4.6 SUMMARY

This chapter is designed to assist researchers with the development and implementation of a tag-recovery program for elasmobranch species. As previously described, it is possible to initiate either an angler-based cooperative program or an agency-based program, and in most cases, the objective(s) of the study and available funding typically dictate the appropriate choice. Also, there are advantages and disadvantages associated with each type of program that should be given consideration during the design phase. Described in this chapter are several data analysis methods that can be used to infer various aspects of the biology and life history of elasmobranch species. A wide variety of methodologies are described in part to demonstrate the utility and usefulness of a tag-recovery program. Some inferences can be drawn in the absence of data reflecting tag recoveries (e.g., habitat utilization, species and size composition, sex ratio, etc. derived from catch data), while others require analysis of data from both first capture and tag recovery (e.g., movement, growth, survival/mortality, etc.). Of particular importance to the validity of any type of data analysis and to the overall success of a tag-recovery program is an assessment of the potential for assumption violation. As a result, efforts should be directed at conducting auxiliary studies to determine if the defined sampling, handling, and tagging protocol minimizes the potential for assumption violation.

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CHAPTER 5. GENETICS: STOCK IDENTIFICATION

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5.1 INTRODUCTION

When members of a fish species are segregated into multiple reproductive stocks, allele frequencies at neutral genetic markers diverge under genetic drift such that the variance in gene frequencies reflects the magnitude of reproductive isolation among these stocks. Thus, gene frequency differences among geographic samples can be used to indirectly estimate patterns of gene flow and hence stock structure of the species. Molecular markers have been used to infer stock structure in fishes for over forty years (Utter, 1991). A brief glossary of genetic terms is included at the end of this chapter for those readers who may be less familiar with the subject.

Application of molecular markers to the estimation of stock structure in marine elasmobranchs can be very challenging for several reasons. Genetic stock structure is less pronounced in marine species, which experience few barriers to migration, than in freshwater species (Ward et al., 1994). Stock structure is especially weak in highly motile pelagic fishes (Waples, 1998). Furthermore, sharks exhibit relatively low levels of genetic variation at some molecular markers, perhaps owing to a slowed mutation rate and/or low long-term effective population sizes (Smith, 1986, Martin et al., 1992). Markers that are not sufficiently variable will not provide the necessary data for a statistically powerful test of stock structure and fish from two geographic regions that are fixed for the same allele may not necessarily be members of the same stock.

The choice of molecular marker depends on the quality and type of tissue available as well as the equipment and expertise. Even a small amount of reproductive migration among stocks is sufficient to prevent genetic divergence at neutral molecular markers. Thus, stocks that are independent from the fisheries perspective may exhibit negligible genetic differentiation (Waples, 1998). Traditional tag/recapture studies performed in concert with molecular genetics studies can provide more information than either approach can individually.

5.2 ESTIMATING STOCK STRUCTURE WITH MOLECULES

The degree to which stocks are reproductively isolated is typically estimated using various estimator's of Sewell Wright's F_{ST} statistic (Wright, 1931). In the case of a codominant locus that exhibits only two alleles F_{ST} is equal to

$$F_{ST} = \frac{H_t - H_s}{H_t} \tag{5.1}$$

where H_t is the expected heterozygosity in the population based on the mean allele frequency across populations and expectations of Hardy-Weinberg equilibrium (i.e., $H_t = 2pq$ where p = the frequency of one allele and q = 1-p) and H_S is the mean heterozygosity within populations. Thus, the greater the variance in allele frequencies among populations the greater the deficit of heterozygosity within each population, and F_{ST} can be determined directly from the variance in allele frequencies as

$$F_{ST} = \frac{Var(p)}{pq} \tag{5.2}$$

where *Var(p)* is the variance in the frequency of an allele among subpopulations. Expected values of F_{ST} range from zero when each sample possesses identical gene frequencies and hence there is a single genetic stock, to unity when isolated stocks are fixed for alternate alleles.

Either of these measures is sensitive to sampling error and in the absence of distinct stocks will result in positive F_{ST} values, the magnitudes of which are inversely proportional to sample size. Waples (1998) observed that in highly migratory species, such as many sharks, the magnitudes of F_{ST} estimates resulting from sampling error alone may be larger than the parametric F_{ST} values among stocks. Various unbiased estimators of Wright's F_{ST} include Weir and Cockerham's θ estimator, which includes corrections for several types of sampling error and sometimes produces negative F_{ST} estimates when the true value of F_{ST} is very small or zero (Weir and Cockerham, 1984). Many recent studies employ analysis of molecular variation (AMOVA) (Excoffier et al., 1992), which provides an unbiased estimator of F_{ST} known as Φ_{ST} and also permits partitioning of genetic variation to multiple hierarchical levels. These estimators are computationally demanding but are incorporated into a variety of freely available software packages (see below). Statistical tests of the hypothesis that $\Phi_{ST} = 0$ (and hence samples are drawn from a single genetic stock) are calculated using algorithms that either model or resample the data and determine the significance level of Φ_{ST} as the likelihood that a larger Φ_{ST} value could be produced via a random allocation of the genotypes or alleles (Rousset, 2001).

Several software packages are freely available for analyzing molecular genetic data including Arlequin (http://lgb.unige.ch/arlequin/) (Schneider et al. 2000), Genepop (http://wbiomed.curtin.edu.au/genepop/) (Raymond and Rousset, 1995), and GDA (http://lewis.eeb.uconn.edu/lewishome/software.html) (Lewis and Zaykin, 2001). The capabilities of these and several other programs were recently reviewed by Labate (2000). Arlequin can be downloaded in Microsoft Windows, Macintosh or Linux format and can handle haploid (e.g., mtDNA) as well as diploid (allozyme and microsatellite) data. Genepop can be downloaded to run in a windows environment or can be run directly from the web page. GDA is only available in windows format and determines significance of θ by bootstrapping across loci, which is only applicable to studies that employ a large number of loci.

Under the assumptions of the island model of migration (Wright, 1931), which assumes a large number of discrete populations with equal amounts of migration among each population, F_{ST} can be related to migration as

$$F_{ST} = \frac{1}{4N_e m + 1} \qquad (5.3)$$

where $N_e m$ is the product of the effective population size and the migration rate. $N_e m$ can be thought of as the effective number of migrants, that is the number of reproductive animals exchanged among populations. It may seem counterintuitive that the magnitude of F_{ST} would be related to the number of migrants and not migration rate. However, the degree to which allele frequencies among isolated populations diverge due to genetic drift is inversely proportional to the effective population size. Thus populations with

a large N_e require a smaller migration rate to produce the same magnitude of genetic variance among populations (F_{ST}). The above relationship is derived with several simplifying assumptions that are unrealistic for shark populations (e.g., equal migration among each of the many populations). However, deviations from these assumptions have only minor effects on the relationship between F_{ST} and $N_e m$. For example, the more realistic case of increased migration among geographically proximate locations and a small number of populations produces slightly lower F_{ST} values for the same rate of migration (Mills and Allendorf, 1996).

Mitochondrial (mt) DNA is potentially a more powerful marker than nuclear DNA. Because mtDNA is maternally inherited as a haploid molecule it has approximately ¼ the effective population sizes of a nuclear marker (Birky et al., 1983). The relationship between F_{ST} and migration is

$$F_{ST} = \frac{1}{2N_e m_f + 1} \qquad (5.4)$$

where $N_e m_f$ refers to the effective migration rate of females only. In species with equal rates of male and female migration the magnitude of F_{ST} will be greater for mitochondrial markers than nuclear markers. Furthermore, because of the smaller effective population size mtDNA reaches equilibrium levels of F_{ST} more quickly and thus a recently established pattern of stock structure will be more accurately represented by mitochondrial data than by nuclear DNA data. In species that exhibit female reproductive philopatry and outcrossing with males from widespread localities, such as several species of marine mammals and sea turtles, mtDNA exhibits stronger differentiation than nuclear markers (Karl and Bowen, 1992; Palumbi and Baker, 1994; Gladden et al., 1999). However, the differences in the rates of genetic drift, mutation, and intraspecific variation among mitochondrial and nuclear markers are sufficient to produce vast differences in estimates of F_{ST} between the marker types without any differences in male- and female-mediated gene flow (Buonaccorsi et al., 2001). Thus larger F_{ST} values for mitochondrial markers relative to nuclear markers do not necessarily indicate female philopatry against a backdrop of male roaming.

5.3 MOLECULAR MARKERS

Several types of molecular markers have been applied to the estimation of stock structure in sharks and many other types used in other marine fishes have yet to be employed in elasmobranchs. The choice of marker depends on the experience of the researcher and the types of equipment available and also on the types and quality of tissue that are available. It would be impossible to provide specific protocols in such limited space, but fortunately several excellent published volumes contain protocols for these and other techniques including Hillis et al. (1996), Ferraris and Palumbi (1996) and Hoelzel (1998).

5.3.1 Allozymes

Allozymes were the first molecular markers to gain widespread use for distinguishing among stocks of fishes (Utter, 1991). Allozymes are distinct allelic forms of enzymes that are separated by charge and in some cases three-dimensional shape on a separatory medium, typically starch gels, poly-

acrylamide gels or cellulose acetate plates, and visualized with histochemical stains that indicate the migration of molecules with specific enzyme activities (Murphy et al., 1996; May, 2003). Allozymes degrade rapidly after death, especially at high temperatures, and the use of allozymes as molecular markers requires fresh or frozen tissue (maintained at -20°C or preferably colder). Because tissue types vary in enzyme expression, it is often useful to collect multiple tissue types (e.g., white muscle, heart, liver, brain) to score a large number of loci. Thus allozyme electrophoresis is not the best technique where lethal sampling and immediate freezing (e.g., with dry ice or liquid nitrogen) of tissue samples are not possible.

Resolution of allozyme banding patterns requires considerable interpretation (Buth, 1990). Homozygotes for different alleles produce single bands with varying motilities while heterozygotes take on an appearance that is determined by the subunit structure of the active enzyme. Monomeric enzymes produce two-banded heterozygotes while dimeric and tetrameric enzymes (those possessing two and four peptides per active enzyme) exhibit three- and five-banded heterozygotes. Many enzymatic reactions are catalyzed by products of multiple loci heteropolymers which can further complicate the banding patterns. Resolution of allozyme patterns as discrete bands rather than smears requires the screening of multiple running buffer conditions to identify the optimal conditions for each locus.

Several studies of allozymes have detected low levels of variation in sharks. In the first published study of allozymes in sharks Smith (1986) reported relatively low variation in seven species. Low levels of allozyme variation and geographic heterogeneity in carcharhinid sharks were observed by Lavery and Shaklee (1989) and by Heist et al. (1995). Relatively high levels of heterozygosity and heterogeneity were found in Pacific angel sharks (*Squatina californica*) (Gaida, 1997) and gummy sharks (*Mustelus antarcticus*) (Gardner and Ward, 2002).

Resolution of allozyme loci can be more of an art than a science and variation in the methodology and experience among labs result in differences in the amount of variation that can be resolved on allozyme gels. Gardner and Ward (1998) found that on average 25.5% of allozyme loci in gummy shark were polymorphic with a mean heterozygosity of 0.099. For the same species over a somewhat smaller geographic range MacDonald (1988) detected variation in only one of 32 presumed loci (3%) with a mean heterozygosity of 0.006 in the same species. Certainly some of this discrepancy must be due to the increased resolution of the study by Gardner and Ward.

The relative simplicity of the materials needed to perform the allozyme technique (i.e., many rigs are “homemade”) make allozymes an attractive tool for labs with little research funding. However, as PCR-based techniques are becoming more affordable, the low variation and high tissue quality demands of allozymes make techniques that score variation at the DNA-level more attractive. Plans for manufacturing allozyme equipment can be found in Aebersold et al. (1987) and Murphy et al. (1996).

5.3.2 Mitochondrial DNA

Mitochondrial DNA of elasmobranchs and other fishes is a single closed loop of double stranded DNA approximately 16,500 base pairs (bp) in length and presumably inherited only from the maternal

parent (Billington, 2003). The haploid, uniparental inheritance of mtDNA results in a fourfold reduction in the effective population size and therefore an accelerated rate of genetic drift, which in turn increases the rate and magnitude of genetic differentiation among isolated fishery stocks (Birky et al., 1983). Data derived from sequencing or restriction fragment length polymorphism (RFLP) analysis of mtDNA permit estimation of the relative divergence time of any two mtDNA haplotypes and can be used to provide evidence of deep historic divisions or cryptic species (Figure 5.01).

If relatively large quantities (several grams) of fresh or ultrafrozen tissue and an ultracentrifuge are available, mtDNA can be isolated in its pure circular form and subjected to restriction enzymes that cleave the circular DNA at specific four- to six-base motifs. The resultant population of restriction fragments can be resolved on agarose or polyacrylamide gels and visualized using radiolabeling or UV illumination of ethidium bromide stained bands (Figure 5.01). This is the technique that was performed by Heist et al. (1995; 1996a, 1996b) on sandbar (*Carcharhinus plumbeus*), shortfin mako (*Isurus oxyrinchus*) and Atlantic sharpnose (*Rhizoprionodon terraenovae*) sharks. In the sharpnose shark study, whole molecule mtDNA prepared from tiger shark was used to probe Southern blots of Atlantic sharpnose shark hearts that did not provide sufficient whole-molecule mtDNA.

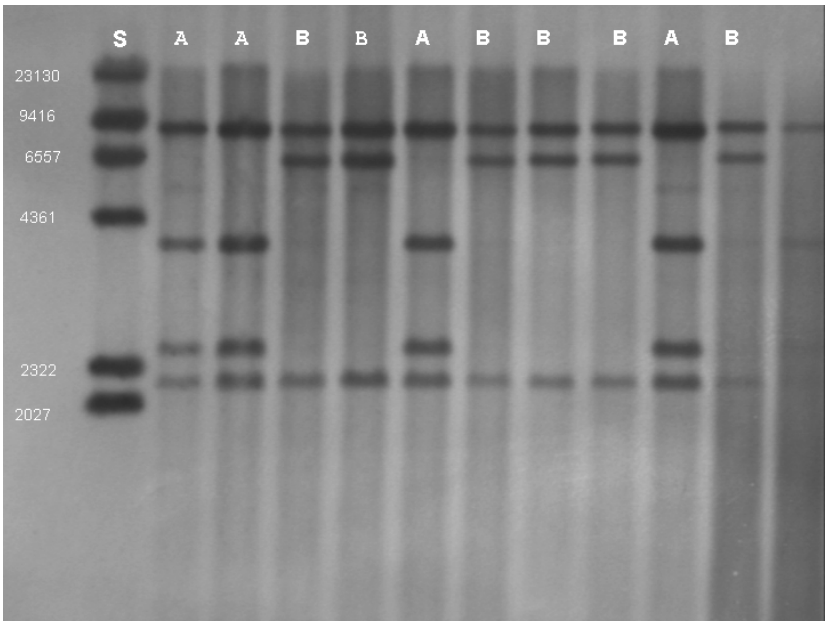

Figure 5.01 Mitochondrial DNA variation in shortfin mako (*Isurus oxyrinchus*). Lane "S" is a size standard lane. Numbers at left refer to the size (in base pairs) of each size standard. Whole molecule mtDNA digested with the restriction enzyme *Bst*E II produces two haplotypes (A and B). Haplotype "A" differs from "B" in that a fragment of approximately 7000 base pairs in "B" is digested into two smaller fragments of approximately 4400 and 2600 in "A".

With the advent of PCR more studies are employing restriction digestion or sequencing of discrete regions of mtDNA. Perhaps the most useful region for analyzing stock structure in elasmobranchs is the D-loop or control region, which contains the largest stretches of noncoding DNA in the elasmobranch mtDNA genome, and in many fishes studied it exhibits the highest nucleotide substitution rate presumably due to the lack of purifying selection. In my lab we routinely use a primer designed by Martin and Palumbi (1993) located in the cytochrome-b protein coding region (CB6H 5' CTC CAG TCT TCG RCT TAC AAG where "R" represents equal quantities of A and G) and a mammalian primer designed in the highly-

conserved 12S ribosomal gene (282 5' AAG GCT AGG ACC AAA CCT) (J. C. Patton, unpublished data) to amplify the entire D-loop region in a variety of sharks. The resultant PCR product can then be analyzed using restriction enzymes or direct sequencing. The widespread availability of inexpensive thermal cyclers and gel rigs make PCR-RFLP a viable method of analysis for labs with a limited research budget.

The genetic diversity present in mtDNA can be represented as haplotype diversity which is estimated as

$$\hat{h} = \frac{n(1-\sum_{i=1}^{l} x_i^2)}{n-1} \qquad (5.5)$$

where *h* is the haplotype diversity, n is the number of individuals scored, x_i is the frequency of each allele, and *l* is the number of unique haplotypes detected (Nei and Tajima, 1981). This equation is essentially the same as that for estimating heterozygosity at a diploid locus and can be thought of as the likelihood that two randomly sampled haplotypes differ. Because haplotype diversity is affected by the number of bases surveyed (i.e., amount of sequence data or number of restriction enzymes employed) a more universal gauge of variation is nucleotide sequence diversity (π) which can be estimated as

$$\hat{\pi} = \frac{n}{n-1} \sum \hat{x}_i \hat{x}_j \hat{\pi}_{ij} \qquad (5.6)$$

where $\hat{x}_i$ and $\hat{x}_j$ are the frequencies of haplotypes i and j and $\hat{\pi}_{ij}$ is the genetic distance between each pair of haplotypes (Nei and Tajima, 1981). AMOVA (Excoffier et al., 1992) can then be used to estimate Φ_{ST} by partitioning the genetic diversity into among and between sample components. The REAP software package (McElroy et al., 1991), which is available at http://bioweb.wku.edu/faculty/mcelroy/, can be used to estimate π and to construct a distance matrix between haplotypes for AMOVA.

Sharks possess relatively low levels of intraspecific mtDNA heterogeneity, presumably due to the low rate of mtDNA evolution relative to that of other vertebrates (Martin et al., 1992). Levels of nucleotide sequence diversity based on whole-molecule RFLP in sharks range from 0.036% in sandbar shark (Heist et al., 1995) to 0.347% in shortfin mako (Heist et al., 1996a). In order to detect a sufficient amount of variation one must either perform the whole-molecule technique with a large number (e.g., eight or more) restriction enzymes or perform direct sequencing. In our lab we are sequencing the entire mtDNA D-loop in blacktip sharks (*C. limbatus*) to produce a haplotype diversity of 0.71 (Keeney et al., In Press "A").

5.3.3 Microsatellites

DNA microsatellites are among the most recent types of markers developed for estimating stock structure and are highly repetitive segments of nuclear DNA that are amplified via PCR and typically resolved on polyacrylamide gels (O'Connell and Wright, 1997). Microsatellite alleles differ in size based upon differences in the number of repeat units present. Alleles differ in size by multiples of the core

repeat motif (typically two to four bases) and thus very high resolution is required to score microsatellites. Typically PCR products are end-labeled with radionuclides (e.g., ^{32}P or ^{33}P) and resolved via autoradiography (Figure 5.02) or fluorescently tagged and resolved on automated DNA sequencers. Either of these techniques may be beyond the capabilities of labs with limited budgets and/or without access to radionuclides.

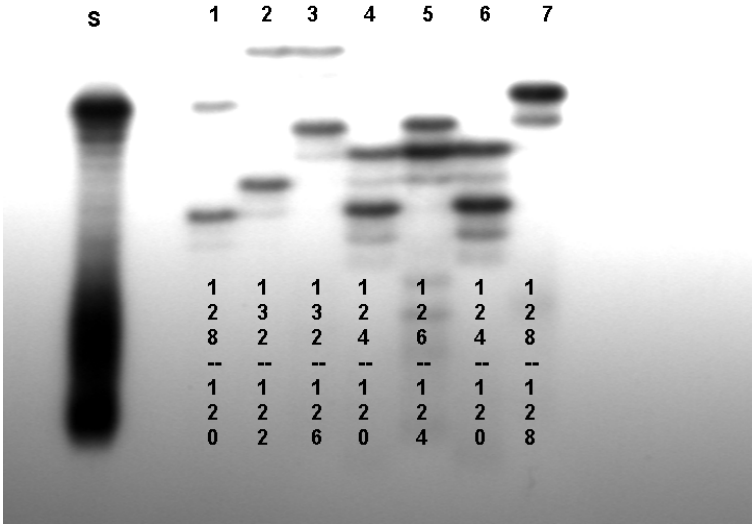

Figure 5.02 Microsatellite DNA variation in nurse shark (*Ginglymostoma cirratum*). Lane "S" is a 128 base pair size standard. Individuals 1 through 6 are heterozygous (genotypes shown below bands). Individual 7 is homozygous for allele 128.

The major hurdle to scoring microsatellites in any species is the development of PCR primers that will amplify polymorphic loci. To date polymorphic microsatellite loci have been developed in sandbar shark (Heist and Gold, 1999), white shark (*Carcharodon carcharias*) (Pardini et al., 2000), lemon shark (*Negaprion brevirostris*) (Feldheim et al., 2001a; Feldheim et al., 2001b), shortfin mako (Schrey and Heist, 2002) and nurse shark (*Ginglymostoma cirratum*) (Heist et al., 2003). Primers developed in one species often work on congeners and sometimes members of related genera but either fail to amplify or amplify only monomorphic products in other families or in more distantly-related taxa. Of sixteen polymorphic microsatellite loci developed from the blacktip shark between five and eleven loci were polymorphic in each of ten other species of *Carcharhinus,* and several loci were polymorphic in tiger shark, lemon shark, blue shark (*Prionace glauca*), Atlantic sharpnose shark and two species of hammerhead sharks (*Sphyrna* spp.) (D. Keeney, In Press "B"). Primers developed in shortfin mako amplified polymorphic microsatellites in salmon (*Lamna ditropis*), porbeagle (*L. nasus*) and white sharks (Schrey and Heist, 2002).

Microsatellite data are analyzed much like allozyme data although the very high heterozygosity and large number of alleles (e.g., 20 or more) can cause a deflation of F_{ST} (Hedrick, 1999). Microsatellites evolve via mutational increases and decreases in the number of times the core motif is repeated in each allele. Thus microsatellites exhibit a finite number of alleles and alleles are often shared even among completely isolated gene pools (e.g., among species). The maximum value F_{ST} can be expected to achieve is equal to homozygosity, which for loci with 20 or more alleles may be less than 0.05. Thus, the maximum value that can be achieved for F_{ST} is comparable to the expected amount of error associated with mea-

surements involving small sample sizes (Waples, 1998). An obvious way to alleviate some of this problem is to employ loci with moderate numbers of alleles and moderate heterozygosities and to obtain sufficiently large sample sizes to reduce the amount of noise in estimating F_{ST}.

A common problem that attends the high genetic diversity of microsatellites and the statistical power of modern estimators is the detection of very small but nevertheless statistically significant F_{ST} values. Low but significant F_{ST} values can arise through a small amount of gene flow (e.g., 1-10 individuals per generation) between stocks that are essentially discrete in terms of recruitment, or it can be an artifact of sampling (e.g., inclusion of close relatives in a sample) and scoring (e.g., null alleles) and thus constitutes a statistical (type I) error. Dizon et al. (1995) warned that the consequences of failing to reject the null hypothesis of $F_{ST} = 0$ when it is false (type II error) may be more deleterious to the management of a species than falsely concluding that multiple stocks are present and recommended that power analyses be used to adjust the rejection (α) level upward to a level that balanced the effects of both types of statistical error. Feldheim et al. (2001b) concluded that a statistically significant ($p < 0.05$) θ value of 0.016 based on highly polymorphic (Heterozygosity = 0.69 to 0.90) microsatellite loci was too low to consider lemon sharks from the Florida, the Bahamas and Brazil as distinct stocks. Tagging data (Kohler et al., 1998) indicate that lemon sharks move between the Bahamas and Florida, but no lemon sharks tagged in either Florida or the Bahamas moved to the Caribbean or beyond. Thus, it seems very unlikely that lemon sharks from Florida and Brazil do not comprise distinct fishery stocks. While gene flow has apparently been high enough to prevent evolutionary divergence among lemon sharks in the western Atlantic, statistically significant differences in allele frequency, regardless of their magnitude, indicate that samples are drawn from different populations (Knutsen et al., 2003).

5.3.4 Other molecular markers

Several other types of molecular markers are used to assess stock structure in fishes but have yet to be applied to elasmobranchs. Random Amplified Polymorphic DNA (RAPD) employs one or more short primers (typically about ten bases) to amplify a population of fragments that are resolved on agarose or polyacrylamide gels (Hadrys et al., 1992). The degree to which bands are shared among individuals can be used to assess the relatedness of individuals within and among populations. While this method is attractive because it does not require taxon-specific primers like mtDNA RFLP and microsatellites do, there are several serious shortcomings that have prevented this technique from gaining widespread acceptance as a tool for analysis of stock structure. PCR is a finicky process that often produces inconsistent results, especially with short primers and low annealing temperatures. Whether a faint band is present or absent may depend on the quality of the tissue used to prepare the DNA or the dynamics of the specific PCR reaction that produced the profile. If tissue quality varies among sample locations, there can be a systematic bias in the data leading to an erroneous conclusion of stock structure.

Another available technique, Amplified Fragment Length Polymorphism (AFLP) analysis, is performed by attaching oligonucleotide adapters to nuclear DNA restriction fragments and amplifying with

longer PCR primers that anneal mostly to the adapters but also the first one to three bases of the genomic DNA (Vos et al., 1995). While this approach is far more work than RAPD, the data are more repeatable because of the use of longer PCR primers and higher annealing temperatures. Both RAPD and AFLP produce dominant data (i.e., there is generally no way to distinguish between bands that are present in heterozygous or homozygous dosages), and as a result statistical treatment of the data are not as powerful as those for codominant data (e.g., allozymes and microsatellites).

5.3.5 Tissue collection

The kinds of tissue samples available and the method of preservation determine what kinds of molecular markers can be used. PCR-based methods are most forgiving and can even be performed on dried fins (Shivji et al., 2002). For PCR-based analyses we routinely collect fin clips by excising approximately ½ cm^2 from the trailing edge of the first dorsal fin using a scalpel. The thin trailing edge of the fin produces far better yields of DNA than do muscle tissue or thick skin from other parts of the body. Fin clips can be stored in either 95% ethanol or 20% dimethyl sulfoxide saturated with NaCl. Tissues are stable in either medium at room temperature for several months, however long-term storage of ethanol-preserved tissues is best done at 4°C or colder. Tissues for whole molecule RFLP need to be kept fresh or frozen once and not subjected to freeze-thaw cycles as each freezing cycle produces ice crystals that linearize the mitochondria making mtDNA purification very difficult. Tissues for allozymes are most demanding in that enzymes degrade rapidly after death. Tissues need to be frozen (preferable in dry ice or liquid nitrogen) and maintained as cold as possible until homogenized for electrophoresis.

Many sharks undergo seasonal and reproductive migrations and may segregate by sex and life stage. Thus, a careful choice of where, when and from which animals to collect tissue can influence the outcome of a study. For example in the study of blacktip sharks described below (Keeney et al., submitted), all tissues were collected from neonate sharks near or within continental shelf nursery areas. Thus, any signal that resulted from reproductive philopatry could be filtered from the noise of adult movement. Such studies can be biased because a sample from a single nursery may contain siblings, which would tend to inflate estimates of gene frequency differences among samples. However, because sharks like the blacktip shark have low fecundities and do not reproduce every year, the number of potential sibling pairs is low and comparisons across sequential years can be used to determine whether a sampling of siblings is influencing estimates of F_{ST}.

5.4 SELECTED CASE STUDIES

5.4.1 Gummy shark

The gummy shark is a small coastal species continuously distributed around the southern two-thirds of Australia. Gardner and Ward (1998) found statistically significant differences in allozyme allele and mtDNA haplotype frequencies in gummy sharks collected from the southern and southeastern coasts of Australia including Tasmania. Measures of G_{ST} (an analog of F_{ST}) were significantly greater than the values expected due to sampling error for three of seven polymorphic loci and for RFLP haplotypes of

whole-molecule mtDNA. Both molecular markers indicated that gummy sharks from the southern coast of Australia, ranging from Bunbury to Eden and including Tasmania, comprised a single stock while gummy sharks from the east coast of Australia from Eden north comprised one or more additional stocks. Vertebral counts did not differ throughout southern Australia. However, there appeared to be a gradual increase in the number of precaudal vertebrae corresponding to decreasing latitude on the east coast. Thus, despite the continuous distribution and great potential for movement in *M. anarcticus*, there exist multiple fishery stocks in Australian waters. Subsequently, Gardner and Ward (2002) reported data from additional *Mustelus* including *M. lenticulatus* from New Zealand and two putative undescribed species from Australia. Allozyme, mtDNA, and vertebral count data all confirmed the presence of four species of *Mustelus* in the waters of Australia and New Zealand.

5.4.2 Blacktip shark

The blacktip shark is a migratory species that is the most important component of the US longline shark fishery operating in the southeastern United States in the Atlantic Ocean and Gulf of Mexico. Neonate blacktip sharks from the west coast of Florida migrate south in the fall, presumably to southern Florida, and have been shown to return to specific nursery areas in subsequent years (Hueter et al. submitted). Whether adult females return to their natal nurseries for parturition is unknown. A study of mtDNA sequences and microsatellites in young-of-the-year blacktip sharks collected from four nursery areas, west coast of Florida, South Carolina, Texas and Mexican Yucatan, revealed significant heterogeneity in mtDNA ($F_{ST} = 0.111$, $p < 0.001$) but not microsatellite loci ($F_{ST} < 0.001$, $P = 0.316$) (Hueter et al., submitted). Neither marker revealed significant differences among three Florida nurseries separated by less than 250 km. Thus, blacktip sharks comprise multiple fishery stocks in US and Mexican waters, and while females may tend to return to natal nurseries, the fidelity to do so is not high enough to result in significant structuring among proximal nurseries.

5.4.3 White shark

The white shark is a wide-ranging globally distributed species with populations clustered around localities with abundant marine mammals. Pardini et al. (2001) compared mtDNA and nuclear (microsatellite) markers in white sharks from South Africa, Australia and New Zealand. The mtDNA data indicated two divergent clusters of haplotypes that were nearly clustered into two highly divergent clades. One clade (type A) was found in 48 of 49 individuals surveyed in Australia and New Zealand while the other clade was found in 39 individuals from South Africa and in one of the 49 individuals surveyed in the Australia/New Zealand sample. F_{ST} analogs (θ) based on five microsatellite loci were all non-significant. Based on the discrepancy in estimates of stock structure between nuclear and mitochondrial data Pardini et al. (2001) concluded that female white sharks are much more philopatric than males.

5.4.4 Shortfin mako

The shortfin mako is a highly migratory cosmopolitan species found throughout the Atlantic, Pacific and Indian Oceans. Heist et al. (1996a) examined whole molecule mtDNA RFLP data in 120

shortfin makos from the North Atlantic (US and Canada), South Atlantic (Brazil), North Pacific (California) and South Pacific (Australia) and found small but significant differences in haplotype frequencies between the North Atlantic and all other samples. Subsequently, Schrey and Heist (2003) examined microsatellites in 433 mako sharks including the individuals from Heist et al. (1996a). They also re-analyzed the data from Heist et al. (1996a) using a more powerful statistical approach. Among ocean basins, F_{ST} estimates from the mitochondrial data were significant and two orders of magnitude larger than the estimates of F_{ST} based on microsatellites. A power analysis indicated that if the amount of heterogeneity present in the mtDNA data accurately represented the magnitude of gene flow of both sexes a statistically significant F_{ST} would have been detected using microsatellites, assuming that the stock structure was stable long enough for nuclear markers to reach equilibrium. The discrepancy in the levels of resolution in mtDNA and microsatellites is likely due to sex-biased dispersal, but they could also be influenced by differences in the resolving powers of the two markers. The shortfin mako results differed from those of white sharks (Pardini et al., 2002) in that no strong phylogeographic signal is present in the mtDNA data, only minor frequency differences among locations. Shortfin mako does not comprise a single worldwide population, but there has been a sufficient amount of historical migration among ocean basins to make detection of stock structure using molecular markers (and especially nuclear DNA markers) very challenging.

5.5 CONCLUSION

Using molecular markers to estimate stock structure in sharks can be very challenging owing to the great potential for migration among shark stocks, the difficulty in detecting genuine but small differences in gene frequencies in the presence of recent or episodic migration among stocks, and inappropriate (too low or too high) levels of variation provided by some molecular markers. Nevertheless several studies have ably demonstrated stocks in sharks and even in highly migratory species across seemingly continuous distributions. Comparisons between markers with different modes of inheritance (e.g., nuclear vs mitochondrial) may indicate differences in male- versus female-mediated gene flow. Because many sharks are viviparous k-strategists that produce well-formed young at a time and place conducive to survival, stocks that overlap during part of the year may segregate into discrete stocks for mating and/or parturition. Thus, a careful selection of where and when tissues are collected (e.g., from neonates in nursery areas) coupled with a wise choice of a molecular marker can provide very valuable information about the stock structure of sharks that can not be obtained from other methods. Molecular detection of stock structure is a complementary technique to tagging and morphology based studies of stock structure. While tagging reveals gross movements of individuals, genetics measures the flow of genes over many generations and can be used, for example, to study fidelity to nursery or breeding grounds in animals whose distributions may sometimes overlap with those of other stocks. Morphological and life history differences may be due to different environmental influences and hence may or may not be reflected in gene frequency differences at neutral loci.

5.6 GLOSSARY OF GENETIC TERMS USED IN THIS CHAPTER

Allele – Alternate forms of a gene at a particular locus. Each diploid organism may possess either one (homozygote) or two (heterozygote) alleles at a locus; however, there may be more than two alleles in a population.

Codominant markers – Markers that exhibit both alleles in a heterozygous state. Codominant markers are more powerful than dominant markers in which a heterozygous individual is indistinguishable from an individual homozygous for the dominant allele.

Fixed allelic differences – The absence of shared alleles between two populations.

F_{ST} – An index of the magnitude of allele frequency difference among populations. At a locus with two alleles the maximum value of F_{ST} is unity and occurs when each population bears only a single allele not found in any other population. If allele frequencies are identical across populations, $F_{ST} = 0$.

Genetic drift – Random change in gene frequencies due to random stochastic sampling of alleles from generation to generation.

Heterozygosity – The fraction of individuals that exhibit two different alleles at a locus or alternately the fraction of loci over which an individual exhibits two different alleles.

Heterozygous – Possessing two different alleles at a locus.

Homozygous – Possessing two identical alleles at a locus.

Locus – A particular location on a chromosome where a gene or other DNA sequence resides. Diploid organisms possess two copies of each locus that may exhibit either the same (homozygote) or different (heterozygote) alleles.

Mitochondrial DNA (mtDNA) – DNA found in the mitochondria in cells. In animals including sharks mtDNA is a double stranded molecule approximately 16500 base pairs in length. Mitochondrial DNA is inherited strictly from the female parent and thus is a haploid (one copy per cell) marker.

Molecular marker – A polymorphic heritable trait that can be scored for variation within or between species.

Neutral genetic markers – Polymorphic genetic traits that are presumed not to be influenced by natural selection and thus are sensitive only to mutation, migration, and genetic drift. Most models that relate gene frequency differences with stock structure assume that the markers examined are selectively neutral.

Nuclear DNA – The vast majority of DNA in animal cells is found in the nucleus. Nuclear DNA is inherited equally from both parents and thus is a diploid (two copies per cell) marker.

Polymerase Chain Reaction (PCR) – A technique for producing millions of copies of a chosen segment of DNA by repeatedly annealing sequence-specific primers on either side of the region of interest and performing (typically) thirty or more cycles of DNA synthesis. This procedure allows the characterization of a particular segment of nuclear or mitochondrial DNA using only minute amounts of tissue.

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CHAPTER 6. AGE AND GROWTH OF ELASMOBRANCH FISHES

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6.1 INTRODUCTION

The ability to perform age determinations based on the examination of hard anatomical parts is of fundamental importance in fisheries research. Precise and accurate age information is the key to obtaining quality estimates of growth and other vital rates such as natural mortality and longevity, and is essential for successful fisheries management. The effect of inaccurate age determinations on population dynamics studies can lead to serious errors in stock assessment resulting in overexploitation (Hoenig and Gruber, 1990; Hoff and Musick, 1990; Officer et al., 1996; Musick, 1999; Campana, 2001). Fish age and growth are also critical correlates with which to evaluate many other biological (and pathological) processes, such as productivity, yield per recruit, prey availability, habitat suitability and even feeding kinematics (DeVries and Frie, 1996; Campana, 2001; Robinson and Motta, 2002). While age and growth are always used together in phraseology, it is important to remember that each term has its own distinct meaning, which was eloquently stated by DeVries and Frie (1996):

> *"Age refers to some quantitative description of the length of time that an organism has lived, whereas growth is the change in body or body part size between two points in time, and growth rate is a measure of change in some metric of fish size as a function of time."*

Concentric growth bands have been documented in the vertebral centra of most elasmobranchs for over 80 years (Ridewood, 1921). Counts of opaque and translucent banding patterns in vertebrae, dorsal spines, caudal thorns and neural arches have provided the only means of information on growth rates in these fishes as they lack the hard parts, such as otoliths, scales and bones typically used in age and growth studies of teleost fishes (Cailliet et al., 1986; Cailliet, 1990; Gallagher and Nolan, 1999; McFarlane et al., 2002). Unfortunately, the vertebral centra of many elasmobranch species (such as numerous deep water species) are too poorly calcified to provide information on age, most species have no dorsal spines and there may be no tangible relationship between observed banding patterns and growth (Caillet et al., 1986; Cailliet, 1990; Natanson and Cailliet, 1990; McFarlane et al., 2002). These circumstances continue to cause difficulties in making age estimates for many species.

Centrum banding patterns may be related to physiological changes induced by changes in environmental parameters such as temperature and photoperiod (Cailliet et al., 1986; Branstetter, 1987). However, some species such as the little skate, *Leucoraja erinacea* (Natanson, 1993), and the Pacific angel shark, *Squatina californica* do not reflect such relationships (Natanson and Cailliet, 1990; Cailliet et al., 1992). Vertebral growth is inevitably linked to food intake, and a lack of food for short periods of time can cause subtle bands to appear in vertebral centra of some species (J. Gelsleichter pers comm., pers. obs.). Considerable variability exists in the amount and pattern of calicification within and among taxonomic groups of elasmobranch fishes, and much of the variation observed in several species has not yet been explained (Branstetter, 1990; Branstetter and Musick,

1994; Wintner and Cliff, 1999). These factors make it inherently risky to assume that the vertebral banding pattern of one species is representative of another species or under all conditions, necessitating a species-specific approach.

The age determination process consists of the following steps: collection of hard part samples, preparation of the hard part for age determination, examination (age reading), assessment of the validity and reliability of the resulting data and interpretation (modeling growth). The purpose of this chapter is to provide a concise overview of basic methodologies and statistical analyses that can be used to quantify age and estimate rates of growth from vertebral centra and dorsal fin spines in elasmobranch fishes. I provide a few web-based references at the end of the chapter, and cite additional literature sources throughout that can be obtained to conduct specific staining techniques and age validation methods that are more expensive, complex and technology based. Additional methods of assessing the age-length relationship can also be conducted, but as the purpose of this chapter relates solely to age and growth via hard part analysis, alternative methods such as size mode or length frequency analysis and monitoring captive growth are not covered herein. (See Gulland and Holt, 1959; Francis, 1988; Cailliet et al., 1992; Natanson et al., 2002 and Chapter 4 this volume for size mode and length frequency analysis; see Van Dykhuizen and Mollet (1992), Mollet et al. (2002) and Mohan et al. (in press) for monitoring captive growth).

6.2 VERTEBRAL OR FIN SPINE COLLECTION AND PREPARATION

Whole vertebral centra, as well as transverse and sagittally (i.e., longitudinally) sectioned centra have been used for ageing elasmobranchs (Figure 6.01). Transverse sectioning will prevent bands on opposing halves from obscuring each other when illuminated from below. However, determining the age of older animals can still be problematic as bands become more tightly grouped at the outer edge of vertebrae, and may be inadvertently grouped and counted together thereby causing underestimates of age (Cailliet et al., 1983a; Branstetter, 1987). As such, sagittally sectioned vertebrae should be used for ageing unless it can be unequivocally demonstrated that identical ages can repeatedly be obtained from a given species using whole centra.

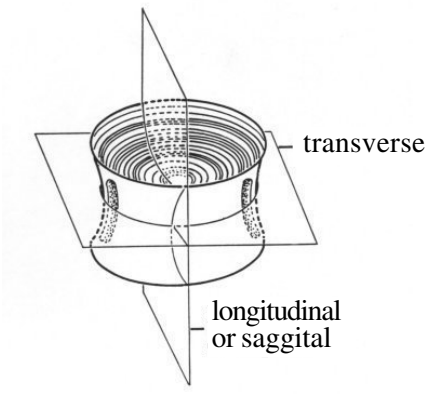

Figure 6.01 Diagram of the two sectioning planes that can be used on vertebral centra (courtesy of G.M.Cailliet, Moss Landing Marine Laboratory).

Dorsal fin spines have been another useful hard part for ageing some elasmobranchs, most notably dogfish sharks of the family Squalidae (Ketchen, 1975; Nammack et al., 1985; McFarlane and Beamish, 1987a). Spines from the second dorsal fin are preferred for ageing as the tips of first dorsal fin spines tend to be more worn down, which leads to an underestimation of age.

Novel approaches to ageing various elasmobranchs continue to arise, and researchers may want to begin collecting additional hard parts from specimens in the field to be experimented with in the lab. For example, Gallagher and Nolan (1999) used caudal thorns along with vertebral centra to determine age in four bathyrajid species, demonstrating high precision in ages between the two parts, and Gallagher et al. (in press) further elaborated on the structure and seasonal growth processes in the caudal thorns of the broadnose skate, *Bathyraja brachyurops*. Comparing counts in more than one hard part is a common age verification technique used in teleost ageing studies. However, it is not often conducted on elasmobranchs due to the lack of multiple hard parts for comparison. The use of thorns as a reliable hard part for ageing, where appropriate, has the potential to greatly aid in our understanding of the life histories of several species of skate and ray. Additionally, McFarlane et al. (2002) have provided preliminary evidence that neural arches stained with silver nitrate may be useful in assessing the ages of sharks with poorly calcified vertebral centra (see section 6.2.2.2).

6.2.1 Field sampling and storage

Upon capture, precaudal, fork, and total length (PCL, FL and TL, respectively) of sharks should be measured on a straight line, while disc width at its widest point and total length should be measured for skates and stingrays (see Chapter 3, section 3.1 this volume). While disc width is likely to be the more statistically useful length measurement for skates and rays, total length can be taken for comparison (and used in growth models if it provides better statistical results). Sex should be recorded and clasper length of males should be measured (see Chapter 7 this volume). Weights should be obtained from all specimens prior to the removal of any tissues, organs or hard parts.

The location in the vertebral column from which samples are taken for ageing can have a statistically significant effect on increment counts (Officer et al., 1996). This emphasizes the importance of standardizing the vertebral sampling region for all ageing studies, allowing for precise, valid comparisons among individuals within a population and for more accurate comparisons between populations. A section numbering between 10 and 15 of the largest (usually thoracic) vertebrae should be removed from the fish. The largest vertebrae may be located in slightly different areas depending upon the species, but they are typically located directly in front of or under the first dorsal fin in sharks, and at the thickest body point in skates and rays. The vertebral section should be bagged, labeled and stored frozen until ready for preparation (see section 6.1.2). If freezing is not an option, vertebrae can be fixed in 10% formalin for 24 h and preserved in alcohol.

Second dorsal fin spines should be removed by cutting horizontally just above the notochord to ensure that the spine base and stem are intact. Spines can be bagged, labeled and frozen until returned to the lab or placed immediately in 70-95% ethyl alcohol or 95% isopropyl alcohol.

6.2.2 Cleaning, cutting and mounting

Vertebral samples need to be thawed if frozen, or washed if preserved in alcohol, and cleaned of excess tissue and separated into individual centra. While the removal of all muscle tissue is required, I recommend that the neural arches (Figure 6.02) be removed from only ½ of the vertebral sample, and that the vertebrae with neural arches attached, along with a subsample of the fully cleaned (whole) centra, be kept frozen. Neural arches may be useful for ageing if centra are not (see section 6.3.2.2), and additional centra will be needed if staining is necessary. Haemal arches (sometimes referred to as transverse processes) should be removed. If manual cleaning is not sufficient to remove all of the surrounding tissue, or if working with dried vertebrae, several options are available to assist in complete cleaning of vertebral sections. However, soaking them in a 5% sodium hypochlorite solution is a simple and effective method. Soak times can range from five minutes to one hour depending on the size of the vertebrae and should be followed by soaking centra in distilled water for 30 to 45 minutes (Johnson, 1979; Schwartz, 1983). This method also assists in removal of the vertebral fascia between centra and does not affect the staining process, should any be conducted. Centra are typically permanently stored in 70-95% ethyl alcohol or 95% isopropyl alcohol; however, a sub-sample of centra should be permanently stored in a freezer as long-term exposure to alcohol may reduce the resolution of the banding pattern (Allen and Wintner, 2002; Wintner et al., 2002). Centra that are to be analyzed should remain in one of the above alcohol solutions for at least 24 h prior to any further preparation (i.e., being sectioned). Vertebrae should not be permanently stored in formalin as it may damage centra making them unreadable, nor should they be stored dry (in air) as this may result in cracking. Ages can be obtained in most cases from cracked vertebrae, however, accurate centrum measurements may be difficult to obtain from them.

Vertebral sectioning is typically done with a low-speed diamond-bladed saw (e.g., Isomet rotary diamond saw), but can be made with small handsaws and even scalpels when working with very small centra. Each centrum should be sagittally sectioned immediately adjacent to the center of its focus (Figure 6.02) (so that the center of the focus is at the edge of the cut) and then cut again approximately 1.5 mm off-center. Accuracy and precision in these cuts (i.e., always including the center point of the focus) will reduce centrum measurement error among individuals. A double-bladed saw can be used to eliminate the problem of cutting a small section off of one-half of a vertebral centrum (Figure 6.03). Spacing between blades should be no less than 0.6 mm to allow for some sanding and/or polishing. Large vertebrae can be hand-held for cutting, whereas imbedding small

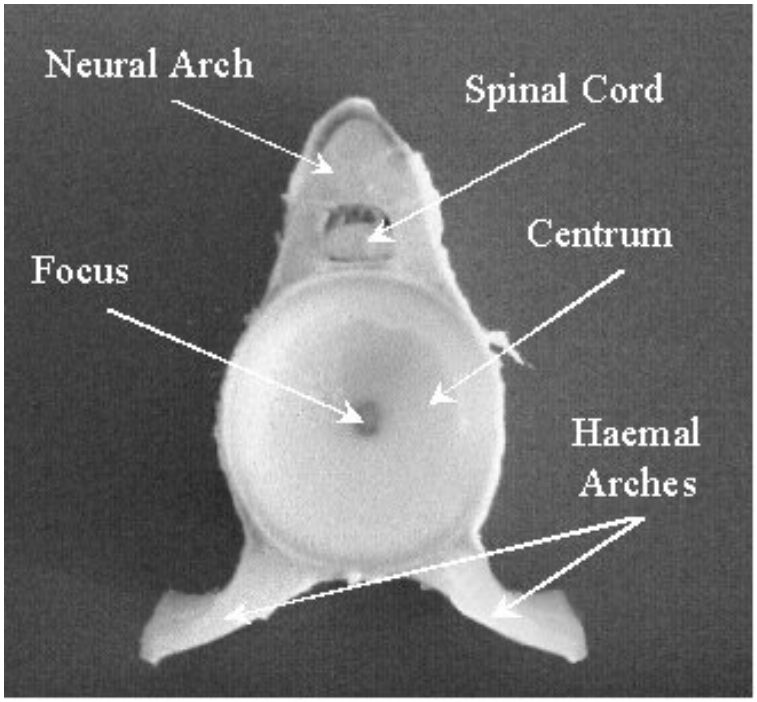

Figure 6.02 Photograph of an individual vertebral centrum showing neural and haemal arches, spinal cord and focus (courtesy of S.E. Campana, Bedford Institute of Oceanography).

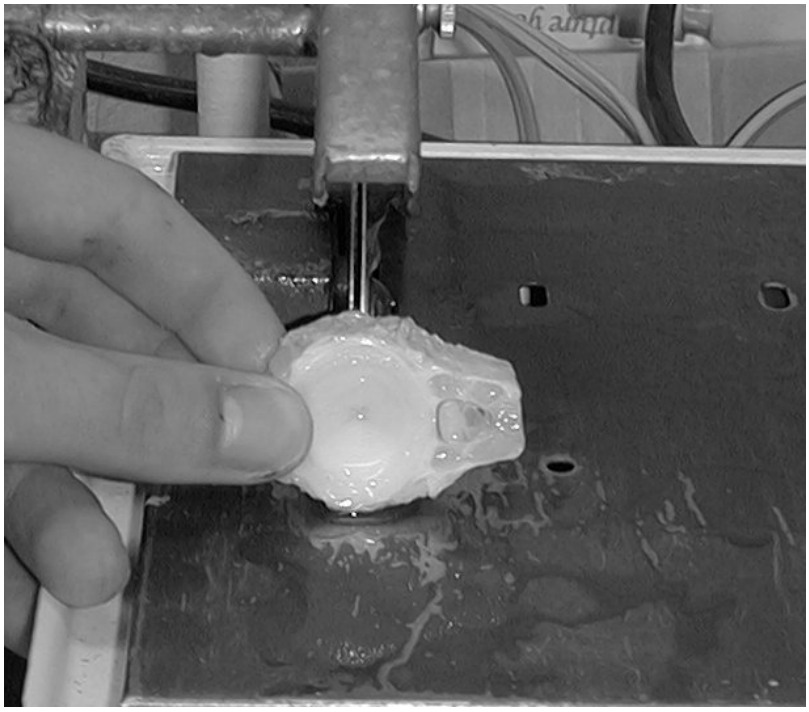

Figure 6.03 Photograph showing a vertebral centrum being sectioned (side-to-side) with a double bladed saw (courtesy of S. E. Campana, Bedford Institute of Oceanography).

vertebrae in resin (thermoplastic cement) and then cutting may prove easier. If not using a rotary saw, small vertebrae can be sanded in half, mounted, sanded thin and polished. A grinder may be used to section large vertebrae, which can then be mounted, sanded thin and polished.

If working with lamniform or other vertebrae with small numbers of radials, pressing the sagittally cut (bowtie-shaped) sections between two pieces of Plexiglas and placing weight on the top sheet during drying will prevent warping, which can effect increment and centrum radius measurements. Sectioned vertebrae should be air-dried for 24 h (under a ventilation hood if possible), and then

mounted onto microscope slides. The focus side of the vertebral section must consistently be placed face down on the slide when mounting in order to avoid adding to centrum measurement error that will lead to subsequent analysis error. Any typical slide-mounting medium (e.g., Permount™) will suffice for attaching vertebral sections. After the mounting medium is completely dry (24-36 h), sections should be sanded with wet fine grit sand paper in a series (grades 320, 400 and finally 600 for polishing) to approximately 0.3-0.5 mm and air-dried. A binocular dissecting microscope with transmitted light is generally used for identification of growth rings and image analysis (see section 6.3).

It is important to the age-determination process that at least the majority of vertebral sections include the calcified radials of the intermedialia, but this is not always easy (Figure 6.04). For example, the radials of the intermedialia of carcharhinid sharks are relatively hard, robust and numerous, making centra nearly solid. In contrast, the radials of the intermedialia in lamnoid sharks are less numerous, softer and quite fragile. Large interstitial spaces between radials can prevent intermedialia from being present in a sectioned centrum. Conducting several preliminary "test cuts" should reveal the best location to make a sagittal cut that will include intermedialia. Once the best location is found, all cuts need to be consistent (i.e., made in the same location on each centrum) in order to minimize error in centrum measurements, which are critically important for centrum edge analyses and back-calculations. In the experience of the author, the best "cut" to obtain the radials of the intermedialia has most frequently been obtained from a side-to-side cut from the vertebral centrum vs. a top-to-bottom one (Figure 6.03).

Second dorsal fin spines can be permanently stored dry or in 70-95% ethyl alcohol or 95% isopropyl alcohol, but should be air-dried for at least 24 h before reading. Spines can be read whole (without further preparation), by wet-sanding the enamel and pigment off the surface and polishing the spine or from the exposed surface resulting from a longitudinal cut (Ketchen, 1975; McFarlane and

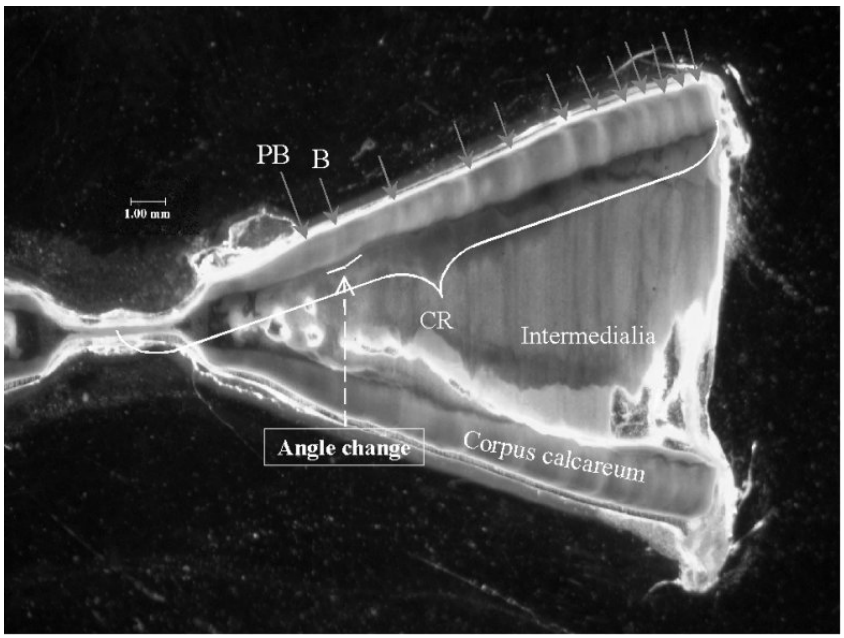

Figure 6.04 Sagittal section of a vertebral centrum from a 10 yr old salmon shark, *Lamna ditropis*, showing the typical banding pattern in this species. CR = centrum radius. PB = pre-birth ring, B = birth ring, and arrows indicate rings or age (photograph K.J. Goldman).

Beamish, 1987a). Spines should also be cross-sectioned as this has provided age assessments for some squaloids and chimaeras (Sullivan, 1977; Freer and Griffiths, 1993; Clark et al., 2002a and b; Calis et al., in press).

6.3 AGE DETERMINATION

The most commonly distinguishable banding pattern in sectioned centra when viewed microscopically is one of wide bands separated by distinct narrow bands (Figure 6.04). The terms opaque and translucent are commonly used to describe these bands, and they tend to occur in summer and winter, respectively. However, the opacity and translucency of these bands varies considerably with species, light source and methodology (Cailliet et al., 1986; Cailliet, 1990; Wintner et al., 2002; pers. obs.). It should not be assumed that the opaque and translucent nature of vertebral bands in different species will be similar; however, the pattern of wide/narrow banding tends to be very consistent (Figure 6.04). In temperate waters, the wide bands represent faster fish growth during the summer months when water temperatures are warmest, and the narrow bands represent slower growth during the colder winter months. An annulus is usually defined as the winter band. The difference in appearance between summer (wide) and winter (narrow) growth bands provides the basis for age determinations. In many species, this so-called winter band actually forms in the spring (Sminkey and Musick, 1995). While tropical teleosts have sometimes proven more difficult to age (due to the lack of seasonality and relatively consistent photoperiod), this does not appear to be the case with tropical elasmobranchs, such as the lemon shark, *Negaprion brevirostris* (Brown and Gruber, 1988).

In elasmobranch vertebral sections, each pair of wide/narrow bands that extends across one arm of the corpus calcareum, across the intermedialia and across the opposing corpus calcareum arm is considered to represent an annual growth cycle; the narrow bands, hereafter referred to as “rings” or “annuli”, are what are counted (Figure 6.04). It must be noted that counting these rings, at this point in the process, carries with it the assumption that each one represents a year’s growth; however, the validity of this assumption must be tested (see section 6.4). (The term annulus is defined as a ring-like figure, part, structure or marking, but annuli must be shown to be annual in their deposition). The age determination process (i.e., enumeration of rings, measurements and back-calculations) for spines is virtually identical to that for vertebrae (Figure 6.05); however, Ketchen’s (1975, see also Nammack et al., 1985) method for calculating age from worn spines should be used instead of discarding them. This method uses an age to spine-base-diameter regression for unworn spines to allow an estimation of age for individuals with worn spines. The best-fit regression line is used to obtain the number of years that are to be added to the age of an individual based on the diameter of a spine at its “no wear point” (see Ketchen, 1975 for details on worn spine criterion and specific examples).

While transmitted light is the most commonly used method of illuminating sectioned centra, I strongly recommend comparing transmitted light with reflected light, translucent and other filtered light,

as well as ultraviolet (UV) illumination even if staining or tetracycline injection has not been conducted (see sections 6.2.2 and 6.3.2, respectively). Altering the intensity of each type of light and making finite adjustments to the optical focus of the microscope can often provide visual enhancement of the banding pattern.

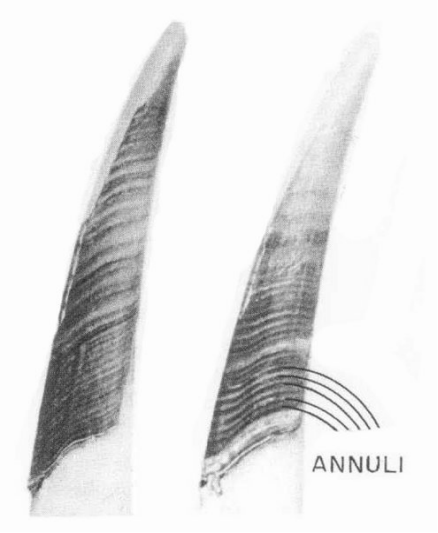

Figure 6.05 Photograph of spiny dogfish, *Squalus acanthias*, second dorsal fin spines showing annuli. First spine was aged at 42 yrs.; second spine aged at 46 yrs (courtesy of G.A. McFarlane, Pacific Biological Station).

6.3.1 Ageing protocols

Age and growth studies require interpretation of banding patterns in the hard parts of fishes. As such, they incorporate several sources of variability and error. While the individuals used in an ageing study provide a source of natural variability, variability between sexes and among geographic locations may also exist (Parsons, 1993; Carlson and Parsons, 1997; Yamaguchi et al., 1998). Other potential sources of variability and error include the method used to count growth increments, effects of within- and between-reader variability and bias, effects of staining, variation in increment counts from different hard parts and variation in increment counts from within the same region of the vertebral column and from different regions of the vertebral column (Officer et al., 1996; Campana, 2001). Developing an ageing protocol brings consistency in the ageing process leading to better precision thus minimizing error. The most important aspect of any ageing protocol is that it produces repeatable ages within and between readers (i.e., precision). Ageing protocols have two key components: 1) determination of which marks on vertebral centra or spines will be counted (see section 6.3 and below), and 2) checking for reader agreement and precision, and testing for bias within and between readers after age determinations are completed (see section 6.3.3). A standard part of every ageing protocol, whenever possible, should be to have two readers independently age all centra two times in blind, randomized trials without knowledge of each specimen's length or disc width (see section 6.3.3).

One of the more common problems in age determination occurs due to deviations in typical growth patterns observed in vertebral centra, which can lead to inaccurate counts. These deviations can result from false checks or split bands occurring within the corpus calcareum, the intermedialia or both, and the vertebral intermedialia of many species possess a great deal of "background noise". As such, it is important that these accessory bands be recognized as anomalies when assigning an age to a specimen. Checks tend to be discontinuous, weak or diffuse, and inconsistent with the general growth pattern of true annuli. Developing some familiarity with the typical "look" of the banding pattern in a given species' centra to aid in distinguishing checks from annuli is recommended. If the ageing study is

an ongoing one, regular review of reference collections and comparing summaries of age-length data from one season to the next also helps maintain accuracy, precision and reduce bias in age determinations (Officer et al., 1996; Campana, 2001). In addition, because the intermedialia of the centrum in many species is not very robust, it may warp in a concave manner during the drying process. When this occurs, the rings near the outer edge of the intermedialia become "bunched up" and indistinguishable. The rings on the corpus calcareum also become more tightly grouped at the outer edge, particularly in larger/older animals; however, they have a tendency to remain distinguishable due to the stronger (more robust) nature of the structure (see Figure 6.04). For these reasons, the corpus calcareum should always be used as the primary counting and measuring surface, with the distinct rings in the intermedialia and any additional features (see below) used as "confirmation" of a ring or annulus.

Additional difficulties in ageing elasmobranch fishes can include determining the birthmark and first growth ring. Birthmarks are usually represented by an angle change along the centrum face of whole vertebrae or along intermedialia-corpus calcareum interface with an associated ring on the corpus calcareum in sectioned centra (Figures 6.04 and 6.06), but this feature may not be distinct in either. While the birthmark usually can be found on the whole centrum surface (i.e., the outside wall of the corpus calcareum), the variability in this mark is such that it may appear distinctly only within the sagittally cut section (Figure 6.04). Additionally, "pre-birth rings" have been reported in some species (Branstetter and Musick, 1994; Nagasawa, 1998; Goldman, 2002) (Figure 6.04). Once the angle change is located, pre-birth rings can easily be distinguished from the first growth ring. The first growth ring may consist of minimal growth around the focus of a vertebra, can be faint relative to other annuli (Campana, 2001), and can also differ in its opacity or translucency (Wintner and Dudley, 2000; Allen and Wintner, 2002). Being able to consistently locate a birthmark and (particularly) the first annulus are obviously of critical importance to accurate age assessment. Knowledge of the pupping (or hatching) time of a given species can help in determining if the first annulus is expected to be very small (first winter is soon after birth) or large (first winter is a considerable time after birth).

The vertebral centra of some species may also possess features that can assist in ageing specimens. For example, sagittally cut vertebral sections of some species reveal distinct notches along either the inside or outside edge of the corpus calcareum at each ring providing an additional ageing feature (Figure 6.06). This can be particularly useful in ageing vertebral sections where the cut has excluded the radials of the intermedialia and in distinguishing growth checks from annuli.

If examination of vertebral centra reveal no discernable banding patterns or reveal rings that are difficult to interpret, centra (either whole or sectioned) can be stained to attempt enhancement of growth bands for enumeration.

6.3.2 Staining methods

Numerous techniques have been used in attempts to enhance the visibility of growth bands in elasmobranch vertebral centra. The list includes alcohol immersion (Richards et al., 1963), xylene impregnation (Daiber, 1960), histology (Ishiyama, 1951; Casey et al., 1985; Natanson and Cailliet, 1990), X-radiography (Aasen, 1963; Cailliet et al., 1983a and b; Natanson and Cailliet, 1990), X-ray spectrometry (Jones and Green, 1977), cedarwood oil (Cailliet et al., 1983a; Neer and Cailliet, 2001), alizarin red (LaMarca, 1966; Gruber and Stout, 1983; Cailliet et al., 1983a), silver nitrate (Stevens, 1975; Schwartz, 1983; Cailliet et al., 1983a and b), crystal violet (Johnshon, 1979; Schwartz, 1983; Carlson et al., 2003), graphite microtopography (Parsons, 1983; Parsons, 1985; Neer and Cailliet, 2001), a combination of cobalt nitrate and ammonium sulfide (Hoenig and Brown, 1988) and the use of copper, lead and iron based salts (Gelsleichter et al., 1998a). Many of these studies used multiple techniques on a number of species for comparison, particularly Schwartz (1983) and Cailliet et al. (1983a). These studies show that the success of each technique is often species specific and that slight modifications in technique may enhance the results.

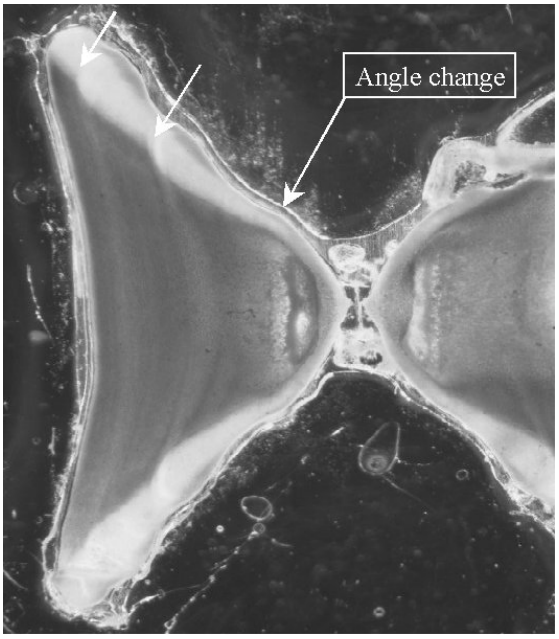

Figure 6.06 Sagittal section of a vertebral centrum from a 2 yr old smooth dogfish, *Mustelus canis*, showing the distinct notching pattern (white arrows) that accompanied the distinct banding pattern (courtesy of C. Conrath, Virginia Institute of Marine Science).

In addition to their effectiveness, the various techniques mentioned vary in their simplicity, cost and technological requirements. Histological processes have proven useful, but require specialized equipment, a number of chemicals and are relatively time consuming. However, the resulting staining process resulted in no color change in vertebral sections after 15 yrs (Casey et al., 1985). X-radiography has proven useful in many studies, but has the obvious necessity of an appropriate X-ray machine and film processing capabilities, and while X-ray spectrometry may hold promise (Jones and Geen, 1977; Casselman, 1983), it is time consuming and expensive. Simpler, less expensive and time-efficient staining techniques, such as crystal violet, silver nitrate, cedarwood oil, graphite microtopography and alizarin red should be used first prior to considering other, more elaborate methods. While these techniques have been tried, many have not yet been thoroughly evaluated. For example, the cobalt nitrate and ammonium sulfide stain suggested by Hoenig and Brown (1988) is easy to use, time efficient and provided quality results for two species (Figure 6.07), but has not been extensively applied. A microradiographic method using injected fluorochrome dyes to aid in resolving individual

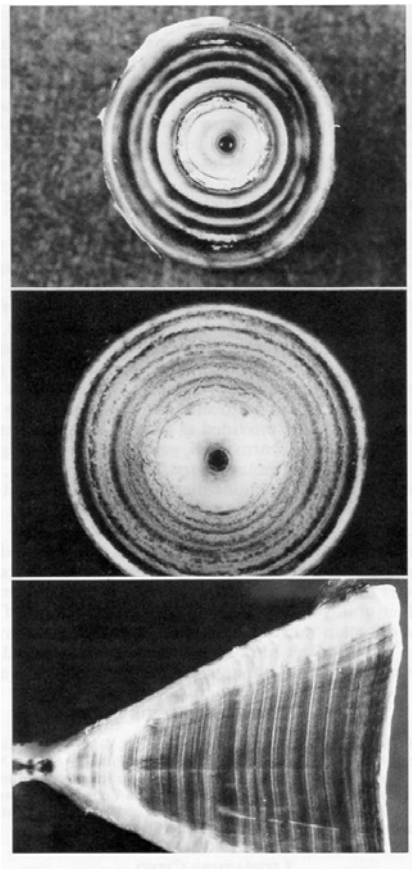

Figure 6.07 Vertebrae stained using the cobalt nitrate and ammonium sulfide method of Hoenig and Brown (1988). The top image is a smooth dogfish, *Mustelus canis*, centrum, the middle and bottom images are of lemon shark, *Negaprion brevirostris*, centra (courtesy of J.M. Hoenig, Virginia Institute of Marine Science).

hypermineralized increments was applied to captive gummy sharks, *Mustelus antarcticus*, with success (Officer et al., 1997), but this method has also not been extensively applied. This method may also have application as a validation technique, but this needs to be investigated.

Two of the simplest staining techniques are crystal violet and silver nitrate, which are described below. The appropriate literature (provided herein) should be acquired for detailed directions for other staining or enhancement techniques as well as modifications of the techniques presented. The wide-ranging subtle differences between studies using the same staining technique and the use of whole vs. sectioned vertebrae make presenting a single formula difficult. As such, a general timeline range for the methods is presented and may require some tinkering for the best results. Mini-modifications are made by many researchers in attempts to accentuate the vertebral rings in the centra of their study species.

6.3.2.1 Crystal violet protocol

Perhaps the simplest staining technique involves the use of crystal violet (Figure 6.08). An advantage of this technique is that it can be performed on fresh vertebrae as well as those stored in alcohol. After each vertebra has been cleaned of excess tissue, it is soaked in a 0.01% solution of

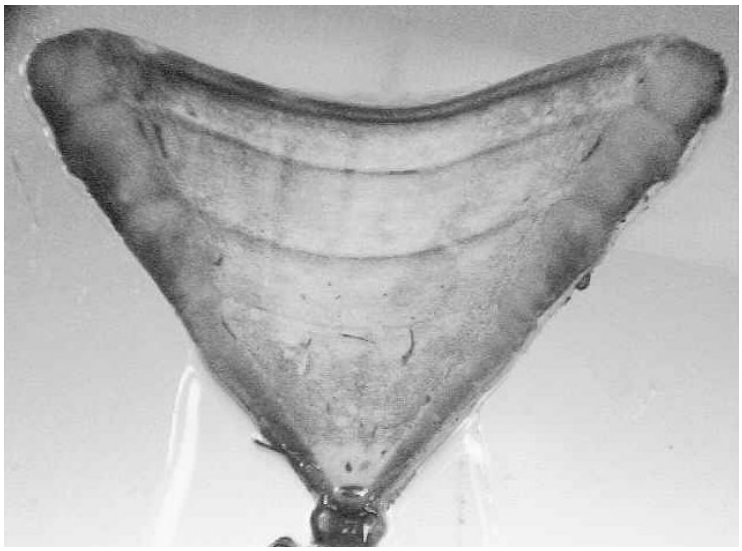

Figure 6.08 Sagittal section of a vertebral centrum from a 3 yr old fine-tooth shark, *Carcharhinus isodon*, stained with crystal violet (courtesy of J.K. Carlson, NOAA/NMFS/SEFSC Panama City Laboratory).

crystal violet. Johnson (1979) suggested soak times ranging from 0.2 to 4.0 hrs depending on the size of vertebrae, but this was for teleost fishes. Schwartz (1983) used soak time ranging from 10-15 min for 12 different elasmobranch species (10 min for sharks < 70 cm FL, 15 min for sharks > 100 cm FL). Carlson et al. (2003) used similar soak times as Schwartz (1983) for sectioned finetooth shark, *Carcharhinus isodon*, vertebrae (Figure 6.08), and on whole centra for the blacknose shark, *Carcharhinus acronotus* (J.K. Carlson, pers. comm.). The best ring definition may occur if vertebrae are initially overstained and then destained for no more than 1 min in 50% isopropyl alcohol (Schwartz, 1983).

6.3.2.2 Silver nitrate protocol

The silver nitrate technique replaces calcium salts in the centrum with silver, providing bands that darken when illuminated with ultraviolet light (Figure 6.09). As with crystal violet, this technique can be performed on fresh vertebrae as well as those stored in alcohol. All connective tissue must be removed from the centrum to ensure chemical substitution. While Cailliet et al. (1983a) soaked vertebral centra in 88% formic acid for 2-4 min to remove any traces of bleach they had used in the cleaning process and etch the centrum surface for staining, this may not be required, as neither Stevens (1975) or Schwartz (1983) conducted this step. Regardless of whether this step is taken, all centra should be repeatedly washed for 5-15 min in distilled water prior to applying the stain. Centra can then be placed in 1% silver nitrate solution for 1-3 min and simultaneously illuminated with an ultraviolet light source for anywhere between 2-4 min and depending on the species and size of the centrum (Stevens, 1975; Schwartz, 1983), although times used by Cailliet et al. (1983a) ranged from 3-15 min. Submerging whole centra in solution is recommended for ensuring the extreme edges of the vertebra are stained. Checking the centrum every 30 s or so will allow determination of the proper immersion time and prevent over-staining, which can easily occur (Schwartz, 1983). Centra should then be rinsed with distilled water to remove excess silver nitrate, and may then be read or sagittally sectioned and read.

Cailliet et al. (1983a) used a dissecting scope with reflected illumination focused laterally on the centra to make counts; however, either reflected or transmitted light can be used for sectioned vertebrae. After counts are completed, centra should be soaked in a 5% sodium thiosulfate solution for 2-3 min, rinsed with distilled water and stored in 70% isopropyl alcohol (Stevens, 1975; Schwartz, 1983; Cailliet et al., 1983a and b). This process fixes the chemical substitution, but may also eradicate very narrow rings. Counts should be made before and after fixation to estimate the bias caused by the process (Cailliet et al., 1983b)

Calcium deposits have been documented in the neural arches of elasmobranch fishes (Peignoux-Deville et al., 1982; Cailliet, 1990), but they had not been used for ageing. McFarlane et al.

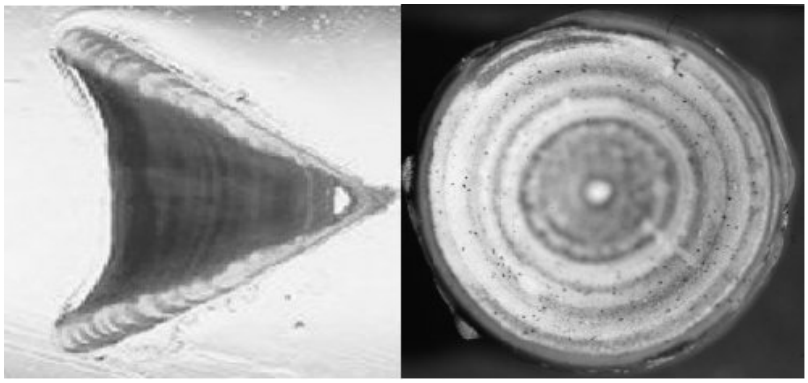

Figure 6.09 Images of two vertebrae stained with silver nitrate. Left-hand image is a sagittal sectioned centrum of an 11 yr old leopard shark, *Triakis semifasciata* (courtesy of G.M. Cailliet, Moss Landing Marine Laboratories) and the right-hand image is of a 4 yr old spot-tail shark, *Carcharhinus sorrah* (courtesy of J.D. Stevens, CSIRO Australia).

(2002) recently introduced the first attempt using this structure for ageing elasmobranchs by silver nitrate staining the neural arches of sixgill sharks, *Hexanchus griseus*. The results from this preliminary study indicate that neural arches may provide another ageing structure for elasmobranch species where their vertebral centra are poorly calcified, but the method has not been validated. Attempts are currently underway to refine this method by determining the most appropriate sectioning methods and thickness, staining times and solution concentration (McFarlane et al., 2002). The technique is also being applied to several other elasmobranchs with poorly calcified vertebrae (McFarlane, pers. comm.).

6.3.3 Reader agreement, precision and bias

Precise and accurate age estimation is a critical component of any ageing study. It is important to keep in mind that the consistent reproducibility of age estimates from vertebral centra will achieve high precision, but that these age estimates may not be accurate (i.e., reflect the true or absolute age), and that precision should never be used as a substitute for accuracy. Accurate age determination requires validation of absolute age not just the frequency of increment formation in vertebral centra or spines (Beamish and McFarlane, 1983; Cailliet, 1990; Campana, 2001) (see section 6.4).

Two readers independently ageing all centra two times in blind, randomized trials without knowledge of each specimen's length or disc width allows two calculations of between-reader agreement and precision, and helps prevent reader bias that can be caused by "predetermination" of age based on knowledge of length (i.e., prevent subjectivity). When there is a disagreement between readers, a final age determination should be made by the two readers viewing the centrum together, as a single age is needed from each specimen for input into growth models. If no consensus can be reached, the sample should be eliminated from the study.

The most commonly used methods for evaluating precision in age determination have been the average percent error (APE) technique of Beamish and Fournier (1981) and the modification of their method by Chang (1982). However, Hoenig et al. (1995) and Evans and Hoenig (1998) have demonstrated that there may be differences in precision that these methods obscure because the APE

assumes that the variability among observations of individual fish can be averaged over all age groups and that this variability can be expressed in relative terms. Also, APE does not result in values that are independent of the age estimates. APE indices do not test for systematic differences, do not distinguish all sources of variability (such as differences in precision with age) and do not take experimental design among studies into account (i.e., number of times each sample was read in each study) (Hoenig et al., 1995). Within a given ageing study, however, APE indices may serve as good relative indicators of precision within and between readers provided that each reader ages each vertebra the same number of times. However, even this appears only to tell us which reader was less variable, not which one was better or if either were biased. The comparison of precision between ageing studies would appear to have limited value, and I can find no references that compare precision estimates for a given species (APE or otherwise) to other studies, although a conversion factor relating the two precision estimators has been derived based on 14 papers that used both APE methods (Campana, 2001). Comparing precision between studies would seem to hold importance only if the study species is the same, but caution should be used if samples are from different geographic areas.

A simple and accurate approach to estimating precision is to 1) calculate the percent reader agreement (PA=[No. agreed/No. read]•100) within and between readers for all samples, 2) calculate the percent agreement plus or minus one year (PA +/- 1 yr) within and between readers for all samples, 3) calculate the percent agreement within and between readers, with individuals divided into appropriate length or disc width groups (e.g., 5-10 cm increments) as an estimate of precision (this should be done with sexes separate and together), and 4) test for bias using one or more of the methods below. The criticism of percent agreement as a measure of precision has been that it varies widely among species and ages within a species (Beamish and Fournier, 1981; Campana, 2001). However, there is validity in using percent agreement with individuals grouped by length as a test of precision because it does not rely on ages (which have been estimated), but rather on lengths, which are empirical values. Age could be used if, and only if, validation of absolute age for all available age classes had been achieved (see section 6.4).

Several methods can be used to compare counts (ages) by multiple readers such as regression analysis of the first reader's counts vs. the second reader's counts, a paired t-test of the two readers' counts and a Wilcoxon matched pairs signed-ranks test (DeVries and Frie, 1996). Campana et al. (1995) stated the importance of a separate measure for bias, and that bias should even be tested for prior to running any tests for precision. They suggest an age bias plot, graphing one reader vs. the other, which is interpreted by referencing the results to the equivalence line of the two readers (45^{o} line through the origin) (Figure 6.10). Similarly, Hoenig et al. (1995), and Evans and Hoenig (1998), state that comparisons of precision are only of interest if there is no evidence of systematic disagree-

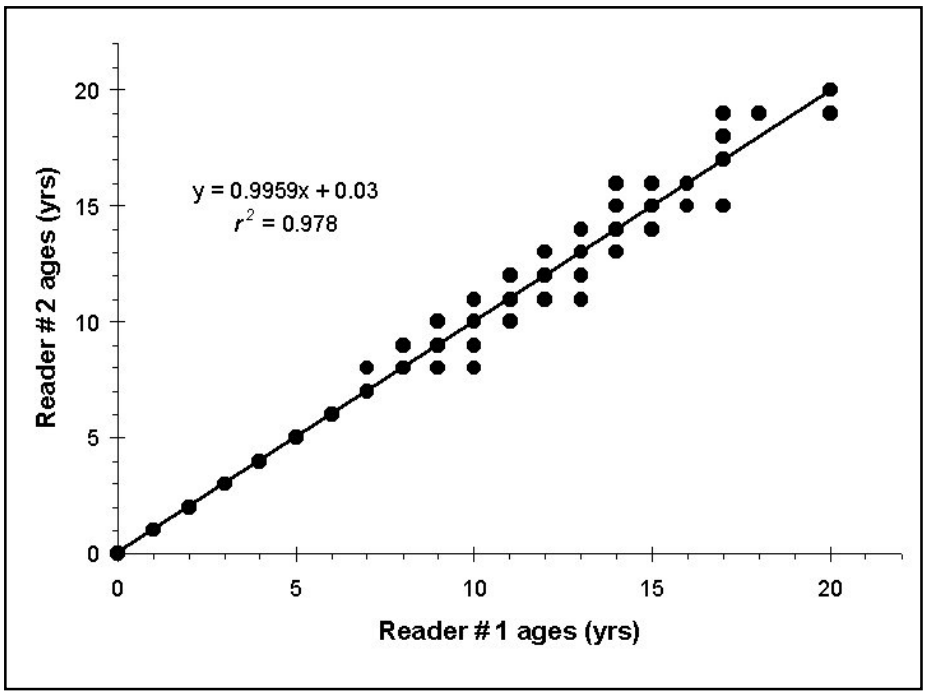

Figure 6.10 An age bias plot, graphing one reader vs. the other, showing good agreement and no bias. Chi-square tests of symmetry were also conducted on these data and gave no indication that differences between and within readers were systematic rather than due to random error (from Goldman, 2002).

ment among readers or methods, and suggest testing for systematic differences between readers using Chi-square tests of symmetry such as Bowker's (Bowker, 1948), McNemar's (McNemar, 1947), and their Evans-Hoenig test to determine whether differences between and within readers were systematic (biased) or due to random error. This is of particular importance if initial percent agreement and precision estimates are low. I recommend these tests of symmetry for testing for bias regardless of precision as they place all age values in contingency tables and test the hypothesis that values in a given table are symmetrical about the main diagonal, and because they can be set up to test among all individual age classes or groups of age classes. The test statistic (the Chi-square variable) will tend to be large if a systematic difference exists between the two readers.

6.3.4 Back-calculation methods

Back-calculation is a method for describing the growth history of each individual sampled, and numerous variations in methodology exist (see Francis (1990) for a thorough review). Back-calculations estimate lengths-at-previous-ages for each individual and should be used if sample sizes are small and if samples have not been obtained from each month. Regression methodologies are ill advised because they discard information and frequently produce back-calculated lengths that overestimate fish length at capture (Francis, 1990), and they will not be presented here. Back-calculation formulas that follow a hard part or body proportion hypothesis are recommended (Campana, 1990; Francis, 1990; Ricker, 1992). The proportional relationship between animal length or disc width and the radius of the vertebral centrum among different length animals within a population is used as a basis for empirical relationships regarding population and individual growth, as is the distance from the focus to each annulus within a given centrum (see below and section 6.3.1). Centrum radius (CR) and distance

to each ring should be measured as a straight line from the central focus to the outer margin of the corpus calcareum (Figure 6.04) to the finest scale possible. If using a compound video microscope with the image analysis system (e.g., UTHSCSA Image Tools 1997 or Optimus - Media Cybernetics 1999), distances can be measured to the nearest 0.001 mm. If no image analysis system is available, measurements should be made with an ocular micrometer (which is easily inserted into an eyepiece of the microscope). Lengths or disc widths should then be plotted against CR to determine the proportional relationship between somatic and vertebral growth (Figure 6.11), which will assist in determining the most appropriate back-calculation method.

Four different proportion-based back-calculation methods are presented here that can be used to compare to sample length-at-age data, depending on the relationship between CR and length. (Length and disc width are interchangeable in the following equations, but length will be the term used). The results of the method best representing sample data should be used in subsequent growth models (see section 6.5).

1) The Dahl-Lea direct proportions method (Carlander, 1969):

This is the most commonly applied proportions method. While it should theoretically only be conducted when the linear fit to the relationship between CR and length passes through the origin, it may still provide the most accurate results when compared to sample length-at-age data. Hence, it should be conducted, but at least one of the other three methods below should also be conducted for comparison. The Dahl-Lea direct proportions equation is:

$$L_i = (L_c/CR_c)\bullet CR_i \qquad (6.1)$$

where L_i = length at ring 'i', L_c = length at capture, CR_c = centrum radius at capture, and CR_i = centrum radius at ring 'i'.

2) Linear-modified Dahl-Lea method (Francis, 1990):

This method should be applied if the relationship between CR and length is best described by a linear equation and the CR-length relationship does not pass through the origin (Figure 6.11). Parameter estimates from the specific linear fit are incorporated into the back-calculation estimates. The linear-modified Dahl-Lea equation is:

$$L_i = L_c\bullet[(a+bCR_i)/(a+bCR_c)] \qquad (6.2)$$

where 'a' and 'b' are the linear fit parameter estimates (Figure 6.11).

3) Quadratic-modified Dahl-Lea method (Francis, 1990):

This method should be applied if the relationship between CR and length is best described by a quadratic fit (Figure 6.14), as parameter estimates from the specific quadratic fit are incorporated into the back-calculation estimates. The quadratic-modified Dahl-Lea equation is:

$$L_i = L_c\bullet[(a+bCR_i+cCR_i^2)/(a+bCR_c+cCR_c^2)] \qquad (6.3)$$

where 'a', 'b', and 'c' are the quadratic fit parameter estimates (Figure 6.11).

4) Size-at-birth-modified Fraser-Lee method (Campana, 1990):

Both Ricker (1992) and Campana (1990) suggested that the point of origin of proportional back-calculations should be related to a biologically derived intercept (i.e., length at birth). This equation is recommended for u anytime the linear fit to the relationship between CR and length does not pass through the origin. The "size-at-birth-modified" Fraser-Lee equation is:

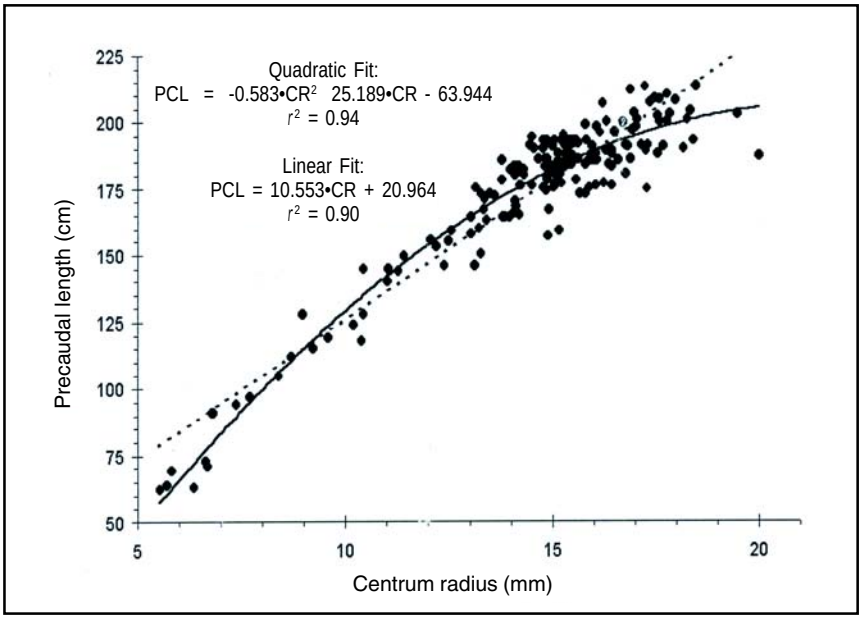

Figure 6.11 Relationship between centrum radius and precaudal length for eastern North Pacific salmon sharks, *Lamna ditropis*, showing significant fits given by linear and quadratic equations (sexes combined, n=182). PCL = precaudal length, CR = centrum radius (from Goldman, 2002).

$$L_i = L_c + [(CR_i - CR_c) \bullet (L_c - L_{Birth})/(CR_c - CR_{Birth})] \quad (6.4)$$

where L_{Birth} = length at birth and CR_{Birth} = centrum radius at birth.

Providing biological and statistical reasoning behind the choice of a back-calculation method is extremely important for obtaining accurate life history parameter estimates from a growth function (e.g., von Bertalanffy) when using back-calculated data. While one method may show itself to be more statistically appropriate for back-calculation, researchers should conduct several methods for comparison to available sample length-at-age data to verify that statistical significance equates to biological accuracy. Biological accuracy can be determined by plotting the sample mean length-at-age data against the difference between mean back-calculated length-at-age estimates and the sample mean length-at-age data to see which method provides the best results (Goldman, 2002). This plot will show which mean back-calculation length-at-previous-age estimates (from each method) most accurately reflect mean lengths-at-age of sampled individuals.

6.4 VALIDATION

Estimates of age, growth rate and longevity in sharks assume that the vertebral rings are an accurate indicator of age. While this is probably true for most species, few studies on elasmobranch growth have validated the temporal periodicity of band deposition in vertebral centra and even fewer have validated the absolute age (Cailliet et al., 1986; Cailliet, 1990; Campana et al., 2002; Natanson et al., 2002). Cailliet (1990) stated that the process of evaluating growth zone deposition in fishes can be

categorized into the terms “verification” and “validation,” where verification is defined as “confirming an age estimate by comparison with other indeterminate methods,” and validation as “proving the accuracy of age estimates by comparison with a determinate method,” and these definitions are adhered to herein.

Obtaining the absolute age of individual fish (complete validation) is the ultimate goal of every ageing study, yet it is the frequency of growth ring formation for which validation is typically attempted. The distinction between validating absolute age and validating the periodicity of growth ring formation is important (Beamish and McFarlane, 1983; Cailliet, 1990; Campana, 2001). Validation of the frequency of growth ring formation must prove that the mark being considered an annulus forms once a year (Beamish and McFarlane, 1983). However, it is the consistency of the marks in “number per year” that really matters, be it one or more than one. Two or more marks (rings) may make up an “annulus” if, and only if, consistent multiple marks per year can be proven. Strictly speaking, validation of absolute age is only complete when it has been done for all age classes available, with validation of the first growth increment being the critical component for obtaining absolute ages (Beamish and McFarlane, 1983; Cailliet, 1990; Campana, 2001).

Validation can be achieved via several methods such as chemically tagging wild fish, mark-recapture studies of known-age individuals and bomb carbon dating (see section 6.4.2) (the latter two can also be used to validate absolute age). A combination of using known-aged individuals, tag and recapture, and chemical marking is probably the most robust method for achieving complete validation (Beamish and McFarlane, 1983; Cailliet, 1990; Campana, 2001; Natanson et al., 2002). While this is a rather daunting task to accomplish with most elasmobranch species, the current necessity to obtain age-growth data for fisheries management purposes dictates that it be attempted. The most frequently applied method used with elasmobranchs has been chemical marking of wild fish (see section 6.4.2) even though recaptures can be difficult to obtain for many species. As validation has proven difficult in elasmobranchs, verification methods such as centrum edge analysis and relative marginal increment analysis are frequently employed.

6.4.1 Indeterminate methods (verification)

Centrum edge analysis and relative marginal increment analysis are simple, indeterminate methods that can be used to verify the temporal periodicity of ring formation in vertebral centra. Each uses the centrum edge in a different manner to assess the timing of band deposition. While relative marginal increment analysis may be slightly more robust, as the technique makes all age classes comparable on a relative scale, it is advantageous to conduct both methods, particularly if electron microprobe spectrometry can be applied (see below) (Cailliet, 1990; Wintner and Dudley, 2000; Wintner et al., 2002).

Centrum edge analysis compares the opacity and translucency (width and/or density) of the centrum edge over time in many different individuals to discern seasonal changes in growth. The centrum edge is categorized as opaque or translucent, and the band width is measured or graded, then compared to season or time of year (Kusher et al., 1992; Wintner and Dudley, 2000; Wintner et al., 2002). A more detailed centrum edge analysis can be conducted by analyzing the levels of calcium and phosphorous at the centrum edge using X-ray or electron microprobe spectrometry (Cailliet et al., 1986; Cailliet and Radtke, 1987), which according to Cailliet (1990) has only been conducted in a single study on recaptured nurse sharks that had been injected with tetracycline (Carrier and Radtke, 1988 in Cailliet, 1990).

Relative marginal increment analysis (RMI)—sometimes Marginal Increment Ratio (MIR)—is a useful, direct technique with which to assess seasonal band and ring deposition. The margin, or growth area of a centrum from the last (ultimate) growth ring to the centrum edge, is divided by the width of the last (previously) fully formed (penultimate) annulus (Branstetter and Musick, 1994; Natanson et al., 1995; Wintner et al., 2002). Resulting RMI values are then plotted against month of capture to determine temporal periodicity of band formation. Age-zero animals cannot be used in this analysis since they have no fully formed increments.

6.4.2 Determinate methods (validation)

Validation of absolute age is extremely difficult to achieve with elasmobranch fishes, hence the few studies that have attempted validation in these fishes have focused on validating the temporal periodicity of ring (growth increment) formation. The tetracycline validation method is a standard among fisheries biologists for marking free-swimming individuals (Cailliet, 1990; DeVries and Frie, 1996; Campana, 2001) to test the assumption of annual periodicity of growth rings. Oxytetracycline (OTC), a general antibiotic that can be purchased through veterinary catalogs, binds to calcium and is subsequently deposited at sites of active calcification. It is typically injected intramuscularly at a dose of 25 mg kg^{-1} body weight (Tanaka, 1990; Gelsleichter et al., 1998b) and an external identification tag is simultaneously attached to each injected animal. OTC produces highly visible marks in vertebral centra and dorsal fin spines of recaptured sharks when viewed under ultraviolet light (Holden and Vince, 1973; Smith, 1984; McFarlane and Beamish, 1987a and b; Brown and Gruber, 1988; Tanaka, 1990; Kusher et al., 1992; Gelsleichter et al., 1998b; Natanson et al., 2002; Simpfendorfer et al., 2002; Smith et al., 2003) (Figure 6.12). The combination of body growth information and a discrete mark in the calcified structure permit direct comparison of time at liberty with growth band deposition, such that the number of rings deposited in the vertebra or spine since the OTC injection can be counted and related to the time at liberty. Although there may be problems associated with using captive growth as a surrogate to growth in the wild and with recapturing animals that have been at large for long enough

periods of time, this method has been used on a number of species in the field and laboratory (Cailliet et al., 1986; Branstetter, 1987; Cailliet, 1990; Cailliet and Goldman, in prep.). While growth in captive animals may be influenced by constant environmental parameters (e.g., water temperature and photoperiod) and food availability, laboratory studies can provide valuable information on growth rates (Tanaka, 1990; Mohan et al., in press) assist in verifying or validating the timing of growth ring deposition (Branstetter, 1987; Goldman, 2002), and the results may resemble growth rates observed in field experiments (Branstetter, 1987).

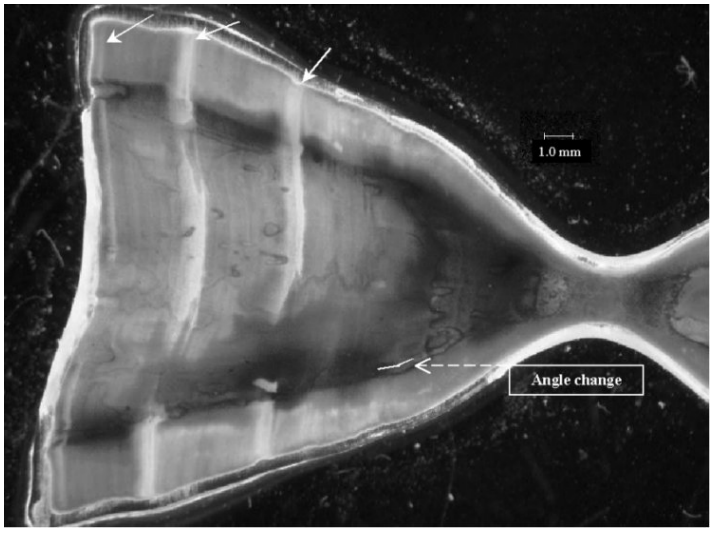

Figure 6.12 Sagittally cut vertebral section of OTC injected captive sand tiger shark, *Carcharias taurus*. White arrows indicate three clearly visible OTC marks at the sight of ring formation (photograph K. J. Goldman).

Several other chemical markers such as fluorescein and calcein have been used to validate growth ring periodicity in teleost otoliths, but very few studies have evaluated these in elasmobranchs (Gelsleichter et al., 1997; Officer et al., 1997). Gelsleichter et al. (1997) found that while doses of 25 mg kg^{-1} body weight (typical dose for teleosts) induced physiological stress and mortality in elasmobranchs, doses of 5-10 mg kg^{-1} body weight produced suitable marks without causing physiological trauma or death. Based on this evaluation, any alternative chemical markers tested should consider that doses for teleosts might be too high for elasmobranchs.

Bomb carbon dating is a technique that has recently been applied to age validation in elasmobranchs. A rapid increase in radiocarbon (^{14}C) occurred in the world's oceans due to atmospheric atom bomb testing in the 1950's and 1960's (Druffel and Linick, 1978). Its uptake was virtually synchronous in marine carbonates including corals and fish otoliths, which allowed the period of increase to serve as a dated marker in structures exhibiting growth bands (Druffel and Linick, 1978; Weidman and Jones, 1993; Kalish, 1995; Campana, 1997; Campana, 1999). Hence, all fish born prior to 1958 contain relatively little ^{14}C, all those born after 1968 possess elevated levels of ^{14}C and individuals born in the interim period have intermediate levels of ^{14}C. Matching the ^{14}C chronology in the fish hard part with the published ^{14}C chronologies for the region allows interpretation of age and validation. While this method has been used for ageing several teleost fishes, Campana et al. (2002) reported the first application of bomb radiocarbon to validate ages in long-lived sharks, specifically the porbeagle shark, *Lamna nasus*, and (preliminary results for) the mako shark, *Isurus oxyrinchus*. This method may

provide one of the best approaches to age validation of long-lived fishes; however, it is not viable for short-lived species or younger individuals, and appropriate reference chronologies are not available for some environments (Campana, 2001). Bomb carbon dating requires at least some of the fish in the sample to have been born (or hatched) prior to 1965; it is expensive and requires the use of relatively high technology equipment such as a mass spectrometer, which may make this method unavailable for many researchers. It may, however, be a key technique in resolving certain ageing discrepancies such as questions regarding single vs. double ring formation annually in some species, if vertebrae from the appropriate time period can be obtained.

6.5 GROWTH MODELS

A number of models and variations of models exist for estimating growth parameters in fishes, of which the von Bertalanffy (1938) and Gompertz (1825) growth models are the most commonly applied (see Ricker, 1979; Summerfelt and Hall, 1987; and Haddon, 2001 for thorough reviews). The von Bertalanffy growth function has mostly been used to describe fish growth, while the Gompertz curve is often used to describe larval and early life growth of fishes and growth in many invertebrates (Zweifel and Lasker, 1976; Ricker, 1979). These two models are presented in standard form below; however, weight can be used in place of length in the von Bertalanffy model, and length may be substituted for weight in the Gompertz model. Many statistical packages include modules (i.e., functions) that can be used to calculate the best fitting growth parameters for the available length-at-age or weight-at-age data pairs from the equations given in sections 6.5.1 and 6.5.2. For example, a nonlinear least squares regression algorithm (e.g., 'nls' in S-Plus, Mathsoft Inc., 2000), a maximum likelihood function or the PROC NLIN function in SAS can be used to fit the von Bertalanffy and Gompertz curves to the data (SAS Institute Inc., 1999), and programs such as PC-YIELD (Punt and Hughes, 1989) can calculate a wide range of growth models for comparison (Wintner et al., 2002). Additionally, FISHPARM (Prager et al., 1987), a fishery based statistics program, is simple to use and provides quality statistical results for the two models presented herein. Both models can also be fit to data on a spreadsheet via a non-linear regression using the "solver" function in Microsoft Excel.

Sample size can have considerable influence on growth model results. Additionally, pooling the sexes into one sample can mask differences in sex-specific growth, so growth parameters should be estimated for the sexes separately and combined and tested for significant differences (see below). If smaller and-or medium size age classes are not well represented in the sample size of one or both sexes, lengths at previous ages should be back-calculated from centra measurements for all animals. Sample (observed) length-at-age data, back-calculated length-at-age data, mean back-calculated length-at-age data, and a combination of back-calculated lengths-at-age and sample data should then each be separately fitted with the appropriate growth function, and the resulting parameter estimates

compared. As long as large animals are well represented in the sample size, close parameter estimates from these four growth curves would indicate that a relatively reliable overall sample size (n) has been obtained. The best parameter estimates in these cases will be those with the smallest standard error; however, significant differences between curves can be tested with a likelihood ratio test. A likelihood ratio test should always be conducted if the resulting four curves have not produced very similar parameter estimates and if standard errors are high.

Several methods exist for evaluating differences in growth curves (Gallucci and Quinn, 1979; Kimura, 1980; Bernard, 1981; Kappenman, 1981; Francis, 1996; Wang and Milton, 2000). While several techniques can provide reasonable results, a likelihood ratio test will always equal or surpass other methods in accuracy and reliability and should be used to determine whether significant differences exist between growth curves, such as to see if female and male growth parameter estimates are significantly different or if a single set of growth parameters better describe the data (Kimura, 1980; Cerrato, 1990; Quinn and Deriso, 1999; Haddon, 2001). Likelihood ratio tests can be conducted in a multitude of programs, such as Microsoft Excel following the Kimura (1980) method (Haddon (2001) provides an excellent step-by-step instruction guide to the Kimura, 1980 method) or using the PROC NLIN function in SAS (SAS Institute Inc., 1999).

6.5.1 von Bertalanffy growth function

The von Bertalanffy (1938) growth function has been widely used since its introduction into fisheries by Beverton and Holt (1957), and although it has received much criticism over the years, it is the most widely used growth function in fisheries biology today (Roff, 1982; Haddon, 2001). It maintains its attractiveness, in part, because its approach to modeling growth is based on the biological premise that the size of an organism at any moment depends upon the resultant of two opposing forces: anabolism and catabolism. Additionally, it is convenient to use and allows for much easier comparison between populations and several alternate forms of the model can be fit to the age-length data. [Haddon (2001) presents a variety of growth models including generalized models as possible alternatives.]

The von Bertalanffy (1938) growth function is:

$$L_t = L_4 \, (1\text{-}e^{-k\,(t\text{-}to)}) \qquad (6.5)$$

where L_t = predicted length at age 't', L_4= asymptotic or maximum length, k = the growth coefficient, and t_o = age or time when length theoretically equals zero. The growth rate, k, is often misrepresented in its description; it should be remembered that when fitted, this curve represents the average growth rate of population members (i.e., the 'k' coefficient is best described as the average rate at which an organism in the population achieves its maximum length [or size] from its length at birth). The exponent t_o is an extrapolation from available data and is not biologically interpretable.

Small sample size, particularly of small and/or large individuals can cause poor parameter estimates using the von Bertalanffy model (Cailliet and Tanaka, 1990; Francis and Francis, 1992). In lieu of using t_o (due to its lack of biological meaning) some researchers suggest using an estimate of length at birth (L_o) rather than t_o as a more robust method (Goosen and Smale, 1997; Carlson et al., 2003; H. Mollet, pers. comm.). This method was first introduced by Fabens (1965) as an alternate equation to the von Bertalanffy growth model. While only a few studies have used Faben's (1965) equation to estimate growth parameters in elasmobranchs, it has provided more realistic parameter estimates for some species when the sample size was small (Goosen and Smale, 1997), and extremely similar results to the von Bertalanffy model when sample size was adequate (Carlson et al., 2003). This appears to be an excellent alternative to the von Bertalanffy model and should be applied where appropriate for comparison to other models.

The Fabens (1965) equation is:

$$L_t = L_4(1-be^{-kt}) = L_4 - (L_4 - L_o)e^{-kt}, \qquad (6.6)$$
$$b = (L_4 - L_o)/L_4 = e^{kto},$$

where L_o is the length at birth.

6.5.2 Gompertz growth function

The Gompertz (1825) growth function is an S-shaped model function (similar to the logistic function—for use of the logistic function and several alternatives to the Gompertz function, see Ricker 1975 and Ricker 1979). The estimated instantaneous growth rate in the Gompertz function is proportional to the difference between the logarithms of the asymptotic disc width or length and the actual disc width or length (Ricker, 1975; 1979). This growth function has been used most often for skates and stingrays (Mollet et al., 2002) and may be better suited to elasmobranchs that hatch from eggs, but it may also be the most appropriate model for some shark species (Wintner et al., 2002). This model may offer a better option when the volume of an organism greatly expands with age, such as myliobatiform rays where considerable thickness is added to the animal over time, but not so much disc width or length (W. Smith, pers. comm.). The body mass may be distributed differently than would be readily detectable by length measurement and by the von Bertalanffy model. Additionally, captive growth rates (particularly when starting with young, small animals) may be better estimated by this function as newly captured specimens may not grow in their typical fashion due to physiological stress or a reduction in feeding that often accompanies that stress, which may cause growth rates to slow (Mollet et al., 2002).

Three commonly used integral forms of the Gompertz growth function (Gompertz, 1825 as presented by Ricker, 1979) are:

1) $w_t = W_0 \exp(k(1-\exp(-gt)))$

2) $w_t = W_4\ exp(k(exp(-gt)))$, and

3) $w_t = W_4\ exp(-exp(-g(t-t_o)))$

where: w_t = biomass at any time t, W_0 = hypothetical size (weight or length) at $t = 0$ (not t_o), W_4= Maximum estimated weight, k = dimensionless parameter such that "kg" is the size-specific instantaneous rate of growth at $t = 0$, g = instantaneous growth rate when $t = t_o$, where t_o = the time at which the absolute growth rate starts to decrease (i.e. the inflection point in the curve), and t = age. Equations 2 and 3 are simply alternate expressions of equation 1, but the same three parameters (w, k, and g) are solved.

6.6 SAMPLING COVERAGE

The goal of every age and growth study is to accurately and thoroughly describe (through validation) the age-length relationship of a species. In order to achieve that goal, a solid experimental design beginning with field sampling and ending with the calculation and comparison of growth rate estimates is necessary. Thorough sampling coverage is imperative to the successful outcome of ageing studies. The dramatic effect that sample size can have on growth parameter estimates makes it imperative that a representative sample of the population be obtained for ageing studies. It is obvious that a larger number of specimens (i.e., larger sample size) is beneficial to gaining a thorough understanding of the age and growth process of any species. The desired content of this sample is to have specimens from both sexes for each month of the year for the entire size and geographic range of the species. This can be a difficult sample base to obtain for many elasmobranchs, but the goal should be to come as close to it as possible. Back-calculations can help to "fill in" the gaps for a low sample size of young and middle age classes, but it must be remembered that while there is considerable value in using back-calculated data, this is a false increase in sample size, as back-calculation data are not independent values.

A wide range of techniques is available for conducting ageing studies on elasmobranch fishes (Casselman, 1983; Cailliet et al., 1986; Cailliet, 1990; Cailliet and Goldman, in prep), and studies should utilize as many of the available techniques as possible. I have tried to encompass the majority of options available in this paper, but resources cited herein should be consulted for more detailed information on specific topics. Researchers more frequently follow the advice given by Beamish and McFarlane (1983) (and reiterated in Cailliet et al., 1986 and Cailliet, 1990) regarding the need to combine techniques, such as the use of OTC marking and tag-recapture data from the field and-or laboratory to validate relative (timing of increment formation) and absolute age. However, much work still needs to be done on this group of fishes. These practices along with the development of new techniques will be needed to further elucidate the nature of growth increment deposition in the vertebral centra, dorsal fin spines, neural arches and caudal thorns and to validate age. Research on physi-

ological aspects related to age and growth, such as the function of the endocrine system in calcium regulation and the deposition of growth increments, should simultaneously be undertaken, as we know little about these mechanisms as they relate to growth in elasmobranchs (Cailliet, 1990; Gelsleichter and Manire, 1997).

6.7 WEB-BASED RESOURCES

- Canadian Shark Research Laboratory, Bedford Institute of Oceanography, Nova Scotia Canada:
  http://www.mar.dfo-mpo.gc.ca/science/shark/english/index.htm
- NMFS/NOAA/SEFSC Shark Population Assessment Program, Panama City, FL, U.S.A.:
  http://www.sefscpanamalab.noaa.gov/shark/shark_final_1.htm
- NOAA/NMFS/NEFSC Apex Predator Program, Narragansett, RI, U.S.A.:
  http://na.nefsc.noaa.gov/sharks/

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CHAPTER 7. REPRODUCTIVE BIOLOGY

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7.1 INTRODUCTION: MODES OF REPRODUCTION

Several reproductive specializations are found within the elasmobranchs. All elasmobranchs utilize internal fertilization and produce a relatively small number of large eggs. Elasmobranch fecundity generally ranges from one to two offspring produced per year up to a possible maximum of 300 in the whale shark (Compagno, 1990; Joung et al., 1996). Elasmobranch reproductive strategies include oviparity, aplacental viviparity, and placental viviparity (Wourms, 1977). Oviparous species enclose eggs in an egg case and deposit them into the environment, where embryos will develop external to the body of the mother. Embryos remain in the egg case to develop for a period of time ranging from less than two months to over one year (Compagno, 1990). Viviparous species retain eggs within the uteri where the embryos will develop. The yolk sac of placental viviparous species interdigitates with the uterine wall to form a placenta in which nutrients from the mother are transferred to the embryo directly. In most species the egg envelope is retained and incorporated into the uteroplacental complex (Hamlett et al., 1985). Gestation for viviparous species ranges from less than six months to greater than two years (Compagno, 1990). Viviparous species may have either lecithotrophic or matrotrophic development. Lecithotrophic development occurs when embryos derive their nutrition solely from yolk reserves and occurs in many aplacental viviparous species. Matrotrophic development occurs when embryos supplement the yolk reserves by obtaining maternally derived nutrients during gestation and also occurs in many aplacental species and all placental viviparous species (Wourms and Lombardi, 1992). The advantage of matrotrophy may be the increase in juvenile size at birth and therefore increased survivorship of young. Another important consideration in the evolution of elasmobranch reproductive strategies is the presence or absence of uterine compartments. Uterine compartments are formed in all species with placental development and some species with aplacental development and are proposed to be an important step in the evolution of placental viviparity (Otake, 1990).

7.1.1 Oviparity

Oviparity occurs in all batoids of the family Rajidae and six families and over 100 species of sharks in the orders Heterodontiformes, Orectolobiformes and Carcharhiniformes (Compagno, 1990; Compagno, 2001). In oviparous species, eggs are enclosed within an egg case and deposited in the environment. Two types of oviparity occur, extended oviparity and retained oviparity. Almost all oviparous species have extended oviparity in which large egg cases are fertilized, enclosed in an egg case, deposited and, after a period of up to 15 months, hatch out. In this reproductive mode almost all of the embryonic development occurs within the egg case outside of the mother's body. Retained oviparity occurs much more rarely and refers to species in which cased eggs are retained in the oviduct and development proceeds for a longer period before the eggs are released into the environment. One form of retained oviparity occurs in some scyliorhinid catsharks when multiple egg cases are retained within the oviduct before being released (Compagno, 1988; Compagno, 1990).

The egg case generally has tendrils and sticky filaments that aide in attaching the egg to some sort of structure or substrate where the eggs incubate. The egg case also hardens after being deposited to protect the embryos from predation. All oviparous chondrichthyan eggs are laid in pairs (Mellinger, 1983). Oviparous embryos tend to be relatively smaller than viviparous embryos as growth of the embryo is constrained by the amount of yolk initially present in the yolk sac (Hamlett, 1997). Compagno (1990) suggests egg-laying elasmobranchs may select appropriate substrates for egg deposition as occurs in the bullhead shark in which the female picks up the egg after it is laid and wedges it into rocks or marine vegetation. Development time within the egg case is likely dependent on external temperatures. Differences in the length of the incubation period of eggs laid by female thornback rays, *Raja clavata*, held at different temperatures have been noted in at least two aquarium experiments (Clark, 1922; Ellis and Shackley, 1995).

7.1.2 Aplacental viviparity

Embryos from species with aplacental viviparous development are retained within the mother for the duration of development, but no placental connection is formed between the mother and the embryo. A wide range of developmental forms occur within this reproductive mode and Wourms (1977) separated them into three groups: those dependent entirely on yolk reserves, those which feed on other eggs or embryos, and those which possess placental analogues. Animals within the first group are considered lecithotrophic as the embryo receives no extra nutrition from the mother, and animals in the last two groups are considered matrotrophic as the embryo's nutrition is supplemented with either ovulated eggs or uterine milk (histotrophe).

7.1.2.1 Aplacental yolk sac

Embryos from species within this group are entirely dependent on yolk reserves to complete development. This type of development is the most common reproductive strategy employed by sharks. It occurs in the orders Hexanchiformes, Squaliformes, Pristiophoriformes, Squatiniformes, Rhinobatiformes, Pristiformes, Torpediniformes and some species in the orders Orectolobiformes and Carcharhiniformes (Compagno, 1990). This form of development offers protection from predators for a longer period of time than oviparous development (Hamlett, 1997).

7.1.2.2 Oophagy and adelphophagy

Oophagy occurs when embryos within the uterus hatch out of the egg capsule after a few months and then consume additional eggs that continue to be ovulated while the embryo develops. Oophagy is thought to occur in all sharks in the order Lamniformes (Compagno, 1990; Gilmore, 1993), specific examples described within the literature include the bigeye thresher shark, *Alopias superciliosus*, the pelagic thresher shark, *A. pelagicus*, the shortfin mako shark, *Isurus oxyrinchus* and the porbeagle shark, *Lamna nasus* (Moreno and Moron, 1992; Francis and Stevens, 1999; Liu et

al., 1999; Mollet et al., 2000). In the sand tiger shark, *Carcharias taurus*, the first embryo to develop in each uterus consumes all the other embryos within that uterus (adelphophagy or intrauterine cannabilism), as well as additional ovulated eggs (Gilmore et al., 1983). This type of development may facilitate the development of very large embryos and may prepare the embryo for a predatory life style (Wourms, 1977). Yano (1992) found that embryos of the false catshark, *Pseudotriakis microdon,* also ingest yolk material from other ova but that they transfer ingested yolk to an external yolk sac rather than forming the extended stomach of lamniform oophagous embryos. Female slender smooth-hounds, *Gollum attenuatus*, form egg capsules which contain 30-80 ova, and only one ovum within each egg capsule develops with all other ova ingested and packed to an external yolk sac (Yano, 1993). While ova are ingested by the slender smooth-hound embryo during development, this form of reproduction may or may not be considered oophagy as after the initial consumption of ova within the egg sac, the embryo then develops without any additional ova or maternal investment.

7.1.2.3 Placental analogues: histotrophe and trophonemata

This type of development occurs in all rays of the order Myliobatiformes. Trophonemata are long villous extensions of the uterine epithelium that secrete histotrophe or "uterine milk" which can be ingested or absorbed by the embryo. The quantity and composition of the histotrophe varies widely between species. Trophonemata envelope the embryo and may occasionally enter the embryo through the spiracles. As yolk reserves are depleted, trophonemata increase in size and release uterine secretions rich in proteins and lipids (histotrophe) (Wourms, 1981). White et al. (2001) found that trophonemata of the stingaree, *Urolophus lobatus*, increase in length and enter the gill, spiracles and mouths of developing embryos in the uterus about six months after ovulation when yolk reserves from the external yolk sac have been utilized. Trophonemata are also formed in the Atlantic stingray, *Dasyatis sabina*, and increase in length in the late stages of gestation while the developing young are bathed in histotrophe (Snelson et al., 1988). The transfer of nutrients has been found to be much more efficient in species with trophonemata than in species with a yolk sac placenta (Wourms, 1981).

7.1.3 Placental viviparity

Placental viviparity occurs when during the course of embryonic development after an initial period of reliance on yolk from a yolk sac, the yolk sac attaches to the uterine wall and forms a yolk sac placenta and the associated yolk stalk forms the umbilical cord. In most species the egg envelope is retained and incorporated into the uteroplacental complex (Hamlett et al., 1985). Thirty percent of viviparous sharks form a yolk sac placenta (Hamlett, 1997). This type of reproductive development only occurs in sharks of the order Carcharhinformes (Compagno, 1990), and can occur within the same family or genus as aplacental viviparous species. The genus *Mustelus* includes several aplacental viviparous species such as the spotted estuary smooth-hound, *M. lenticulatus,* the gummy shark, *M. antarcticus,* and the starspotted smooth-hound, *M. manazo,* and several placental viviparous

species such as the dusky smooth-hound, *M. canis,* and the spotless smooth-hound, *M. griseus* (Francis and Mace, 1980; Teshima, 1981; Lenanton et al., 1990; Conrath and Musick, 2002). Wourms and Lombardi (1992) estimate the yolk sac placenta has evolved independently 11-20 times within the elasmobranchs. This has led to a large diversity in placental structure. After ovulation placental species undergo a period of dependency on yolk reserves that may last for several weeks to months before the placenta is formed. Teshima (1981) divides the placental species into two groups, those in which it forms in mid-gestation and those in which it forms soon after ovulation.

7.2 BASIC ANATOMY

7.2.1 Male

The male reproductive system is composed of the testes, genital ducts (ductus efferens, epididymis, ductus deferens and seminal vesicle), accessory glands and secondary sex organs (Figure 7.01). Male reproductive organs and tissues have been described and defined using various terminologies, and this account will follow the terminology of Hamlett (1999). The testes are paired structures supported by a mesorchium and in some species enveloped by the epigonal organ. A pre-germinal fold runs the length of the testis and is the origin of the spermatogenesis process. The testes are the location of spermatogenesis and also play a role in creating and secreting steroid hormones. Pratt (1988) identified three types of testes in elasmobranchs: radial, diametric, and compound, defined by their pattern of seminiferous follicle origin and propagation. The epididymis is connected to the testis via the ductus efferens, which are fine tubules which cross the mesorchium at the anterior edge of the testis. Mature sperm are discharged from the testis through the ductus efferens (Wourms, 1977). The efferent ducts join the epididymis, which expands to form a long tube with complex convolutions. The epididymis is continuous with the next section of the genital duct, the ductus deferens also known as the vas deferens or Wolffian duct. The ductus deferens is continuous with the seminal vesicle or ampulla ductus deferens. The ductus deferens and seminal vesicle function as storage areas for seminal products, and in some species sperm is packaged into either spermatozeugmata or spermatophores here (Wourms, 1977). The ureter becomes entwined with the terminal portion of the seminal vesicle, and both end in the anterior wall of the urogenital sinus. The urogenital sinus vents into a common cloaca by means of a single large papilla. Two accessory glands are present, Leydig glands and the alkaline gland. Leydig glands are a series of branched tubular glands that secrete seminal fluids into the epididymis and ductus deferens. The alkaline gland of batoids may be involved in sperm protection (Hamlett, 1999).

The secondary sex organs include the claspers and the associated siphon sacs. Claspers are modified regions of the pelvic fin that act as copulatory organs to transfer sperm and seminal matrix from the male to the female (Figure 7.02). All elasmobranchs have internal fertilization and possess

claspers, but clasper structure varies widely. All claspers have a dorsal longitudinal groove through which semen passes to the female during mating. The clasper consists of two intermediate elements—known as the joint and beta cartilages that extend down from the metapterygium of the pelvic fin, the main stem cartilage to which two marginal cartilages are fused, and four terminal cartilages, the claw, rhipidion, the distal basal and the spur. The two marginal cartilages help to form the clasper groove with a terminal end opening, the hypopyle, and an anterodorsal opening, the apopyle (Compagno, 1988). A good diagram of clasper skeletal structure can be found in Compagno (2001). Most male elasmobranchs possess siphon sacs which are subcutaneous muscular, epithelium-lined bladders situated on each side of the midline between the skin and belly musculature. Each sac ends blindly anteriorly and opens into the clasper groove posteriorly through the apopyle (Gilbert and Heath, 1972). Gilbert and Heath (1972) examined the structure and function of the siphon sacs in piked dogfish, *Squalus acanthias,* and dusky smooth-hounds, *Mustelus canis,* and determined that the siphon sacs' function is to hold seawater, which is used to wash sperm from the clasper groove into the oviduct of the female.

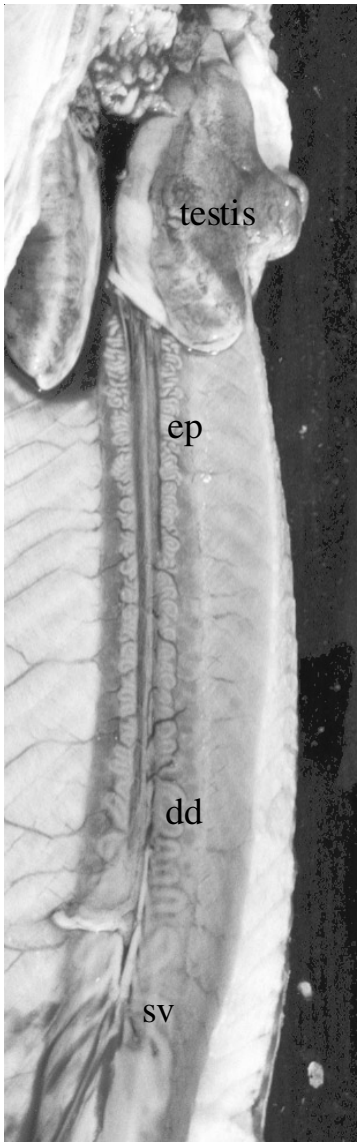


Figure 7.01 The male reproductive tract of a spiny dogfish, *Squalus acanthias*, ep = epididymis, dd = ductus deferens, and sv = seminal vesicle.


Figure 7.02 Male and female little skates, *Leucoraja erinacea*, female on the left, male on the right.

7.2.2 Female

The female reproductive system is composed of either a paired or single ovary and oviducts, which are differentiated into an ostium, the anterior oviduct, the oviducal gland, the isthmus, a dilated terminal region/uterus, a cervix and the urogenital sinus (Hamlett and Koob, 1999) (Figure 7.03). The ovary and the oviducts are in close

association but are not continuous. The female reproductive tract begins as paired ovaries and oviducts, but in many adults the reproductive tract becomes asymmetrical as the animal develops. In many viviparous sharks species only the right ovary develops fully, and in many ray species the right ovary and oviduct are reduced to varying degrees. The ovaries are attached to the body wall by a mesovarium (Wourms, 1977). Pratt (1988) described two types of ovaries: one found in lamniforms in which the ovary was hollow and contained within the epigonal organ, the other found in other elasmobranch species in which the ovary was external and borne on the flat surface of the epigonal organ or suspended directly from the mesovarium. The ovary functions in the generation of germ cells, the acquisition and accumulation of yolk and the biosynthesis and secretion of hormones. The ovary consists of oocytes, developing follicles and embedded loose connective tissue stroma. The epigonal organ is present in most species and supports the ovary or ovaries. The ostium is the anterior funnel-shaped opening of the oviduct which functions to collect the ovulated eggs. The oviducal gland is a specialized portion of the oviduct where egg capsule and egg jelly formation occur and where fertilization may take place although it may occur in the upper oviduct (Hamlett et al., 1998). (The oviducal gland is described more completely in section 7.6.) An isthmus may occur before the widening of the oviduct into a posterior oviducal section or a uterus and may function to isolate the contents of the uterus. The uterus in oviparous species is specialized for egg capsule formation and provides structural modifications for movement of the capsule through the uterine lumen (Koob and Hamlett, 1998). In viviparous species the uterus is highly developed and modified for retention of eggs and the developing embryos. The cervix occurs at the junction of the uterus and urogenital sinus and is a constriction in this area. The uteri independently join the urogenital sinus (Hamlett and Koob, 1999).

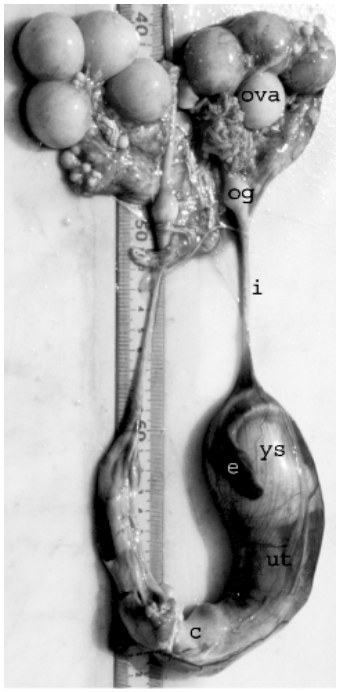


Figure 7.03 The female reproductive tract dissected out of a spiny dogfish, *Squalus acanthias*, og = oviducal gland, ova = ovary, i = isthmus, e = uterine embryo, ys = embryonic yolk sac, ut = uterus, and c = cervix.

7.3 MATURITY

7.3.1 Assessing maturity

The meaning of the term maturity in recent elasmobranch literature ranges from defining the onset of maturation to the period of time when a female elasmobranch undergoes parturition and produces a litter of pups. Since in many elasmobranch species the period between the beginning of the maturation process until pupping can last a period of years, it is important to specifically define the term maturity in an elasmobranch reproductive study. For the purposes of this manual a

mature animal is defined as one that is immediately capable of mating and producing viable offspring or one that has already done so. Therefore, in order to be considered mature, an animal must have previously mated or possess fully developed gametes and all of the secondary structures necessary for successful mating and fertilization. For female elasmobranchs that have not previously mated this requires the presence of fully developed ova in the ovaries that are ready to be ovulated. For male elasmobranchs that have not previously mated this requires not only the presence of mature sperm within the reproductive tract but also the presence of fully developed claspers and siphon sacs. Maturity in sharks is determined by either observation of the reproductive tract organs or secondary sex structures or by noting the presence or absence of reproductive products within the reproductive tract.

7.3.1.1 Male

In order for male elasmobranchs to successfully mate they must have fully developed and functional claspers, and they must have mature sperm ready to be transported by the claspers into the female. Therefore male maturity can be assessed by determining if the claspers are calcified and if sperm products are found within the seminal vesicles of the reproductive tract. Clark and von Schmidt (1965) considered males mature when the clasper head (rhipidion) could be spread open, the clasper proximal to the head was rigid due to calcification of the supporting cartilage, the base of the clasper rotated easily, and when the siphon sacs were fully elongated. Clasper calcification can be a simple and quick way to determine if male elasmobranchs are mature; however, maturity assessments based on calcification alone may be inaccurate as claspers may have developed before spermatogenesis is complete. Pratt (1979), in a reproductive study on blue sharks, *Prionace glauca*, stated that many sharks with claspers that appeared mature lacked sperm aggregations and had small ductus deferentia and were therefore still immature.

Histological evidence or direct observation will confirm the presence of sperm within the reproductive tract. Sperm products can be located and viewed by cutting a cross section of the reproductive tract, or smears of the reproductive tract can be taken, stained, and viewed under a microscope to determine if viable sperm or sperm products are present. Pratt (1979) found the most accurate way to determine maturity in male blue sharks was to note the presence or absence of sperm in the ampulla ductus deferens (seminal vesicle). He found a field test to look for the presence of mature sperm aggregates could be done by cross-sectioning the thickest part of the kidney of the male blue shark. When the cross-section was made four ducts were visible; the largest two were the seminal vesicles, and the presence or absence of spermatophores in a white supportive tissue could be observed with the aid of a magnifying glass. This technique was used to assess the male maturity of smalleye hammerheads, *Sphyrna tudes,* and Pacific angelsharks, *Squatina californica* (Natanson and Cailliet, 1986; Castro, 1989). Pratt and Tanaka (1994) stated that mature male elasmobranchs in a

resting stage may not possess sperm within the ampullae of the reproductive tract but that the size and the shape of the ampullae should be a good indicator of maturity as mature males will have large ampullae. Assessments based on the presence of sperm in the reproductive tract alone may also be somewhat inaccurate as sperm may be present within the reproductive tract before the claspers are fully functional. Clark and von Schmidt (1965) found that individuals of at least two species (the blacktip shark, *Carcharhinus limbatus,* and the tiger shark, *Galeocerdo cuvier*) possessed mature sperm that were produced and present in the seminal vesicles before the claspers and siphon sacs were fully developed. The best approach to determining maturity in male elasmobranchs should therefore combine an examination of clasper calcification and development with a simple field or laboratory test to determine if sperm are present within the seminal vesicles of the reproductive tract or to determine if the seminal vesicles are enlarged indicating a previous mating event.

7.3.1.2 Female

Female elasmobranchs are considered mature if there is evidence of a current or previous pregnancy or evidence that they will be ready to reproduce within a short period of time. For females that are not or have not been pregnant previously, maturity can be determined by assessing the condition of the ova in the ovary and the size of the oviduct. Mature females will have well developed yolky eggs in the ovary, and the oviduct may start to expand and detach from the body wall. Females that have previously been pregnant will have an expanded oviduct containing expanded oviducal glands and well developed uteri. Female maturity can therefore be determined by assessing the condition of the reproductive tract and noting the presence or absence of well developed ova in the ovary, eggs or embryos within the reproductive tract, or expanded oviducts. Bass et al. (1973) defined female sharks with distinct ova in the ovary and an expanded uteri to be mature. In doubtful cases the presence or absence of an intact hymen was used to show if the female was still an adolescent or was in between pregnancies. The hymen is a circular transverse fold that separates the vagina from the cloaca; in virgin elasmobranchs the vagina is sealed by a membrane which is an extension of the hymen (Pratt, 1979). The condition of the reproductive tract has been used to determine maturity in female sandbar sharks, *Carcharhinus plumbeus*, and piked dogfish, *Squalus acanthias* (Springer, 1960; Jones and Geen, 1977).

In many studies an intermediate maturing stage is identified. During this stage the oviduct begins to expand or the ova within the ovary begin to undergo vitellogenesis. Jones and Geen (1977) in their reproductive study of piked dogfish, *Squalus acanthias*, defined a maturing phase and plotted the proportion of animals in this stage versus length to determine the size at the onset of maturity. Natanson and Cailliet (1986) also define three stages of maturity for the Pacific angelshark, *Squatina californica*—immature, maturing and mature—based on the condition of ova in the ovary and the

condition of the oviduct. Also, in many studies mature females are classified according to what stage of the reproductive cycle they are currently undergoing. Jones and Geen (1977) defined three stages of mature females: those between pregnancies, those with candles within the uteri, and those with free embryos within the uteri. Determining maturity in female elasmobranchs is largely dependent on observation, and, therefore, assessing maturity will be most accurate when a large enough number of immature, maturing and mature animals can be observed.

7.3.2 Determining the size or age at maturity

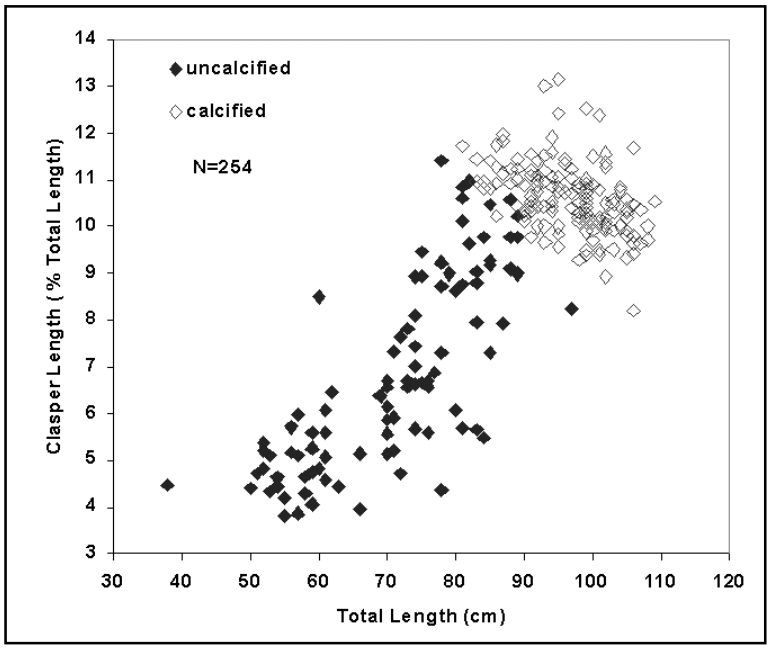
Size or age at maturity is usually determined by either analyzing the growth of reproductive organs relative to size or age or by quantifying the proportion of mature animals at each length or age group and determining the length at which 50% of a class is mature.

7.3.2.1 Male

Clasper length measurements have been used in many studies to estimate the size at maturity because there is a known correlation between the development of secondary sex characters and the reproductive organs, and maturity. Clasper length is most commonly measured from the posterior margin of the anus to the tip of the clasper (clasper inner length) or from the base of the pelvic fin to the tip of the clasper (clasper outer length) (Compagno, 1984). The length of the clasper as a proportion of the precaudal, fork or total length is plotted against the corresponding length. This usually results in a plot that shows a sharp increase in the slope for a range of lengths before leveling off. This portion of the plot with the steeper slope corresponds to the range of lengths at which the shark is becoming mature (Figure 7.04). While the most common reproductive measurement to plot against length is the clasper length in male elasmobranchs, the size or weight of other reproductive structures like the testis and siphon sac are often used and plotted in the same manner (Parsons, 1981; Teshima, 1981; Yano, 1993).

The other method commonly used to determine the size at maturity for male elasmobranchs is to use a maturity ogive. Using this method, the reproductive condition of a large enough sample size of males of different sizes is first determined as in section 7.3.1.1. Then the proportion of mature animals found in each length group is determined. These data can then be fitted with a logistic regression and the length at the point of the curve corresponding to 50% is often used as an indicator of the size at which these animals mature. The logistic equation can take the following form: proportion mature at a specific length or age = $1/(1+e^{a+(b*\text{length or age})})$, where a and b are coefficients estimated by fitting the data to the logistic curve. This equation can then be solved to determine at what length or age 50% of the population is mature (Conrath and Musick, 2002) (Figure 7.05).

Figure 7.04 The relationship between clasper length (as % total length) and total length of *M. canis*.



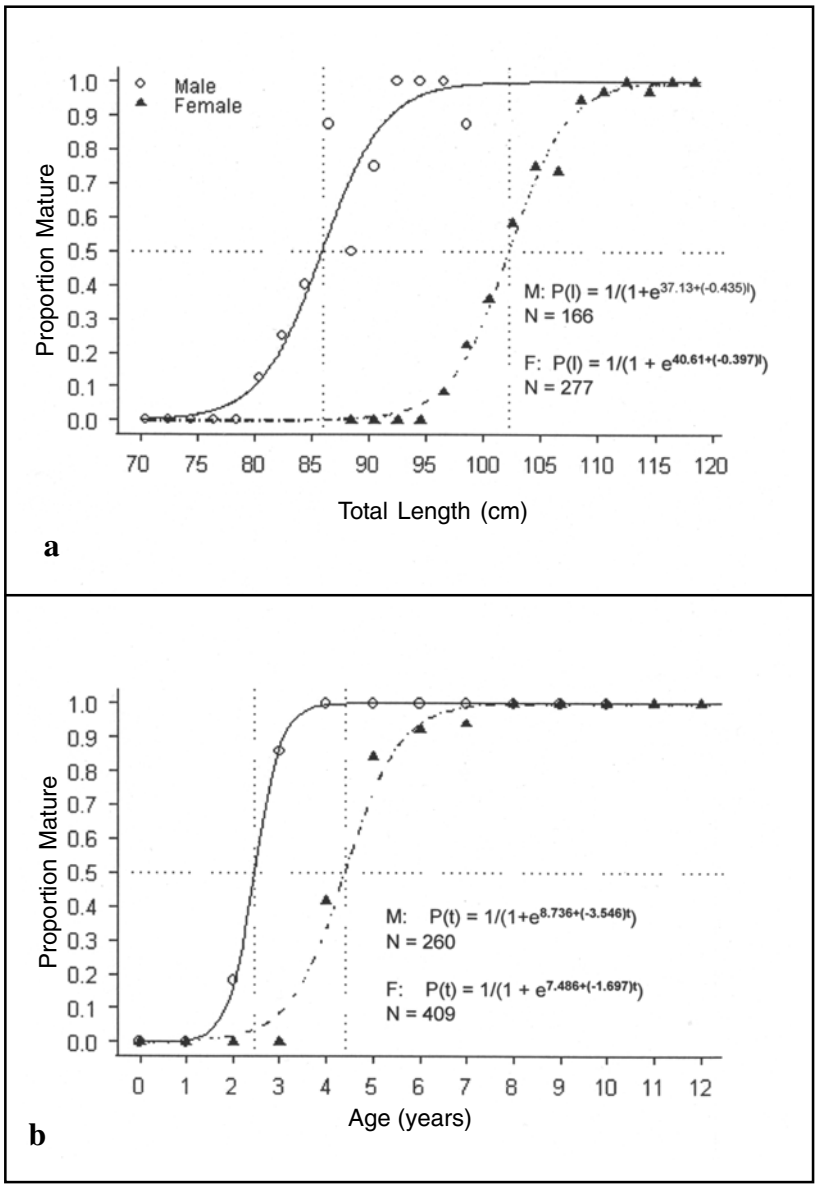


Figure 7.05 a - Maturity ogives for total length (TL) of male and female *M. canis*, b - maturity ogives for age of male and female *M. canis*.

7.3.2.2 Female

The size of oviducal gland or other structures of the female reproductive tract is often used to assess the size at which animals become mature. The size or weight of the ovary, or the size of the oviducal gland, uterus, or other reproductive structure is often plotted against the length of the animal to determine if there is a size range at which the structure in question begins to develop very quickly before growth tapers off again. Similar to the clasper length versus total length plot discussed above the length range at which an elasmobranch population matures is determined by a change in the slope of the plot (Wass, 1973; Parsons, 1981; Castro et al., 1988; Yano, 1993).

As with male elasmobranchs, the other method used to determine length at maturity in female elasmobranchs is to create a maturity ogive. The same procedures and equations as explained above in section 7.3.1.2. are used for females (Figure 7.05) (Conrath and Musick, 2002).

7.3.3 Age at maturity vs. age at first reproduction

It is important to distinguish the difference between the age or length at first maturity with the age or length of first reproduction. This distinction becomes very important in demographic models. The time a fish matures is generally understood as the size or age of first mating, and this needs to be distinguished from the size or age at which the animal actually produces pups. If the species being considered is oviparous or has a very short gestation time there may be no discrepancy or only a slight one. However, if the animal has a gestation time of several months or longer, the delay must be accounted for in the model, and the fecundity term should not be included at the size or age when the animal is first mature but at the age or size when the animal actually undergoes parturition. Dusky smooth-hound, *Mustelus canis*, females mature at four to five years of age, and therefore in a age-based model a fecundity term would not be added until age five to six as gestation lasts nearly one year.

7.4 TIMING OF THE REPRODUCTIVE CYCLE

Wourms (1977) defined three types of reproductive cycles exhibited by elasmobranchs: reproduction continuously throughout the year, a prolonged annual cycle that is not well defined with one or two peaks in activity, or a well defined annual or biennial cycle. Chen et al. (1996) found encapsulated fertilized eggs in the uteri of female blacktip sawtail catsharks, *Galeus sauteri*, all year round indicating this species reproduces throughout the year without a well-defined breeding season. This may be characteristic of some deep sea elasmobranch species as this also occurs in the deep sea black dogfish, *Centroscyllium fabricii* (Yano, 1995). The small-spotted catshark, *Scyliorhinus canicula*, is proposed to have a very extended breeding season, but peak reproductive activity occurs during the winter and spring months (Sumpter and Dodd, 1979). Dusky smooth-hounds, *Mustelus canis*, have a very well-defined annual reproductive season with an 11 to 12 month gestation followed

by ovulation of the next year class of eggs within a period of days to weeks (Conrath and Musick, 2002).

7.4.1 Mating

Determining what time of year a species mates can be quite difficult and is often inferred by assuming mating occurs sometime between parturition of one year class of embryos and ovulation of the next year class of eggs to be fertilized. The timing of mating can also be inferred from viewing female specimens with mating scars. Pratt (1979) found that the skin of mature female blue sharks was twice as thick as that of male blue sharks to accommodate the biting that occurs during mating. Pratt and Carrier (2001) found that biting by males during mating seems universal among elasmobranchs, and therefore during the mating season female elasmobranchs frequently bear mating marks on their bodies with the most common being tooth cuts and abrasions on the pectoral fins. They further found that in some elasmobranch species there is a sexual dimorphism of the teeth with males having teeth designed to make courtship biting more effective. Tricas and LeFeuvre (1985) proposed that biting in the whitetip reef shark, *Triaenodon obesus*, functions as a precopulatory releasing mechanism for females and to maintain contact during copulation. The timing of the reproductive cycle before and after mating is generally considered separately for male and female elasmobranchs.

7.4.2 Male reproductive cycle

The timing of the reproductive cycle of male elasmobranchs is generally determined by using various gonad size indices, through histological examination of the testes, or by noting the presence and amount of sperm products in the reproductive tract throughout the year. Since the contribution of the male to the reproductive effort in elasmobranchs primarily ends with mating and inseminating the female, the following two sections of the chapter are primarily concerned with the timing of mating. The next two sections are not included in the previous mating section as most of the techniques listed track the reproductive condition of the male throughout the year or reproductive cycle.

7.4.2.1 Gonad size indices

A gonadosomatic index (GSI)—or some other relationship between the size of the male reproductive organs and the total size of the animal—is often used to determine when sperm and sperm products are being produced. The GSI is the testis weight expressed as a percentage of the total body weight, GSI = (testis weight/total body weight) * 100. By comparing the GSI from mature males caught during various times of the year, a mating season can be estimated by assuming mating is occurring when the GSI reaches its highest value. This will correlate to the time of year when sperm production has reached its highest level. Peak GSI values may not always coincide exactly with mating season, as sperm products must move down the reproductive tract before mating can occur and sperm may be stored in the reproductive tract for a period of time. Simpfendorfer (1992) found that the peak GSI for male Australian sharpnose sharks, *Rhizoprionodon taylori*, occurred approximately a month

before the mating season. While a GSI can give valuable information about the timing of sperm production in male elasmobranchs, caution should be used when trying to use this data as an approximation of when mating season begins. GSI data is best used combined with other supporting data, like examinations of sperm presence and quantity in the lower portions of the reproductive tract or other evidence of mating activity like the presence of sperm products in the female or the presence of courtship wounds on the female. Stevens and Wiley (1986) defined the mating season by determining the monthly GSI of two carcharhinid shark species and also examined the quantity of sperm in the seminal vesicles, mating scars of females captured during the appropriate time of year and the mean maximum ova diameter of the females.

7.4.2.2 Histological examination of the reproductive tract

A more detailed way to track the formation of sperm in the testis through time is by making histological sections of the testis. The functional unit of the testis is defined by Callard (1991) as, "the germ cell clone plus associated Sertoli cells within a closed spherical unit bounded by a basement membrane." Parsons and Grier (1992) name this unit the spermatocyst and define the sequence of development from the germinal zone to the degenerate zone which includes zones of spermatocysts in various stages of development. Parsons and Grier (1992) define seven stages of development as do Maruska et al. (1996) also. While these two papers differ slightly in the definition of stages, both track the spermatogenesis process from loosely organized germ cell, to spermatogonia, spermocytes, spermatids, and mature spermatozoa.

In order to use this technique a section is removed from the middle of the testis and preserved in either 10% formalin or Bouin's solution. The section is processed using standard histological techniques and stained with hematoxylin and eosin. The section is rinsed in a series of water washes, placed in a tissue cassette, and the Bouin's fixed tissues are rinsed with a solution of 50% ethanol (ETOH) saturated with lithium carbonate to remove soluble picrates, then rinsed in 70% ETOH. The cassettes are then placed in a tissue processor to dehydrate them and infiltrate them with paraffin. A rotary microtome is used to cut 5 µm thick sections of the tissue, which are then stained with hematoxylin and eosin and cover-slipped with a synthetic mounting media. The testis section is then viewed under a compound microscope and the proportion of the testis occupied by each different stage is measured along a straight-line distance across the cross section of the testis, starting from the germinal zone. Or the number of spermotocysts occupied by each stage can be counted across the straight-line distance and compared for various times of the year. The mean proportion of the testis occupied by each stage or the mean number of spermatocysts in each stage throughout different months of the year can then be compared to determine if there is a recognizable seasonal pattern in testis development. Parsons and Grier (1992) suggest using caution with this technique as the peak testicular development may not coincide with the mating season.

Mating season has been determined for the male piked dogfish, *Squalus acanthias*, (Jones and Geen, 1977) and two smooth-hounds, *Mustelus griseus* and *Mustelus manazo* (Teshima, 1981) by examining what percent of the ampullae contain each defined spermatogenic stage throughout the year. The timing and duration of spermatogenesis was determined for the Port Jackson shark, *Heterodontus portusjacksoni*, by examining the migration of the degenerative zone throughout the year (Jones and Jones, 1982).

In the dusky smooth-hound, *Mustelus canis,* the mean proportion of the testis occupied by the seven stages defined by Maruska et al. (1996) was measured and compared for different months of the year to determine if there was a recognizable seasonal pattern in testis development. A cross section of the testis is shown in Figure 7.06, and the stages of the sperm development, modeled after Maruska et al. (1996), are shown in Figure 7.07. Stage one consists of spermatogonia and loosely organized germ cells not yet bound by a basement membrane into a spermatocyst. During stage two a layer of spermatogonia and associated Sertoli cells divide and surround a central lumen and are bounded by a basement membrane forming the spermatocyst. In stage three the spermatogonia undergo mitosis to become primary spermatocytes, which will then undergo the first meiotic division to become secondary spermatocytes. In stage four the secondary spermatocytes have undergone the second meiotic division to become spermatids. Stage five consists of immature sperm, which are spermatids that have undergone spermiogenesis and possess a head and tail region, but individual sperm have not organized into bundles yet. During stage six these spermatozoa organize into tightly shaped packets arranged spirally along the outside of the spermatocysts. Unlike Maruska et al. (1996), the seventh "degenerate" stage was classified by Conrath and Musick (2002) as the area of the testis posterior to stage six, which consists of empty spermatocysts, free spermatagonia and free spermatozoa. During September through October the majority of the testes were primarily occupied by spermatocysts in the spermatocyte stage (stage 3). During November the majority of the testes were occupied primarily by spermatocysts in the spermatid stage (stage 4). By March and continuing through May the majority of the testes were occupied by spermatocysts in the mature spermatozoa stage (stage 6). Thus mating most likely occurs sometime between the months of May and September for this species (Figure 7.08).

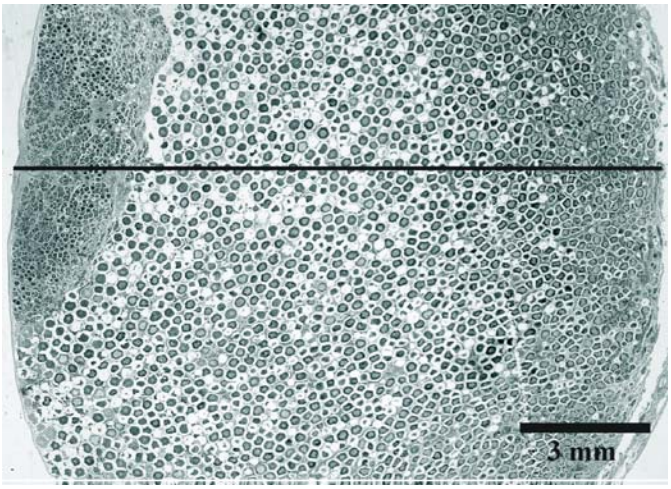


Figure 7.06 Cross section of a *M. canis* testis, stained with hematoxylin and eosin.

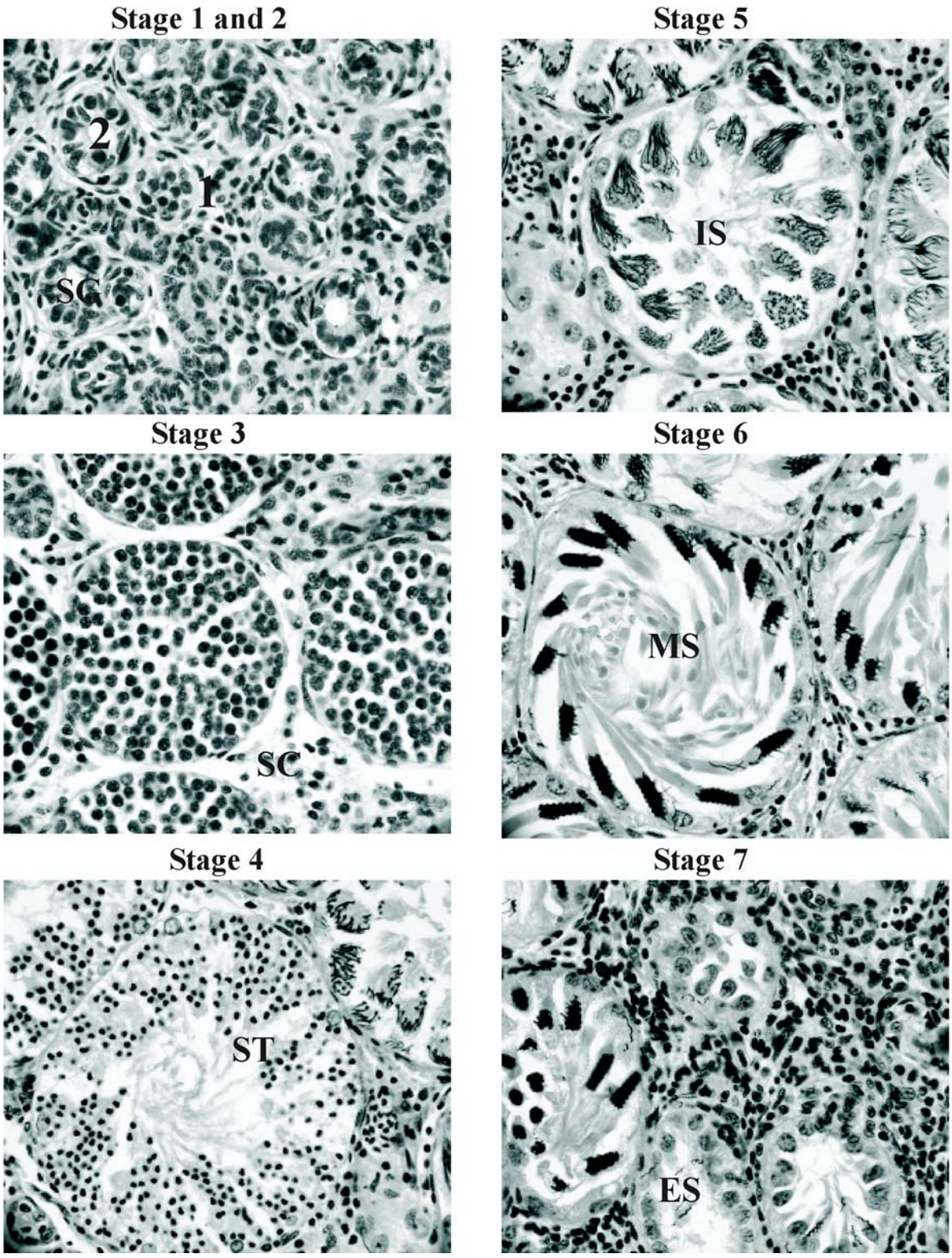


Figure 7.07 Sperm stages of the testis: Stages 1 – 7, SG = spermatogonia, SC = spermatocytes, ST = spermatids, IS = immature sperm, MS = mature spermatozoa, ES = empty spermatocyst, SG = spermatogonia.

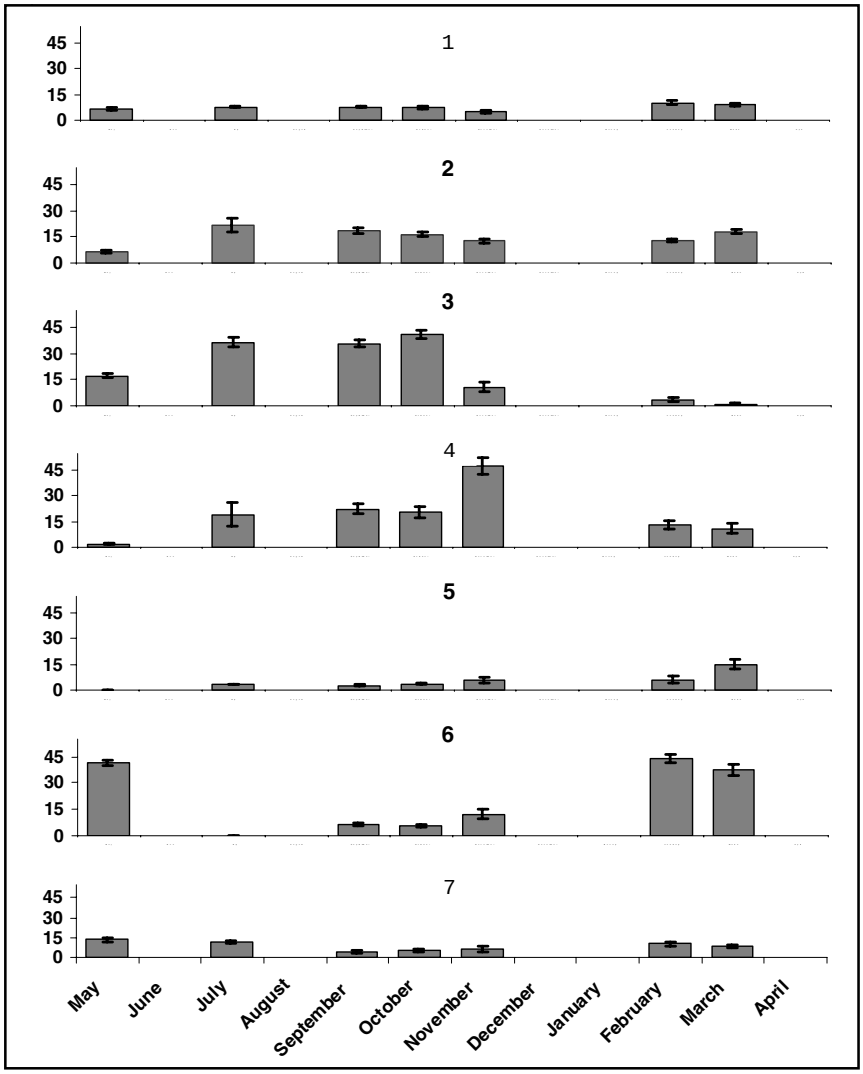


Figure 7.08 The mean proportion of the testis occupied by each stage for May through April (N=62, error bars are standard error).

7.4.3 Female reproductive cycle

In female elasmobranchs the timing of reproductive events is usually determined by direct observation of the reproductive tract, by tracking the size of ovarian eggs throughout the year (ovulation cycle), and by tracking the size of pups within the uterus throughout the year (gestation cycle). A comparison of the timing of the ovulation and gestation cycles can help determine the reproductive resting interval.

7.4.3.1 Ovulation cycle

The ovulation cycle is determined by measuring the largest developing ova in the ovary and comparing their size throughout the year. Usually anywhere from two to five of the largest ova in the ovary are isolated and their diameter is measured using calipers. Then a mean maximum ova diameter (MOD) is calculated and compared for various animals captured throughout the year. Capape et al. (1990) studied two angel shark species and plotted the diameter of oocytes and uterine ova against time to determine the timing of reproductive events. For dusky smooth-hounds the maximum ova diameter was measured and the mean MOD was calculated for each month of sampling. Ova sizes increased until May and then became much smaller by July, indicating ovulation occurs between May and July (Conrath and Musick, 2002) (Figure 7.09a).

7.4.3.2 Gestation cycle and time of birth

For viviparous species the timing and length of gestation is usually determined by following through time the size of eggs and embryos found within the uterus. The length and timing of gestation

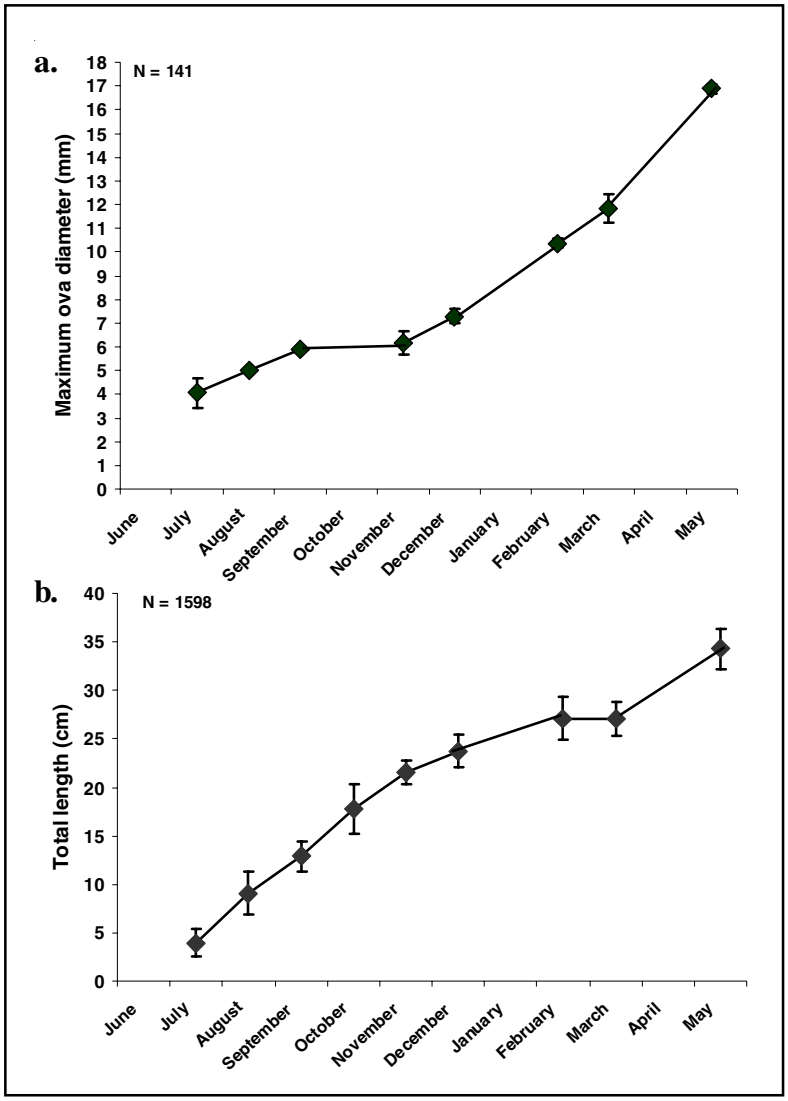


Figure 7.09 a - Mean maximum ova diameter (MOD), June through May, b - mean *M. canis* pup length for May through April (error bars are standard deviation).

has been determined by comparing the length and weight of uterine eggs and embryos throughout the year for Atlantic sharpnose sharks, *Rhizoprionodon terraenovae* and dusky smooth-hounds, *Mustelus canis* (Parsons, 1981; Conrath and Musick, 2002) (Figure 7.09b). This can also be used to determine the size of embryos at birth and the timing of birth. If each period of the year is adequately sampled, the largest size embryos will give a minimum size estimate for size at birth, and the time between the capture of females with the largest uterine embryos and of females with the smallest uterine eggs can give some indication of when parturition is occurring. This approach will give a minimum estimate of size at birth and may underestimate the size at birth and not accurately reflect the timing of mating if all time periods are not sampled adequately. A more accurate way to determine the size at birth and timing of birth is to compare the size of the largest embryos found within the uterus with the size of the smallest free living animals captured throughout the year. This approach has been taken for determining the size at birth of blue sharks*, Prionace glauca,* and of spotted estuary smooth-hounds, *Mustelus lenticulatus* (Pratt, 1979; Francis and Mace, 1980). Females containing the largest embryos should be captured just prior to and possibly during the period of time when the smallest free living animals are captured depending on the length of the parturition period. In studies of the common guitarfish, *Rhinobatos rhinobatos*, and the finetooth shark, *Carcharhinus isodon*, the timing of parturition has been estimated or verified by comparing the time between the capture of females with the largest embryos and the capture of the smallest free living specimens (Abdel-Aziz et al., 1993; Castro, 1993).

7.4.3.3 Reproductive interval

Another factor of interest in studying elasmobranch ecology is determining the length of the reproductive cycle. In addition to having varying lengths of gestation, many species of elasmobranchs have a resting period between pregnancies, which may last up to two years. For species with a well-defined reproductive cycle, the proportion of pregnant females at any given time can be used for a preliminary indication of whether or not the female undergoes a resting phase between pregnancies. If all or nearly all the mature females are pregnant, this may indicate that there is no resting phase. Jensen et al. (2002) proposed that the porbeagle, *Lamna nasus*, has a yearly reproductive cycle based on the fact that all females that were sampled in the month of December were gravid. However, this approach must be used with caution as pregnant females may have a different migratory pattern than nonpregnant females. This appears to be the case with sand tiger sharks, *Carcharias taurus*, sampled by Lucifora et al. (2002), who found that pregnant females occur in Brazilian waters and nonpregnant females occur in Argentinean waters. They propose a one-year resting phase for this population with pregnant and nonpregnant mature females having different migrations.

A more accurate assessment for viviparous species, excluding perhaps oophagous species, can be made by comparing the development of ova and of embryos in the uterus in each individual. A resting cycle is usually apparent by determining if the ovulation and gestation cycles are concurrent or if they are sequential. In the dusky smooth-hound the ovulation and gestation cycles are concurrent; ova are developing at the same time that pups within the uterus are developing, with both maximum ova diameter and pup length reaching a maximum value during the month of May (Conrath and Musick, 2002) (Figure 7.09a and 7.09b). Dusky smooth-hounds likely have a very short "resting period" of days to possibly as much as one month. Simpfendorfer and Unsworth (1998) found that the whiskery shark, *Furgaleus macki*, has a biennial cycle with a one year resting phase by noting the presence of two groups of mature females, one pregnant with undeveloped ova in the ovary and one not pregnant with developed ova in the ovary. They did propose the possibility that larger female whiskery sharks are able to produce a litter of pups yearly with no resting phase.

7.4.3.4 Reproductive cycle examples and embryonic diapause

A wide variety of reproductive strategies are employed by elasmobranch species in regards to the timing of the reproductive cycle; several examples are given here to emphasize the diversity of these strategies. In some populations of elasmobranchs more than one reproductive cycle per year is postulated. Two of the *Dasyatis* rays, *D. centroura* and *D. marmorata*, have very short gestation times of only three to four months and are therefore thought to possibly have two or three gestation cycles per year (Capape, 1993; Capape and Zaouali, 1995). The Eastern Australian shovelnose ray, *Aptychotrema rostrata*, also has a short gestation of three to five months but gestation and vitellogenesis do not proceed at the same time and the gestation period is followed by a resting phase. This

species only produces one litter of pups per year (Kyne and Bennett, 2002). The smalleye hammerhead, *Sphyrna tudes*, has a gestation of approximately 10 months, and as the ovarian and gestation cycles run concurrently is postulated to have a yearly reproductive cycle (Castro, 1989). The piked dogfish, *Squalus acanthias*, has the longest gestation period known in any fish (23 months) but ovulation and gestation cycles run concurrently so female piked dogfish reproduce every two years (Jones and Geen, 1977). The blacktip shark, *Carcharhinus limbatus*, also has a two-year reproductive cycle, but gestation only lasts 12 months, after which these sharks undergo a resting period before vitellogenesis and oogenesis are resumed (Castro, 1996). The tope shark, *Galeorhinus galeus,* has a three-year reproductive cycle with females found in one of three reproductive conditions: either a) gravid, b) first year nongravid with small ovarian follicles, appearing to be in a resting stage with slow vitellogensis, or c) second year nongravid with larger ovarian follicles. Gestation for this species lasts 12 months, with a one-year resting phase, followed by a year of vitellogenesis constituting a three-year reproductive cycle (Peres and Vooren, 1991).

Diapause for the purposes of this manual will be defined as a pause in the development of fertilized eggs or young embryos within the uterus during development. This phenomenon has been documented in at least three species of elasmobranchs. Simpfendorfer (1992) found that the Australian sharpnose shark, *Rhizoprionodon taylori*, has embryos that undergo an approximately seven month diapause. He proposes that this diapause may have been part of the evolution of smaller embryo size and larger litter size within this population. He also proposes the reason for this diapause may be so that embryos are born when water temperatures are maximized and conditions for juvenile growth are optimal. Fertilized uterine eggs of the masked stingaree, *Trygonoptera personata*, undergo a five-month period of embryonic diapause (White et al., 2002). The authors suggest embryonic growth for this species is delayed until water temperatures are at their highest. The bluntnose stingray, *Dasyatis say*, ovulates in May or June but uterine embryos do not begin to develop until the following April (Snelson et al., 1989).

7.5 FECUNDITY

The fecundity of elasmobranch species is often determined by simply counting the number of eggs and embryos within the uterus of viviparous species. Two potential difficulties arise using this method of determining fecundity. First, in some species reproductive failure occurs during gestation, and the number of pups actually surviving to gestation may be considerably smaller than the initial number of ovulated eggs present in the uterus. This occurs in the stingaree species, *Urolophus lobatus*. White et al. (2001) determined the mean number of embryos decreased to less than half of original values throughout the yearly reproductive cycle and attributed this change to embryos being aborted during pregnancy. Therefore it may be preferable to count the number of later term embryos as this may more accurately reflect the number of pups that will survive to gestation. A second poten-

tial difficulty with simply counting uterine eggs or embryos is that many elasmobranchs will abort some of these during the stress of capture, especially if embryos are close to parturition size. For viviparous species placental scars can be counted in the uterus to determine if embryos were aborted or to determine fecundity of animals that are recently postpartum. Therefore counts of embryos in the uterus may be negatively biased and this should be taken into consideration. In situations where the probability of embryos being aborted is unknown and cannot be corrected for by counting placental scars, estimates of fecundity using this method should be considered the lower limit of fecundity.

Fecundity can also be estimated by counting the number of developing ova in the ovary when uterine counts of eggs and embryos are not possible, but this is a less reliable method. Wetherbee (1996) estimated the fecundity of the southern lanternshark, *Etmopterus granulosus*, by counting the number of large ova in mature females. In some species uterine and ovarian fecundity have been found to be very similar. Little differentiation between ovarian and uterine fecundity has been shown for populations of the shortspine spurdog, *Squalus mitsukurii*, two angel shark species, *Squatina squatina* and *S. oculata*, and the tope shark, *Galeorhinus galeus* (Capape et al., 1990; Peres and Vooren, 1991; Wilson and Seki, 1994). However, in other species ovarian fecundity is notably higher than uterine fecundity indicating that some of the developing ovarian eggs will be reabsorbed. A significant difference in ovarian and uterine fecundity has been noted for populations of the finetooth shark, *Carcharinus isodon*, and the common guitarfish, *Rhinobatos rhinobatos* (Abdel-Aziz, 1993; Castro, 1993). While counting developing ovarian eggs will likely give a good estimate of fecundity, in many species not all ovarian eggs are ovulated, and (if possible) using uterine counts of eggs and embryos will be a more accurate indicator of fecundity. However, it is important to note that using ovarian eggs to estimate fecundity will likely lead to an overestimate of fecundity, and using uterine eggs or embryos to estimate fecundity may lead to an underestimate of fecundity.

Determining fecundity for oviparous species is more difficult. Fecundity as previously mentioned can be estimated by counting the number of developing eggs in the ovary, but many oviparous species have a very extended breeding season with eggs continuing to develop throughout the year, and this approach may lead to an underestimation of eggs produced. One method of estimating fecundity for oviparous species is to determine the ovulation rate and the duration of the egg laying period and to use these values to calculate the number of eggs laid by the female during the period. Sumpter and Dodd (1979) studying the small-spotted catshark, *Scyliorhinus canicula,* determined an extended breeding season with a peak in egg laying occurring in winter and spring but did not calculate an ovulation rate. Many estimates of fecundity and egg-laying frequency are determined by keeping animals in captivity. Chain catsharks, *Scyliorhinus retifer*, small-spotted catsharks, and thornback rays, *Raja clavata*, have all been kept in captivity to determine ovulation rates and egg-laying periods.

Estimated annual fecundities for these species range between 20 to 140 eggs per year with egg laying rates (of egg pairs) varying from every 2 days for the thornback ray to every 15.3 days for the small-spotted catshark (Holden, 1975; Mellinger, 1983; Castro et al., 1988; Ellis and Shackley, 1995).

In many species of elasmobranchs there is a positive relationship between fecundity and the size of the female. Presumably, as a female becomes larger this increase in total length and girth results in a larger space in the body cavity to accommodate pups. A positive linear relationship is reported in many species of sharks including populations of scalloped hammerheads, *Sphyrna lewini*, piked dogfish, *Squalus acanthias*, and tope sharks, *Galeorhinus galeus* (Chen et al., 1988; Hanchet, 1988; Peres and Vooren, 1991). The relationships of fecundity and length of a species tend to have low r^2 values and generally, while length is often related to fecundity, it tends to be a poor predictor of fecundity. Negative bias in fecundity estimates based on uterine counts as previously discussed, may obscure correlations between length and fecundity. Fecundity has a significant positive relationship with both age and length in the dusky smooth-hound, *Mustelus canis* (Figures 7.10a and 7.10b) (authors in this study were careful to confirm fecundity estimates in questionable cases by counting placental scars). Fecundity is more closely related to length than to age likely due to the variability in ages of larger animals. Both relationships have a low r^2 value indicating the data do not fit the relationship closely and that neither age nor length are very accurate predictors of fecundity for this species (Conrath and Musick, 2002).

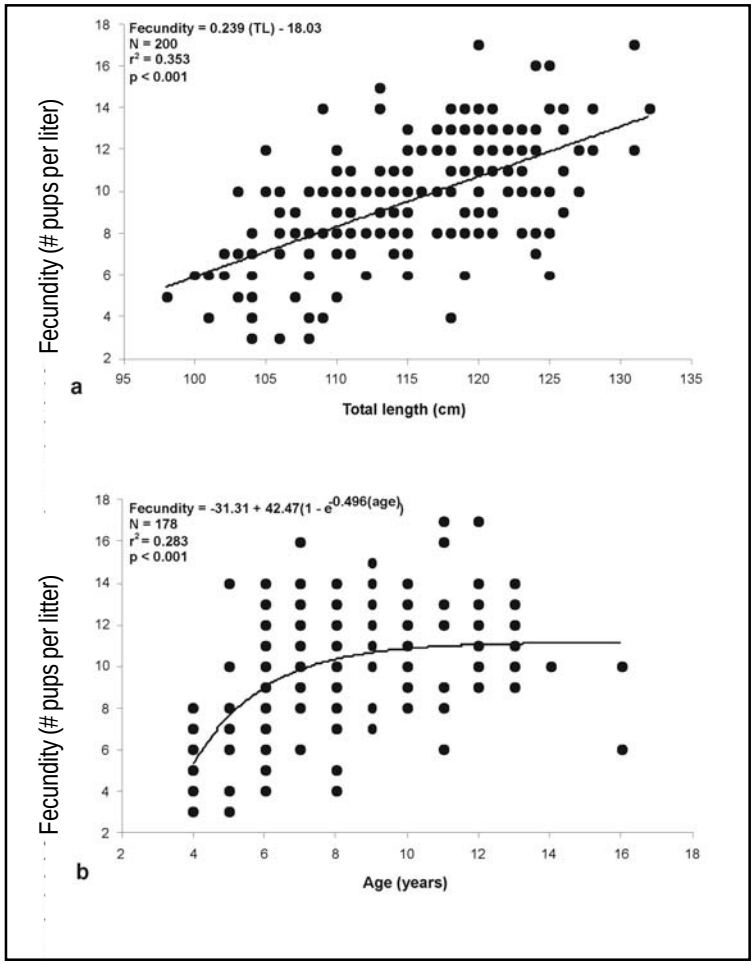


Figure 7.10 a - The relationship between fecundity (number of pups per litter) and total length (TL), b - the relationship between fecundity (number of pups per litter) and age for female *M. canis*.

7.6 SPERM STORAGE IN FEMALE ELASMOBRANCHS AND OVIDUCAL GLAND STRUCTURE

Sperm storage was first proposed to occur when aquarium female specimens of skates of the genus *Raja* continued to lay fertilized eggs after periods of

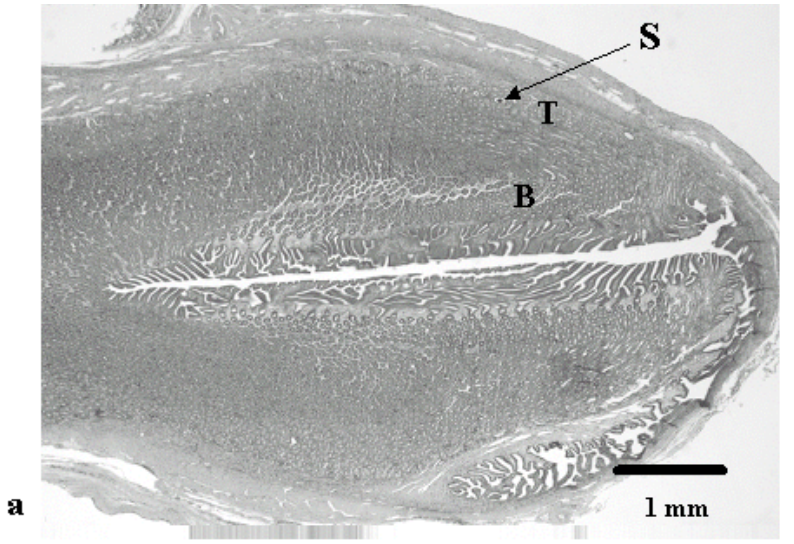
separation from male specimens (Clark, 1922). The storage of sperm in the oviducal gland of the female has been shown by Pratt (1993) to occur in at least nine species of sharks in the western North Atlantic. He proposes three types of fertilization occurring in elasmobranchs: no storage or fertilization occurs immediately following mating, short-term storage in species in which ovulation is prolonged over long periods, and long-term storage for repeated fertilization.

Sperm storage is assumed to occur in species where there is a time lag between mating and ovulation and has been proposed for several species of elasmobranchs. Peres and Vooren (1991) found up to five months passes between mating and ovulation in the tope shark, *Galeorhinus galeus*. Simpfendorfer and Unsworth (1998) propose a six month period of sperm storage for the whiskery shark, *Furgaleus macki*. White et al. (2001) also propose a three month period of sperm storage in the lobed stingaree, *Urolophus lobatus*.

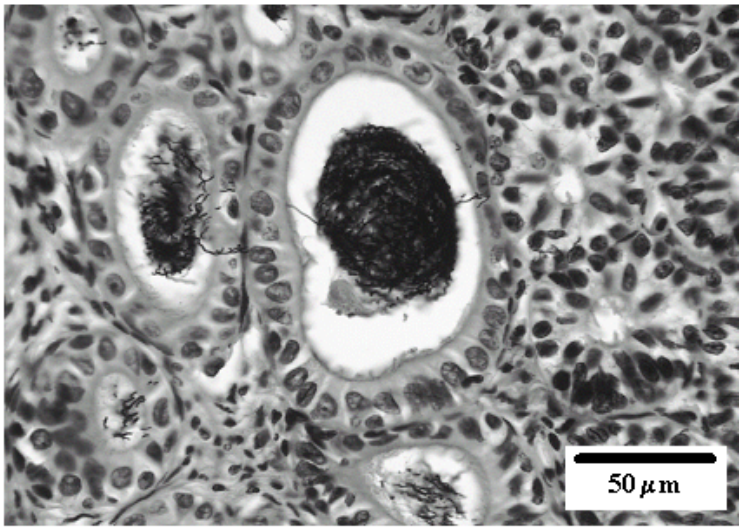
Sperm storage can be examined by sectioning the oviducal gland and examining it using histological techniques. Hamlett et al. (1998) describe four fundamental zones of the elasmobranch oviducal gland based on the morphology of the epithelium: the proximal club zone, the papillary zone, the baffle zone, and the terminal zone. The jelly coats that surround the egg are produced within the proximal club and papillary zones and various types of egg investments are produced within the baffle zone (Hamlett and Koob, 1999). To determine if sperm is present in the oviducal gland, the posterior third of the preserved oviducal gland is sectioned and stained using standard histological techniques, or a sperm smear is taken from this area of the oviducal gland and stained. Pratt (1993) found that most spermatozoa are usually located in the thin walled tubules of the lower oviducal gland. These were subsequently identified by Hamlett et al. (1998) as terminal zone tubules. Hamlett et al. (2002) noted the presence of bundled sperm throughout gestation in the terminal zone of the oviducal gland of the dusky smooth-hound, *Mustelus canis*. Conrath and Musick (2002) also examined the oviducal glands of dusky smooth-hounds by taking samples of the posterior third of the oviducal gland then embedding them in paraffin, sectioning them, and staining them with hematoxylin and eosin. The sections were then viewed with a compound microscope to determine if sperm was present in the oviducal gland. Oviducal glands contained sperm stored throughout the year with every oviducal gland examined containing some sperm. Figure 7.11 shows an oviducal gland section and a typical sperm bundle found within the terminal zone of the oviducal gland.

7.7 ADDITIONAL RESOURCES

One objective of this technical manual was to cite to the greatest degree possible web-based resources to make it easy to obtain literature on the subjects covered by the text. Unfortunately good detailed information about elasmobranch biology on the web seems to be quite sparse and difficult to find. However, there is an abundance of excellent literature about elasmobranch reproductive biology



a



b

Figure 7.11 a - Cross section of the posterior third of a *M. canis* oviducal gland (S = sperm bundle, T = terminal zone, B = baffle zone), b - sperm bundles found within the terminal zone of the oviducal gland.

in the primary literature. I have therefore included a brief section on the primary literature I have found most useful in learning about elasmobranch reproductive biology. As the literature about elasmobranch reproductive biology is quite large, it is undoubtedly incomplete and lacking literature others would name most useful. The few good web resources I located are discussed in the second section. The last section of the chapter includes some guidelines to assist in field data collection.

7.7.1 Literature

Wourms (1977) and Compagno (1990) both provide introductions to elasmobranch reproductive biology with good descriptions of the reproductive modes of elasmobranchs and the various groups that have these modes. Descriptive information on general anatomy can be found in Hamlett (1999) and Hamlett and Koob (1999). Clasper structure in particular is described in Gilbert and Heath's (1972) work on siphon sac and clasper function of piked dogfish and dusky smooth-hounds. Information on defining maturity, reproductive cycles and fecundity are probably best obtained from specific species accounts. Of the many species accounts some of the early ones include descriptions of the reproductive tract such as Pratt's (1979) blue shark paper, Parsons' (1981) Atlantic sharpnose paper, and Teshima's (1981) *Mustelus* paper. Specific information about staging the testes can be found in either Parsons and Grier (1992) or Maruska et al. (1996). Sperm storage and oviducal gland structure are discussed in Pratt (1993) and Hamlett (1999).

7.7.2 Web-based resources

Information from the web was current as of February 14, 2003. A general description of reproductive techniques can be found at the FAO website in the Manual of Fisheries Science (Holden and Raitt 1974), http://www.fao. org/DOCREP/003/F0752E/F0752E00.htm. The Florida Museum of Natural History (http://www.flmnh.ufl. edu/) has much information about elasmobranchs on their website and a link to the IUCN Shark Specialist Group (SSG) can be found here. The SSG publishes an annual newsletter, Shark News, which can be viewed at http://www.flmnh. ufl.edu/fish/organizations/ssg/ssgdefault.html. Hamlett (1997) has a good review of elasmobranch reproductive modes published in Shark News 9 (http://www.flmnh.ufl.edu/fish/organizations/ssg/ 9Newsletter/ shark9news1.htm). Henry Mollet has a web page with some information about various species and a section on oviparous sharks, http://homepage.mac.com/mollet/. Peter Bor also has a website with photographs of various egg laying elasmobranchs as well as some good introductory material on oviparous species, http://www.rajidae. tmfweb.nl/.

7.7.3 Field data collection

This section is provided for the purpose of giving some guidance with what data should be collected in the field in order to accomplish the methods discussed above. A sample data sheet (Figure 7.12) is provided. In addition to standard length and weight measurements, external measurements for males should include clasper length measurements and a note on the extent of clasper calcification. Internal measurement data should include a note about whether reproductive tracts were dissected in the field or preserved for later examination; gonad weight and gonad size (testis weight, maximum ova diameter, uterus width, etc.); presence or absence of sperm in the seminal vesicle of males; and for females the presence or absence of mating wounds, the number of developing ova in the ovary, general observations about maturity (ova size, uterine width, pregnancy, etc.), and uterine content information (number of eggs or embryos, egg and embryo width, sex and lengths of embryos, etc.). This field sheet is meant to be a general guide; each study should have previously defined its objectives and tailored a data sheet to meet those requirements.

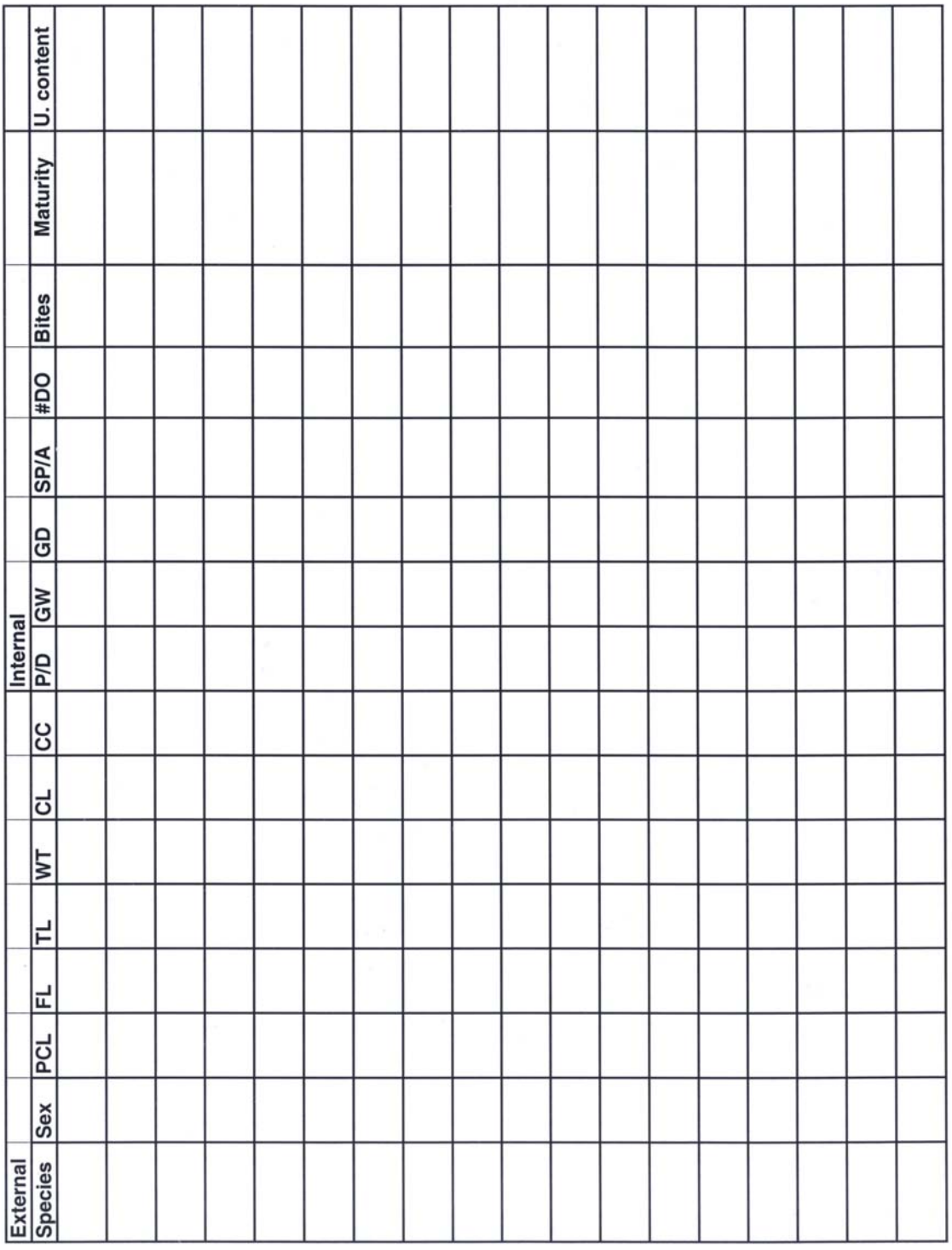


Figure 7.12 Field data collection sheet (PCL = pre caudal length, FL = fork length, TL = total length, CL = clasper length, CC = notes on clasper calcification, P/D = preserved or dissected, GW = gonad weight, GD = gonad size, SP/A = sperm present or absent in the seminal vesicle, #DO = number of developing ova, Bites = presence/absence of mating wounds, U. content = uterine contents).

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CHAPTER 8. MORTALITY ESTIMATION

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8.1 INTRODUCTION

Mortality is a key parameter in understanding the dynamics of any population, and sharks are no exception. Without knowledge of how fast individuals are removed from a population it is impossible to model the population dynamics or estimate sustainable rates of exploitation or other useful management parameters. Two separate types of mortality occur in shark (or fish for that matter) populations: firstly, natural mortality (commonly referred to by the letter *M*), which is the loss to the population from natural sources such as predation, disease and old age: and secondly, fishing morality (referred to by the letter *F*) which, as the name suggests, is the loss to the population from fishing. Together, fishing and natural mortality combine to give total mortality (referred to by the letter *Z*). Values of mortality rates are additive, such that:

$$Z = M + F \tag{8.1}$$

Mortality values are typically expressed as rates that are either instantaneous or finite. Instantaneous (distinguished here by an upper case letter) and finite rates (lower case letter) are related exponentially. For example:

$$f = e^{F} \tag{8.2}$$

Thus, in one year with a finite fishing mortality rate of 0.4, 40% of the population would be removed by fishing. However, it is more convenient to work with instantaneous rates in most situations, and the value of instantaneous fishing mortality that would give a 40% removal if applied over a full year is 0.5 ($e^{0.5}$). Ricker (1975) provides a detailed explanation of instantaneous rates and their use in fisheries.

The simple mathematical expressions above mask some of the more complex issues in relation to mortality rates. For example, it is intuitive that mortality rates are not constant throughout a shark's life. While sharks are young their small size makes them more susceptible to predation from larger sharks, and again as sharks reach their maximum age, they are more likely to die of old age. As a result some researchers have suggested that sharks have a U-shaped natural mortality curve. Similarly, fishing mortality can vary with age due to the size selectivity of fishing gear or differences in the spatial distribution of fish of different ages. These complexities should be kept in mind in relation to the techniques described in this chapter.

Despite the importance of quantifying mortality to understanding the dynamics of shark populations, there have been limited amounts of research directed at this topic. The main reason for this is that accurately quantifying mortality rates is a difficult task, and one that typically requires substantial amounts of data. Since population assessment is such an important part of managing fished or endangered populations, indirect methods of estimating mortality have been developed and are commonly used in the population assessment of sharks and other aquatic organisms. These indirect techniques utilize relationships between life history parameters and mortality (typically natural mortality) from species where research

has been undertaken. Typically the relationships utilized for sharks are based on teleost fishes, although some use data from broader taxonomic groups.

This chapter describes methods for estimating mortality rates in shark populations, starting with the simple indirect methods and then moving on to the more complex and data intensive direct methods. We have attempted to use examples from the shark literature throughout. We also attempt to point out the strengths and weaknesses of each of the methods, and as a conclusion try to provide some guidance on which techniques to use in different situations. The fisheries literature relevant to both direct and indirect methods of estimating natural mortality was reviewed by Vetter (1988), and this reference is a valuable source of information on this topic.

8.2 INDIRECT METHODS

Indirect methods have typically been developed to estimate natural mortality, but in some cases estimates of total mortality can be made. In cases where a method estimates total mortality (e.g., methods of Hoenig and Brander, see below) the total mortality value can be assumed to be equal to natural mortality when the population is unfished (i.e., $F = 0$). If the population is fished, then the value of fishing mortality must be known to determine natural mortality. The majority of these indirect methods assumes that mortality is independent of age, but two methods that give age-dependent values are also described.

8.2.1 Age-independent methods

8.2.1.1 Pauly, 1980

A commonly used indirect method of estimating natural mortality was described by Pauly (1980). He related natural mortality to von Bertalanffy growth parameters (L_∞ or W_∞, and K) and mean environmental temperature (T, in degrees Celsius). This method assumes that there is a relationship between size (measured in either length or weight) and natural mortality. This relationship is quite weak on its own, but the inclusion of mean environmental temperature increases the fit as an animal living in warmer water will have higher mortality rates than an equivalent animal living in cooler water (Pauly, 1980). The relationships developed were based on natural mortality and ambient temperature data for 175 fish stocks, only two of which were sharks (*Cetorhinus maximus* and *Lamna nasus*). The relationship based on length was:

$$\log M = -0.0066 - 0.279 \log L_\infty + 0.6543 \log K + 0.4634 \log T \qquad (8.3)$$

and based on weight was:

$$\log M = -0.2107 - 0.0824 \log L_\infty + 0.6757 \log K + 0.4627 \log T \qquad (8.4)$$

Estimation of natural mortality using these equations is straightforward as long as von Bertalanffy parameter values are available. Jensen (1996) reanalyzed the data of Pauly and used this to produce a simpler relationship (see below).

8.2.1.2 Gunderson, 1980 and Gunderson and Dygert, 1988

Gunderson (1980) used r-K selection theory to develop a relationship between female gonadosomatic index (*GSI*) and natural mortality. This relationship assumes that there is a strong correlation between the amount of energy that a female invests in reproduction and natural mortality. Gunderson's original relationship was:

$$M = 4.64GSI - 0.370 \quad (8.5)$$

This relationship was based on 10 North Sea teleost species, and uses maximum female *GSI*. The calculation of *GSI* is covered in Chapter 7 of this manual.

This relationship was refined by Gunderson and Dygert (1988) who increased the size of the data set on which the relationship was based to 20 species, including one shark (*Squalus acanthias*). The new relationship was:

$$M = 0.03 + 1.68GSI \quad (8.6)$$

Simpfendorfer (1999a) used these two methods in a study of the Australian sharpnose shark, *Rhizoprionodon taylori*. He found that the method of Gunderson (1980) was a poor predictor of natural mortality, but that the method of Gunderson and Dygert (1988) was one of only two methods that produced reasonable values. Simpfendorfer (1999a), however, pointed out that the results from this method may be biased since it is assumed that *GSI* is a proxy for reproductive investment. Since many sharks are viviparous (such as *R. taylori*), not all of the reproductive investment is included in the full size ovarian eggs. Instead, much of the reproductive investment is made later via the placental (or analogous tissues) connection. Thus, it is more likely that this method will work better with oviparous and ovoviviparous shark species.

8.2.1.3 Hoenig, 1983

The most widely used indirect method of estimating mortality in shark species is that of Hoenig (1983) (see Chapter 9). This method uses maximum observed age to predict total mortality, since longer lived species will die at a slower rate than short-lived species. Hoenig (1983) developed three relationships that may be of use to shark researchers (a fourth relationship was developed for mollusks). The most commonly used relationship was for 84 stocks of teleost fishes:

$$\ln Z = 1.46 - 1.01 \ln t_{max} \quad (8.7)$$

Hoenig (1983) also developed a relationship for 22 cetacean stocks:

$$\ln Z = 0.941 - 0.873 \ln t_{max} \quad (8.8)$$

While this relationship is less useful, it may have some applicability since like cetaceans sharks are long-lived, slow-growing and have few young. However, cetaceans are also homeothermic, which may bias the results if applied to sharks.

The third relationship developed by Hoenig (1983) was a combination of all of the mollusk, teleost and cetacean data:

$$\ln Z = 1.44 - 0.982 \ln t_{max} \quad (8.9)$$

The values estimated by the relationships of Hoenig (1983) all predict total mortality. As such they can only be used to predict natural mortality when . Hoenig (1983) also noted that it is possible to use a geometric mean regression in developing the predictive relationships, and provided the values for these parameters. However, it has been standard practice for work with sharks to use the simple teleost relationship.

8.2.1.4 Jensen, 1996

Jensen (1996) used the Beverton and Holt life history invariants (Charnov, 1993) as a starting point in determining the relationships between life history parameters and natural mortality. Using optimal trade-offs between reproduction and survival he showed that:

$$M = 1.65 / x_m \quad (8.10)$$

where x_m is the age at maturity. Similarly, he showed that there was also a simple theoretical relationship between the von Bertalanffy K value and natural mortality:

$$M = 1.5K \quad (8.11)$$

This relationship is much simpler than that provided by Pauly (1980, see above). Jensen re-analyzed Pauly's data and demonstrated that the simple relationship:

$$M = 1.60K \quad (8.12)$$

gives an equivalent fit to the data as the more complex Pauly equation. This simple relationship is very close to the theoretical value (1.5K), suggesting that these relationships may provide a relatively sound method of estimating natural mortality.

8.2.1.5 Brander's equilibrium mortality estimation

Rather than a method to obtain estimates of total, fishing or natural mortality, Brander's (1981) method is an easy way to estimate *threshold* levels of total mortality beyond which stocks will collapse for organisms like sharks and rays in which the actual number of young produced per year is known. Brander (1981) proposed a very simple and intuitive relationship to estimate if the total mortality rates of the juvenile and adult portions of a population are beyond a threshold that would lead to stock collapse. His method relies on previous biological information and some assumptions as detailed below, and is a simple and useful way to perform a quick assessment of the status of exploitation of a stock. This method can be used not only to rapidly estimate if the fishing rate is too high, but also to rank species along a continuum of resilience to exploitation depending on their life-history traits, along similar lines to the demographic methods developed by Au and Smith (1997; see Chapter 9). In addition, and borrowing the conventions of

demographic analysis, Brander's method considers only the female part of the population for purpose of simplicity.

The method calls for three types of information:

- The age of first sexual maturity of the stock. This is usually taken as the age at which 50% of the population is sexually mature. (See section 7.3.3)
- The rate of reproduction (how many offspring are produced per year; in the case of elasmobranchs this would be the number of eggs laid per year for species such as the skates (Rajidae) and sharks of the Heterodontidae and Scyliorhinidae, or the number of pups per year for live-bearing sharks and rays).
- An estimate of the instantaneous total mortality rate of the immature part of the stock.

This method relies on two assumptions:

- First, that the rate of reproduction is constant and not related to the age or size of individuals. Although in many species there is a known relationship between maternal size and fecundity, sometimes this is not the case. In other circumstances, an average number of eggs laid or pups produced can be used as an approximation, or the limits of the range can be used to place bounds on the uncertainty.
- Second, the mortality rate of the immature stock from birth to sexual maturity is considered to be constant. Although this is a stronger assumption as newborn survival is often much lower than for subsequent ages (Manire and Gruber 1993; Heupel and Simpfendorfer, 2002), an estimate of mortality that is representative of the immature part of the stock can be used as this is an approximate method.

Brander's method is based on the fact that for a population to remain at a constant level instead of decreasing or increasing in size (this is usually referred to as being in *equilibrium*), the total rate of mortality of adults or mature fish (Z_m) should equal the net rate of recruitment of mature fish to the stock (R_m):

$$Z_m = R_m \tag{8.13}$$

In turn, the recruitment to the mature stock is equal to the number of eggs developing into females or the number of female pups born (remember that to simplify only females are considered; usually it is assumed that half of the total eggs laid or embryos *in-utero* will develop into females, but it is always advisable to check if this applies to the species being analyzed) multiplied by the survival from birth to maturity:

$$R_m = (E/2)e^{-Z_i t_m} \tag{8.14}$$

where E denotes the rate of reproduction (in number of eggs or embryos produced per year), Z_i is the total mortality of the immature part of the stock (as mentioned above, we generally assume that Z_i is constant throughout immature ages) and t_m is the number of years from birth to sexual maturity. Thus, for the population to remain in equilibrium:

$$Z_m = (E/2)e^{-Z_i t_m} \qquad (8.15)$$

This is Brander's equation, and by substituting the values of the age at maturity, the rate of reproduction, and the total mortality of immature fish for the species being analyzed, we obtain the corresponding equilibrium total mortality rate of the adult stock. This is an important reference point for management that indicates the maximum level of total mortality that the adult stock can withstand before the populations starts to decline.

An additional application of this method involves repeating the above calculations using different values of Z_i to calculate equilibrium curves like those seen in Figure 8.01. In this figure, the mortality thresholds (equilibrium instantaneous total mortality rates of mature and immature fish) of two hypothetical species are plotted. Both species have a t_m of 11 years but different rates of reproduction (20 and 40 offspring per year). Mortality values to the right and above of each curve will eventually drive the population to collapse. Thus, if we can independently determine the actual values of total mortality for the immature and mature parts of the stock in question (Z_i and Z_m), and if the values are to the right of the corresponding curve, management should attempt to reduce total mortality towards an equilibrium level. Catch curves (see section 8.3.1) can be used to estimate the level of total mortality for each part of the stock, but if catch curves can be calculated, then it is usually possible to do a more thorough stock assessment as shown in Chapter 10.

While the two curves in Figure 8.01 illustrate how species with higher fecundity can withstand a slightly higher level of total mortality, they also show that doubling the fecundity has a relatively small effect on the equilibrium mortality. The net rate of recruitment is the most important factor and this depends directly on the cumulative mortality of the immature part of the stock until it reaches maturity.

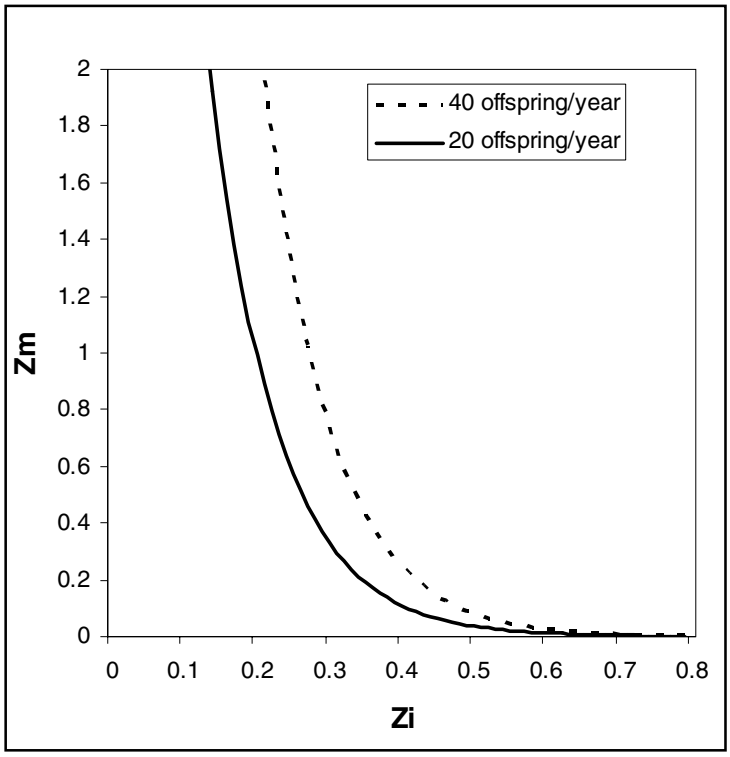

Figure 8.01 Equilibrium mortality curves for two theoretical shark populations as a function of total mortality of the mature (Z_m) and immature (Z_i) portions of the stock. In both cases the age of first sexual maturity is 11 years. Reproductive rate is 40 or 20 offspring per year depending on the case.

Brander's method is an easy and simple way to estimate the maximum total mortality of the mature stock that would guarantee the stability of the population based on age of maturity, rate of reproduction and total mortality of the immature stock. The method was used by Brander to explain why common rays *Dipturus batis* (= *Raja batis*) were virtually extirpated in the Irish Sea and to compare the "resilience" to exploitation of other ray species. For this, he plotted the highest total mortality that could be sustained by the five species he was analyzing as a function of fecundity and age of maturity while assuming that $Z_m=Z_i$. The results showed that the least fecund species could withstand the highest mortality because it had a high net survival to maturity. Brander's method is very useful for deriving reference points and making comparative analyses; however, it has never been adopted for the management of a real elasmobranch fishery.

The main limitations of Brander's approach are: a) it does not provide direct management advice in the form of an appropriate catch or effort level, b) it is not a dynamic model (considering changes in time), but offers only a static view, thus processes like density-dependent compensation cannot be taken into account. Density-dependent compensation is a change in any fundamental process of the population that is directly related to the abundance level of the stock. In reality, most biological processes are density-dependent, especially mortality and recruitment (which is a consequence of pre-recruit mortality), but other processes like body growth, population growth and fecundity are often density-dependent too.

8.2.2 Age-dependent methods

8.2.2.1 Peterson and Wroblewski, 1984

To provide an estimate of natural mortality that varied with age, Peterson and Wroblewski (1984) used dry weight as a scaling factor. Using particle-size theory and data from the pelagic ecosystem (including fish larvae, adult fish and chaetognaths) they showed that the natural mortality for a given weight organism (M_w) is:

$$M_w = 1.92w^{-0.25} \qquad (8.16)$$

where w is the dry weight of an organism. To make this estimate of natural mortality age-specific, weight-at-age data is required. This is normally obtained from a length-weight relationship and length-at-age data from a von Bertalanffy growth function. Such an approach yields wet weight, and Cortés (2002) suggested that a conversion factor of one fifth be used for sharks to give dry weight. One criticism of this method has been that it was developed for smaller pelagic organisms. However, McGurck (1986) showed that it accurately predicted natural mortality rates over 16 orders of magnitude.

8.2.2.2 Chen and Watanabe, 1989

Chen and Watanabe (1989) recognized that natural mortality in fish populations, like most animal populations, should have a U-shaped curve when plotted against age (they referred to it as a bathtub curve). To model this curve, they used two functions, one describing the falling mortality rate early in life and a second describing the increasing mortality towards the end of life. To scale the values of mortality by age ($M(t)$) , Chen and Watanabe (1989) used the K and t_0 parameters of the von Bertalanffy growth function.

$$M(t)=\begin{cases}\dfrac{K}{1-e^{-K(t-t_0)}}, t \le t_m \\ \dfrac{K}{a_0+a_1(t-t_m)+a_2(t-t_m)^2}, t \ge t_m\end{cases} \tag{8.17}$$

where

$$\begin{cases} a_0 = 1-e^{-K(t_M-t_0)} \\ a_1 = Ke^{-K(t_M-t_0)} \\ a_2 = -\dfrac{1}{2}K^2e^{-K(t_M-t_0)}\end{cases} \tag{8.18}$$

and

$$t_M = -\frac{1}{K}\ln\left(1-e^{Kt_0}\right)+t_0 \tag{8.19}$$

Cortés (1999) used this method to estimate the survivorship of sandbar sharks (*Carcharhinus plumbeus*) by age-class. However, he demonstrated no increasing mortality at older age classes due to senescence. The survivorship values that Cortés (1999) estimated using this method were similar to those for the Peterson and Wroblewski (1984), Hoenig (1983) and Pauly (1980) methods. Unlike the Peterson and Wroblewski (1984) method the Chen and Watanabe (1989) method only requires von Bertalanffy parameters, but the mathematics are more involved. This technique can be simply implemented in a spreadsheet using the formulae provided (8.17 – 8.19).

8.2.3 Other indirect methods

The indirect methods described above represent the most commonly used approaches in the elasmobranch literature. However, the fisheries literature contains many other similar techniques, and researchers may wish to investigate the field further. Other published techniques include Ursin (1967), Alverson and Carney (1975), Blinov (1977) and Myers and Doyle (1983). In addition, there are a number of studies that have looked at problems associated with these techniques such as Barlow (1984) and Pascual and Iribarne (1993).

8.3 DIRECT METHODS

Direct methods provide the researcher with the best estimates of mortality because they are based on the actual stock in question. However, they are also data intensive and require unbiased data. Thus, it is important that data are collected so that they are statistically appropriate and that the assumptions and restrictions of each of the methods are understood.

8.3.1 Catch curves

One powerful method of estimating total mortality (natural mortality if $F = 0$) is the use of catch curves. Catch curve analysis assumes that the decrease in observed numbers of individuals across the age-structure of the population is the result of mortality:

$$N_{t+1} = N_t e^{-Z} \qquad (8.20)$$

Thus, if the numbers of individuals in each age class are known then mortality can be estimated. This method requires age data for an unbiased sample from a population and involves six steps:

1. The numbers of animals in each class is determined.
2. The numbers are log (base *e*) transformed.
3. The log-transformed numbers are plotted against age.
4. A linear regression is fitted to the descending limb (right-hand side) of the catch curve.
5. The value of total mortality is calculated as the negative slope of the regression.
6. The error of the estimates is calculated as the error of the slope of the regression.

An example of catch curves from male and female Australian sharpnose sharks from Simpfendorfer (1999a) is given in Figure 8.02.

One of the most important steps in the application of this method is the selection of the points on the descending limb of the catch curve. In the perfect situation the catch curve would be a linear set of points with a negative slope (Figure 8.03a.). However, in reality most catch curves have an ascending limb at the youngest age classes, due to incomplete recruitment of some age classes to the fishing gear or to the population and an asymptote at the older age classes (Figure 8.03b). Ricker (1975) suggested using only the points to the right of the peak ln *N* value. It is also possible to exclude points that are clearly outliers from the line described by most of the descending limb points. This approach was used by Cortés and Parsons (1996) for the bonnethead shark, *Sphyrna tiburo*. In situations where there are only limited numbers of age classes including as many points as possible will provide the most accurate result with a lowest error. To do this, Simpfendorfer (1999a) fitted both a linear and quadratic function to the points including the peak ln *N* value (that Ricker (1975) suggested excluding);

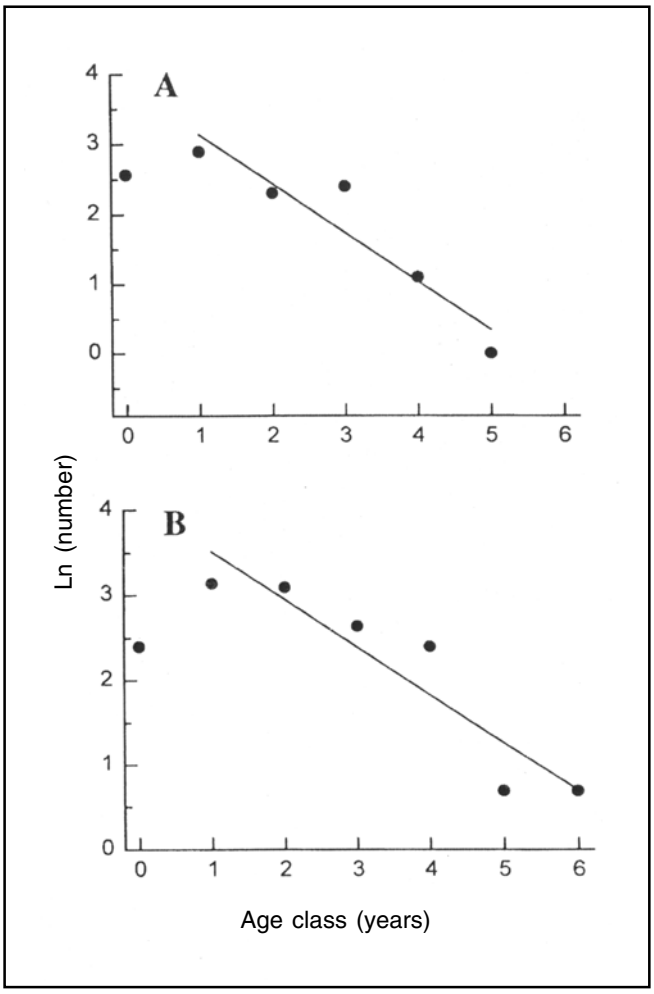

Figure 8.02 Catch curves for (A) male and (B) female *Rhiozprionodon taylori* derived from data from Simpfendorfer (1993). Data points for the first age class were not used to calculate the regression line. From Simpfendorfer (1999a).

where the quadratic function provided a significant increase in fit, it was assumed that including the maximum point increased curvature in the data and so the maximum point was excluded.

The use of catch curves requires a number of assumptions to be made about the sampled population. Firstly, the aged animals are representative of the age structure in the population. Secondly, the ages are accurately determined. Thirdly, the total mortality rate is constant across the age classes to which the linear function is fitted. Fourthly, that the mortality rate is constant between years (if more than one year worth of data is used). Fifthly, recruitment is constant between years. And, sixthly, that vulnerability to fishing gear is equal at all ages and constant over time classes.

Often it is difficult to get a sufficiently large sample of aged animals from a population to get accurate estimates of mortality. However, there may be sufficient age data to develop an age-length (or weight) key. This age-length key can be used to assign ages based on length. More details of age-length keys can be found in Hilborn and Walters (1992). Cortés and Parsons (1996) used an age-based catch curve and an age-length key derived catch curve for the bonnethead shark. Both methods produced very similar results.

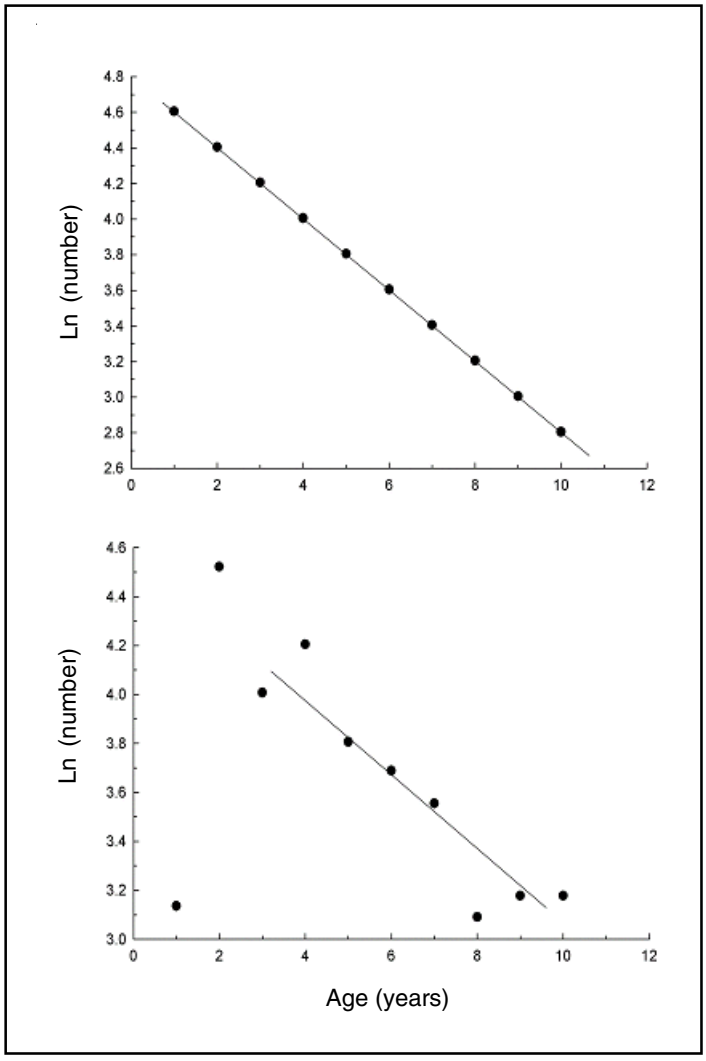

Figure 8.03 Hypothetical catch curves from (a) the "perfect" case based on where Z is constant and the regression can be fitted to all points, and (b) a more typical situation where the regression is fitted only to points to the right of the maximum ln(number) value.

8.3.2 Tagging

Tagging experiments can be separated into two very general categories: 1) studies where the tagged individuals of population are killed upon recapture, as in a commercial fishery, and 2) studies where tagged individuals are recaptured and released several times. The former are referred to as tag-recovery studies, as evident by the fact that fishers recover tags of individuals that are harvested, while the latter are referred to as capture-recapture studies, since it is possible to recapture tagged individuals on multiple occasions. Moreover, tag-recovery studies are typically viewed as fishery-dependent, since the data obtained is strictly a function of fishing activities, while for capture-recapture studies, it is best to use a fishery-independent sampling design to generate capture histories for tagged individuals. Here we focus on the use of multiyear

tag-recovery studies as a method to derive estimates of mortality, and acknowledge that there is a wealth of literature on the analysis of capture-recapture data (e.g., see Burnham et al., 1987, Pollock et al., 1990)

The general structure of a multiyear tag-recovery study is to tag N_i individuals at the start of each year *i,* for $i = 1,\ldots,I$ years. (Note that the tagging periods do not necessarily have to be yearly intervals; however, data analysis is easiest if all periods are the same length and all tagging events are conducted at the beginning of each period.) A total of r_{ij} tag-recoveries are then tabulated during year j from the cohort released in year i, with $j = i, i+1, \ldots, J$ and $J \geq I$ (here, the term "cohort" refers to a batch of similar (e.g., similarly-sized) individuals tagged and released at essentially the same time). The tabulated multiyear tag-recoveries can be displayed in an upper triangular matrix of the following form:

$$r = \begin{bmatrix} r_{11} & r_{12} & \cdots & r_{1J} \\ - & r_{22} & \cdots & r_{2J} \\ \vdots & \vdots & \ddots & \vdots \\ - & - & \cdots & r_{IJ} \end{bmatrix} \tag{8.21}$$

Application of multiyear tag-recovery models involves constructing a matrix of expected values and comparing them to the observed data. The matrix of expected values corresponding to the time-specific parameterization of Brownie et al. (1985), which is referred to as Model 1, takes the form

$$E_r = \begin{bmatrix} N_1 f_1 & N_1 S_1 f_2 & \cdots & N_1 S_1 \cdots S_{J-1} f_J \\ - & N_2 f_2 & \cdots & N_2 S_2 \cdots S_{J-1} f_J \\ \vdots & \vdots & \ddots & \vdots \\ - & - & \cdots & x_J \end{bmatrix} \tag{8.22}$$

where f_i is the tag-recovery rate in year i, which is the probability a tagged individual alive at the beginning of year i is caught during year i and its tag is recovered; S_i is the annual survival rate for year i, which is the probability an individual alive at the start of year i survives to the end of the year, and

$$x_J = \begin{cases} N_I f_J & \text{if } I = J \\ N_I \prod_{k=I}^{J-1} S_k f_J & \text{otherwise} \end{cases} \tag{8.23}$$

Although Model 1 is not the most general formulation of the Brownie et al. (1985) models, it is the most commonly applied since it possesses the flexibility to document annual changes in the tag-recovery and survival rates. In addition to the Brownie et al. (1985) formulation, there are two other types of models (not described here) that can be used to analyze multiyear tag-recovery data (see Seber, 1970 and Hoenig et al., 1998a,b).

Since the data in each row of the tag-recovery matrix follow a multinomial probability distribution, the method of maximum likelihood can be used to derive parameter estimates. Also, since all tagged cohorts are assumed to be independent, an overall likelihood function can be constructed as simply the product of the individual likelihood functions corresponding to each row of the tag-recovery matrix (Brownie et al., 1985; Hoenig et al., 1998a). Software packages that numerically maximize product multinomial likelihood functions have been developed for the use of tag-recovery models. These include programs SURVIV (White, 1983; http://www.mbr-pwrc.usgs.gov/software) and MARK (White and Burnham, 1999; http://www.cnr.colostate.edu/~gwhite/mark/mark.htm).

Application of the Brownie et al. (1985) models requires making the following assumptions: 1) the tagged sample is representative of the target population, 2) there is no tag loss or, if tag loss occurs, a constant fraction of the tags from each cohort is lost and all tag loss occurs immediately after tagging, 3) the time of recapture of each tagged individual is reported correctly (i.e., all tags are returned by fishers during the year in which the individuals were harvested), 4) all tagged individuals within a cohort experience the same annual survival and tag-recovery rates, 5) the decision made by a fisher on whether or not to return a tag does not depend on when the individual was tagged, 6) survival rates are not affected by tagging process or, if they are, the effect is restricted to a constant fraction dying immediately after tagging, and 7) the fate of each tagged individual is independent of the other tagged individuals.

Tag-recovery studies can be plagued by (among others) the following problems:

- Newly tagged individuals may not have the same spatial distribution as previously tagged individuals, especially if tagging takes place in only a few locations. (Note that it is best to tag fewer individuals over a large number of locations rather than many individuals at just a few locations.) This problem of non-mixing (Hoenig et al., 1998b) constitutes a violation of assumption 1 and will lead to unreliable parameter estimates. To determine if non-mixing is present, Latour et al. (2001a) developed a test that can be applied prior to data analysis.
- Individuals are tagged across a range of ages and/or sizes, and these different age and/or size groups experience different survival rates due to selectivity of the harvest. This leads to a violation of assumption 4.
- Individuals within a particular tagged cohort have a different spatial distribution than the other individuals within that cohort, perhaps due to age- and/or size-specific migration patterns (e.g., individuals may leave the estuarine or near coastal nursery grounds once they become sexually mature). This leads to a violation of assumptions 1 and 4 and can be accounted for during data analysis by ignoring the data associated with portions of the tag-recovery matrix (for more details, see Latour et al., 2001b).

Although the Brownie et al. (1985) models are simple and robust, they do not yield direct information about year-specific instantaneous rates of mortality (equation 8.1) or even exploitation rates (u_i),

which are often of interest to fisheries managers. Estimates S_i can be converted to Z_i via the equation (Ricker, 1975):

$$S_i = e^{-Z_i} \tag{8.24}$$

and if information about M is available (say from one of the methods previously described), then estimates of F_i and can be recovered. Given estimates of the instantaneous rates, it is then possible to recover estimates of u_i if the timing of fishing (i.e., single pulse (Type I fishery) or continuous (Type II fishery)) is known (Ricke,r 1975):

$$u_i = \begin{cases} 1 - e^{-F_i} & \text{for Type I fishery} \\ \dfrac{F_i}{F_i + M}(1 - e^{(-F_i + M)}) & \text{for Type II fishery} \end{cases} \tag{8.25}$$

Alternatively, if estimates of the instantaneous rates of mortality are unavailable, it is still possible to calculate year-specific estimates of exploitation (Pollock et al., 1990; Hoenig et al., 1998a):

$$u_i = \frac{f_i}{\phi\lambda}, \tag{8.26}$$

where f_i is as previously defined, ϕ is the short-term probability an individual survives the handling and tagging process with the tag intact, and λ is the tag-reporting rate (i.e., probability the tag will be reported given that that individual is harvested). The parameter ϕ can be estimated by holding newly tagged individuals in cages or holding pens for a short period of time (e.g., 2-4 days) (Latour et al., 2001b), while the tag-reporting rate is best estimated by conducting a high reward study (Henny and Burnham, 1976; Pollock et al., 2001).

Regardless of the goals of a particular tag-recovery study (e.g., estimates of S_i, F_i, etc.), it is advisable to assess the likelihood of assumption violation. This can involve either conducting auxiliary studies to address specific assumptions (e.g., experiments that allow estimation of the rates of tag-induced mortality, both short-term and chronic tag shedding, tag reporting, etc.) and/or by using diagnostic tools to assess model performance (Latour et al., 2001c). Specific to shark tagging studies, a variety of techniques have been used to assess and adjust for assumption violation. For example, Simpfendorfer (1999b) described a method of correcting dusky shark tag return rates for non-reporting by using compulsory catch information and the reporting rates of individual fishers, Xiao (1996) described a model for estimating shedding rates from a double tagging experiment with Australian blacktip sharks (*Carcharhinus tilstoni*), and Xiao (1999) described the tag-shedding rates of school (*Galeorhinus galeus*) and gummy (*Mustelus antarcticus*) sharks .

The use of tagging experiments can provide one of the best methods of estimating both fishing and natural mortality rates in shark populations. There are a wide variety of techniques available for the analysis of these types of data. The increased computing power available to most scientists and the

development of software packages, has opened up increasingly powerful techniques. These techniques, however, have been rarely used for shark populations. Grant et al. (1979) estimated the fishing and natural mortality rates of school sharks (*Galeorhinus galeus*) using animals released in the 1950s, Simpfendorfer (1999b) estimated fishing mortality rates of juvenile dusky sharks based on tag recaptures in a commercial gillnet fishery, and Xiao et al. (1999b) estimated fishing and natural mortality rates of the school shark using a probabilistic model.

8.3.3 Telemetry

Terrestrial biologists often use telemetry methods to estimate mortality rates by regularly monitoring the status of individuals in a population. Despite their popularity in terrestrial biology, these approaches have rarely been used in aquatic studies. In terrestrial systems radio frequency telemetry methods are used that can locate individuals over relatively large distances, whereas in aquatic systems acoustic telemetry methods that have relatively short reception distances must normally be used. This limited reception distance, and the large ranges of individuals, makes it impractical in most systems to monitor the status of individuals. Only one study of a shark population has used this technique. Heupel and Simpfendorfer (2002) used data from an acoustic monitoring system in a nursery area for blacktip sharks (*Carcharhinus limbatus*) to estimate both natural and fishing mortality rates. They used analytical techniques described by Hightower et al. (2001) (Kaplan-Meier and Program SURVIV) to estimate mortality rates for the 0+ segment of the population through time. This type of approach provides some of the most detailed understanding of the mortality process in a population (Figure 8.04), but requires a large amount of data and a high level of effort in the field. The success of the approach used by Heupel and Simpfendorfer (2002) in estimating mortality rates was due to the use of an array of data-logging acoustic monitors that continuously recorded the activity of up to 42 sharks per season within the relatively small and well-confined study site. For more details of this approach, consult Heupel and Simpfendorfer (2002) or Hightower et al. (2001).

8.3.4 Others

Cohort analysis is a popular method of estimating mortalities in fish populations. This often takes the form of Virtual Population Analysis (VPA), but also includes a method described by Paloheimo (1980) that bases mortality estimates on reductions in catches of a single cohort over time. Although commonly used in studies of teleost fish populations, these techniques have rarely been used in shark populations studies. Smith and Abramson (1990) used a reverse VPA to estimate the fishing mortality rates of leopard shark (*Triakis semifasciata*). Walker (1992) used the technique described by Paloheimo (1980) to estimate the natural mortality of gummy sharks (*Mustelus antarcticus*), as did Campana et al. (2002) to estimate total mortality in porbeagle sharks (*Lamna nasus*). These types of analysis are rarely used in studies of shark populations as the data requirements, in terms of the catch-at-age and fishing effort information, are greater than is normally available. However, for populations where good data are avail-

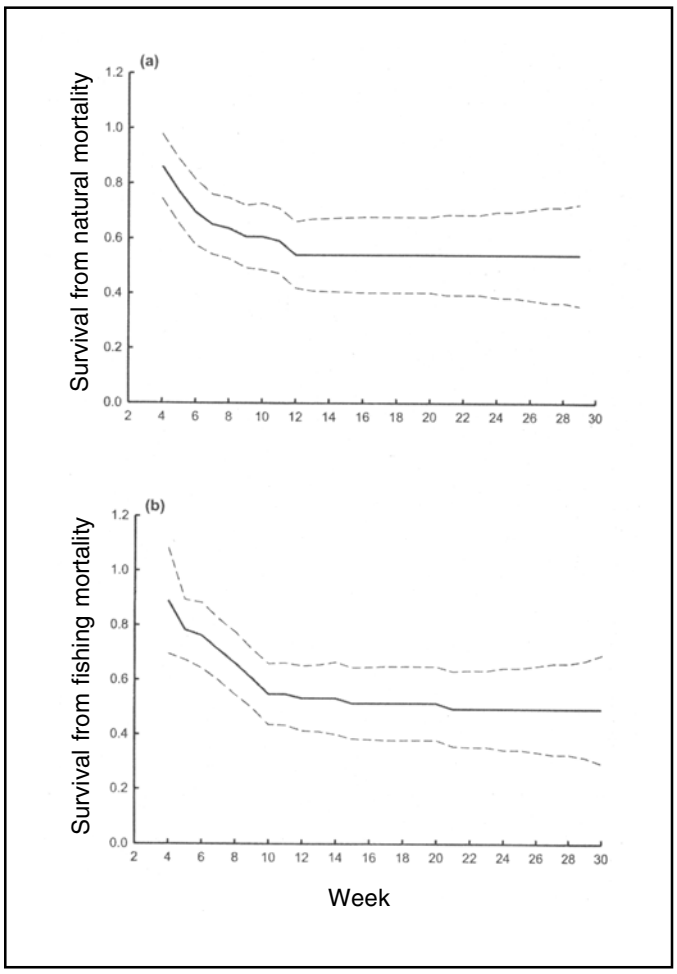

Figure 8.04 Kaplan-Meier estimates of finite rate of survival from (a) natural mortality and (b) fishing mortality for juvenile *Carcharhinus limbatus*. Data for 1999-2001 summers combined. Dashed lines indicate 95% confidence intervals. Graphs use the second week of May as week 1. From Heupel and Simpfendorfer (2002).

able this type of approach can yield valuable information on mortality.

8.4 CONCLUSIONS AND ADVICE

The first choice that a researcher needs to make is whether to use a direct or an indirect method to estimate mortality. Early in the assessment of a population indirect methods are used as they can provide quick and easy results, especially for inclusion in a model. When indirect methods are used for input into a model then it is prudent to construct multiple models that use as many of the indirect estimates as possible. This allows the researcher to include an understanding of the uncertainty associated with the estimates. Keep in mind that each method will provide different results, and in most instances there is no information that can be used to choose between the different values (i.e., they are each as equally likely). In some cases there is little difference between methods. For example, Simpfendorfer (1999b) used five different methods for dusky sharks and all but one of the results fell within the range of 0.081 to 0.086. Alternatively, the estimates of different methods can be very variable. Simpfendorfer (1999a) used seven methods for the Australian sharpnose shark and found a range of values from 0.56 to 1.65.

One of the first things that becomes obvious in population assessments is that the results are always very dependent upon the values of mortality used (both F and M). Thus as a researcher tries to make an assessment more precise and accurate, a direct estimate of mortality will provide a higher level of certainty about the results. It is at this point that direct methods of estimating mortality are normally applied. Unlike indirect methods these estimates require a sampling strategy for the specific species to ensure satisfactory results. Thus they require a much larger amount of field work and data analysis. The reward for this work can be a much better understanding of mortality in a population and so a more accurate assessment of its status.

The choice between different direct methods depends on a couple of factors. Tagging studies probably provide the best data if they can be implemented properly. Of particular importance is the ability

to get tag recapture information, tag shedding rates and tag reporting rates. Without these types of data the estimates of mortality will be biased and may yield results no more accurate than the indirect methods. In situations where tag recapture data may be more difficult to obtain the catch curve approach may prove more useful. Catch curves can produce very accurate results, but the data must meet several assumptions (see section 8.3.1) before the results can be considered accurate. Finally, telemetry methods are best used in situations where the mortality within a given system is required, and this system can be adequately sampled acoustically, normally with data-logging monitors. While this telemetry approach may seem like a dream for some populations, the technological and methodological advances are being made that will make this more and more available to researchers. As such it is likely to represent the future for the estimation of mortality in many situations.

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CHAPTER 9. DEMOGRAPHIC MODELS: LIFE TABLES, MATRIX MODELS AND REBOUND POTENTIAL

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9.1 INTRODUCTION

Information on the status of shark populations and how they respond to increases in mortality (e.g., fishing pressure, predation, disease), is critical to making management decisions about fished or endangered species. It is no surprise, then, that a considerable part of the fish and fisheries literature is devoted to this type of research. In the ideal situation long time series of information about a population—catches, fishing effort, change in abundance, etc—exist. In this situation dynamic fishery models can be applied to derive extensive management related information (see Chapter 10). However, in many situations the data required to support these types of models do not exist. This is often the case with shark populations, where the collection of these data has been uneconomical or overlooked. In this situation population models that rely primarily on life history parameters can provide some useful information for management. The models are normally referred to as demographic models. These demographic analyses became popular for shark stocks in the 1990s and are the most widely used form of population model for this group of fishes (Hoenig and Gruber, 1990; Cailliet, 1992; Cortés, 1995, 1998, 1999, 2002; Cortés and Parsons, 1996; Smith et al., 1998; Simpfendorfer, 1999a,b; Brewster-Geisz and Miller, 2000; Mollet and Cailliet, 2002).

The main parameter estimated by demographic analysis is the intrinsic rate of population increase (r), which is a measure of potential for growth rate in a population. There are two different techniques for estimating r – life tables and matrix models. Life tables are based on the Euler-Lotka equation:

$$\sum_{x=\alpha}^{w} l_x e^{-rx} m_x = 1.0 \qquad (9.1)$$

where l_x is the survival to age x, m_x is the fecundity at age x (female pups per female), α is the age at maturity, and w is the maximum reproductive age. The life table is a way of keeping track of the age-specific mortality and reproductive rates, and estimating r.

The second technique uses matrix algebra to estimate the finite rate of population increase (λ) from reproductive and mortality data. The finite rate of population growth and the intrinsic rate of population growth are related via the simple relationship:

$$\lambda = e^r \qquad (9.2)$$

Matrix methods can be applied to age-structured and stage-based data.

It is interesting to note that both life tables and matrix models were introduced to ecologists by the same person—P. H. Leslie (after whom the age-structured matrix model is named)—in the 1940s (Caswell, 2001). Life tables immediately became popular and were used extensively. However, matrix models did not gain favor with ecologists until the 1970s, but have since become extremely popular. The slow rise in popularity of matrix models was probably the result of the need for an understanding

of matrix algebra and the extra computational requirements. The increased availability of computers enabled researchers to overcome these drawbacks and embrace this powerful technique.

In this chapter I review the use of life table and matrix approaches in modeling shark populations. I restrict this consideration to static assessments of populations. Both life table and matrix approaches can be used to develop dynamic models of populations, but in the shark literature they have been largely restricted to static assessments due to the lack of time-series data. For more general overviews of life table methods several general ecology books provide a more thorough consideration (Krebs, 1985), and for matrix models the revised "Matrix Population Models" (Caswell, 2001), is the authoritative text. In addition to the simple life table approach, I also describe a method developed by Au and Smith (1997) that estimates the rebound potential of a population. This method is based on the life table approach, and is covered as a special case in that section.

9.2 LIFE TABLES

9.2.1 General life table approaches

Life tables were originally developed by life insurance companies as a means of determining life expectancies of humans. Ecologists, however, have adapted them for use in answering biological questions. As described in the introduction, the life table approach is based on the Euler-Lotka equation (9.1). The life table is a simple way of laying out the reproductive and mortality schedule of a population to aid in the solving of this key equation. The classic construction of the life table is shown in Table 9.01. The columns making up the life table can be simply derived from life history studies. Age data are essential to the construction of the table, both for maximum age as well as age at first reproduction. Methods of age determination are covered in Chapter 6 of this manual. The proportion of the population surviving at the beginning of each age class can be derived from estimates of natural and/or total mortality rates:

$$l_x = l_{x-1} e^{-Z} \qquad (9.3)$$

Techniques for estimating mortality rates are covered in Chapter 8 of this manual. The initial value of l_x is normally set to a value of one, making it a "per recruit" analysis that examines if the population will replace that single recruit. The final pieces of data required are the age-specific number of female pups per reproductive event (litter for viviparous species, total eggs laid for oviparous species), and the frequency of reproductive events. In studies of shark populations the number of female pups is used as they are the only group that produces offspring. Thus, in reality this type of life table is only keeping track of the female portion of the population. Rates of female pup production can be derived from total litter size by multiplying by the proportion of female embryos and dividing by the number of years between litters.

The first five columns in the table containing the life history data are then used to calculate the value of *r*. The process of calculating *r* is an iterative one. This process is started by selecting a value

of *r* and calculating the values for the two columns on the right-hand side of the life table. It can be seen that the summation of the final column is identical to the left side of equation 9.1. Thus when the final column is summed it will total 1.0 if the correct value of *r* has been selected. If the value does not equal 1.0, then a new value of *r* is picked and the process repeated until the summation of column 7 equals 1.0. This may seem like a time-consuming and arduous task. However, the process is almost instantaneous with the use of a non-linear optimization routine in a modern spreadsheet. The most commonly used of these routines is the "Solver" add-in that comes standard with Microsoft Excel. The life table can be entered into the spreadsheet and a cell containing the starting value of *r* added. This cell is then used in the formulae of columns 6 and 7 to represent *r*. The solver can then be started and the value of the sum of the final column set to equal 1.0 by changing the value of the cell containing *r*.

Once the life table has been constructed a number of other statistics can be calculated from the life table. The net reproductive rate (R_0) is the total number of female offspring produced per individual in a single cohort:

$$R_0 = \sum_{x=\alpha}^{w} l_x m \qquad (9.4)$$

The mean generation length (G) is the mean period between birth of a parent and the birth of their offspring:

$$G = \frac{\sum_{x=\alpha}^{w} l_x m_x x}{R_0} \qquad (9.5)$$

Krebs (1985) also demonstrated that it is possible to calculate a value related to *r* – the innate capacity for increase for the particular environmental conditions (r_m). This statistic is calculated as:

$$r_m = \frac{\ln(R_0)}{G} \qquad (9.6)$$

The value of r_m, however, is not equivalent to *r* and should not be used as a substitute for it. The value of r_m is a useful starting value for the iterative process of estimating *r*. The population doubling rate can also be simply calculated:

$$t_{\times 2} = \frac{\ln(2)}{r} \qquad (9.7)$$

This statistic is handy for very clearly showing differences between populations, or different mortality or reproductive scenarios within a population. The stable age distribution of the population (the proportion of individuals in each age class, C_x) can be calculated using the equation:

$$C_x = \frac{\left(e^r\right)^{-x} l_x}{\sum_{x=0}^{w} \left(e^r\right)^{-x} l_x} \qquad (9.8)$$

It is an assumption of the life table method that the age structure of the population is stable. In many situations, especially when a population is exploited, this assumption may be violated causing bias in the results. The static nature of life tables also means that they may under estimate the growth rate of a population as they do not include compensatory effects (e.g., decreases in mortality, increases in reproductive rate, decreases in reproductive age, etc. when population size is decreased). In the next section (9.2.2) a life table method is described that attempts to overcome this problem of not including compensation.

Initial use of the life table typically involves using age-specific survival values based only on natural mortality. However, age-specific values of fishing mortality (F) can easily be included by basing survival on total mortality. Several studies of shark populations have used this type of approach to investigate if current (or past) fishing mortality rates were sustainable (Simpfendorfer, 1999b) or at what level of fishing mortality $r = 0$ (i.e., the population will start to decline) (Simpfendorfer, 1999a). This type of information can be useful to resource managers. However, it is often difficult to translate a value of fishing mortality into a catch level without other information (i.e., catch and abundance data). Due to the age-structured nature of life tables it is possible to investigate other management measures. For example, the impact of nursery area closures can be studied by removing fishing mortality from the 0+ age class, or the impact of size regulations can be studied by applying fishing mortality to specific age classes.

9.2.1.1 Example – Australian sharpnose shark

Simpfendorfer (1999a) produced life tables for the Australian sharpnose shark (*Rhizoprionodon taylori*) in northern Australian waters. One of these life tables (Table 9.01) was constructed using natural mortality estimated from a catch curve (for females only, $M = 0.56$ year^{-1}). Based on these data the value of r was 0.271 year^{-1}, the population doubling time (t_{x2}) was 2.554 years, the generation time 2.304 years, and the net reproductive rate 1.758. Simpfendorfer (1999a) calculated the fishing mortality at which the population growth rate would be zero (F_c) to be 0.179 year^{-1}. This was achieved by searching for the value of F that produces $r = 0$. Finally, a contour plot of r was produced for different values of age at first capture and fishing mortality (Figure 9.01) by constructing a large number of life tables. The use of spreadsheet software (e.g., Microsoft Excel) helps to speed the calculation of parameters when multiple life tables are required, with a simple macro being able to construct multiple life tables in almost no time.

Table 9.01 Life table for the Australian sharpnose shark, *Rhizoprionodon taylori*, from northern Australia based on data from Simpfendorfer (1999a).

Age (x)	Proportion surviving(l_x)	Female pups(m_x)	Reproductive rate($l_x m_x$)	$l_x m_x x$	e^{-rx}	$l_x m_x . e^{-rx}$
0	1	0	0	0	1	0
1	0.570638	1.982785	0.64565	0.64565	0.762338	0.492204
2	0.325628	2.588733	0.481027	0.962054	0.581159	0.279554
3	0.185816	2.80877	0.297824	0.893471	0.44304	0.131948
4	0.106034	2.888671	0.174784	0.699137	0.337746	0.059033
5	0.060507	2.917685	0.10074	0.503702	0.257477	0.025938
6	0.034527	2.928221	0.057694	0.346163	0.196284	0.011324
7	0.019703	2.932047	0.032965	0.230757	0.149635	0.004933
8	0.011243	2.933437	0.01882	0.150561	0.114073	0.002147
9	0.006416	2.933941	0.010741	0.096672	0.086962	0.000934
10	0.003661	0	0	0	0.066294	0

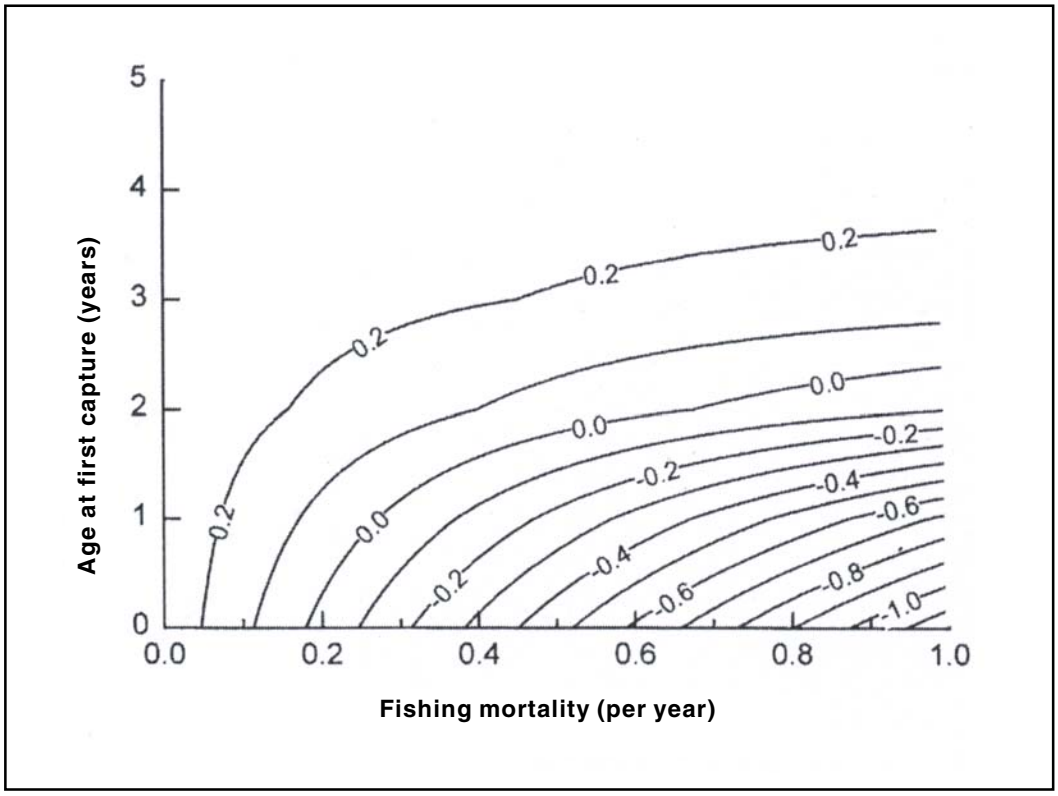


Figure 9.01 Contour plot of intrinsic rate of population increase r as a function of fishing mortality (F) and age at first capture ($AAFC$) for *Rhizoprionodon taylori* from northern Australia. Estimates are based on a life table where natural mortality was calculated by a catch curve. Fishing is sustainable at values of $r > 0$. From Simpfendorfer (1999a).

9.2.2 Rebound potential

Au and Smith (1997) described a modification of the life table approach to estimate what they termed "rebound potential" (r_{2M}). The rebound potential (or rebound rate) is a measure of how fast a population will recover after fishing mortality has been removed from a population. The technique will first be described, and then some potential modifications, assumptions and nuances considered. The description of the technique will be relatively cursory due to space limitations. Those wishing to find more detail on this technique should consult Au and Smith (1997) and Smith et al. (1998).

Au and Smith (1997) began by reformulating the Euler-Lotka equation (9.1) by introducing parameters describing the survival to the mean age at maturity (l_α) and average number of female pups per litter (b). This allows equation 9.1 to be rewritten as:

$$e^{-(Z+r)} = l_\alpha b e^{-r\alpha}\left[1 - e^{-(Z+r)(w-\alpha+1)}\right] = 1.0 \qquad (9.9)$$

The value of Z (total mortality) is substituted for l_x (survival to age x) in equation 9.1. This reformulation allows r to be estimated more simply than the traditional iterative method. However, it requires several assumptions about the mortality and reproductive schedule (see below). Smith et al. (1998) noted that a similar formulation was described by Hoenig and Gruber (1990) in terms of the survival in the first year after birth.

The second step of the technique involves assuming that the maximum sustainable yield (*MSY*) is achieved at $Z = 2M$, and that at this level $r = 0$. They also assumed that all of the compensation in the population growth rate occurs as a result of increased survival to age at maturity (l_α). Thus by substituting $r = 0$ and $Z = 2M$ into equation 9.9 the increased value of l_α ($l_{\alpha,2M}$) can be calculated. Finally, the value of rebound potential (r_{2M}) is calculated by removing the fishing pressure from the population (i.e., $Z = M$) but retaining the increased value of $l_{\alpha,2M}$.

Au and Smith (1997) also considered that in situations where fecundity varied with age the rebounding population is likely to have a different value of b than the fished population. This would occur because the average age of mature animals would decrease as more animals recruited after fishing was stopped. To investigate the impact of these types of changes Au and Smith (1997) and Smith et al. (1998) used sensitivity tests with 1.0b, 1.25b and 1.5b when solving for r_{2M}. Au and Smith (1997) showed that for the leopard shark (*Triakis semifasciata*) that increased values of b resulted in significant changes in r_{2M}.

When using this method, researchers need to be aware of the assumptions and restrictions on its use. In reformulating the Euler-Lotka equation much of the ability to include age-specific rates of reproduction and mortality was lost. The sensitivity of the results to changes in the value of b indicates

the limitations of such an approach. The assumption that *MSY* occurs at $Z = 2M$ also needs to be considered. Shark populations are known to have limited ability to sustain fishing pressure (Holden, 1977; Musick, 1999) due to their low fecundity and late age at maturity. As such *MSY* may occur at lower levels of Z than $2M$. In fact, a value of $Z = 1.5M$ may be a more appropriate level for *MSY*. This change can easily be included into the technique to estimate $r_{1.5M}$. As more research is undertaken on shark populations a clearer understanding of the mortality rates that produce MSY will be gained. As this information becomes available, it may be necessary to address the value of Z used in this technique.

9.3 MATRIX MODELS

Matrix population models are commonly used by researchers in studying the demography of a population. They provide a versatile method that can be used in a wide range of situations. It is not possible here to cover the whole suite of matrix models and how to use them. In this section, two forms of static matrix models will be considered: age-structured and stage-based. In both cases we will only consider static formulations of these models that are equivalent to the life tables discussed above. Matrix models are quickly and easily adapted to produce dynamic population models, but these fall outside the scope of this chapter. For a thorough coverage of all issues related to matrix population models consult Caswell (2001) or Caswell (1989). Like life tables, static matrix models only require life history information. The math involved in producing the estimates of the finite rate of population growth ($\lambda = e^r$) is more complex and requires an understanding of matrix algebra. However, the need for such an understanding can be largely overcome by the use of software developed specifically for use with matrix models. A good example of this type of software is POPTOOLS, a Microsoft Excel add-in that is available free on the internet (http://www.cse.csiro.au/poptools/).

9.3.1 Age-structured models (Leslie Matrix)

Static age-structured matrix models, also know as Leslie Matrices after the scientist who first described their use, have been less commonly used in the assessment of shark populations that have life tables. Hoenig and Gruber (1990) were the first to publish a paper that used a Leslie Matrix to estimate λ for a shark population (lemon shark, *Negaprion brevirostris*). The basis for the Leslie Matrix is:

$$N_{t+1} = AN_t, \tag{9.10}$$

where N is a vector describing the age composition of the population (either at time t or t+1) and A is the transition matrix:

$$A = \begin{bmatrix} m_0 & m_1 & m_2 & \dots & m_w \\ l_0 & 0 & 0 & 0 & 0 \\ 0 & l_1 & 0 & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & l_{w-1} & 0 \end{bmatrix} \tag{9.11}$$

For consistency with the life table section, the same notation has been used: m_x is the number of female pups per female in age class x and l_x is the survival to the end of age x. It is the transition matrix A that is normally referred to as the Leslie Matrix. The matrix columns represent the age classes. The value of λ is determined by finding the dominant eigenvalue of A by using matrix algebra. When the dominant eigenvalue is determined two vectors (the right and left eigenvectors) also can be calculated. The first of these represents the age-specific reproductive values (***v*****,** the left eigenvector), and the second is the stable age/stage structure (***w***, the right eigenvector). These sets of values are functionally equivalent to the $l_x m_x$ and c_x values in life table models.

Like life tables, a Leslie Matrix can be adapted to include information on fishing mortality at specific ages, or changes in the reproductive schedule. In addition, the static nature of the simple Leslie Matrix does not include compensatory effects for a population that is being fished.

9.3.1.1 Example – Australian sharpnose shark

As a direct comparison to the example given in the life table section, a Leslie matrix was constructed from the data provided by Simpfendorfer (1999a) (Table 9.01):

$$\begin{bmatrix} 0.00 & 1.98 & 2.59 & 2.81 & 2.89 & 2.92 & 2.93 & 2.93 & 2.93 & 2.93 & 0.00 \\ 1.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.57 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.33 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.19 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.00 & 0.11 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.06 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.03 & 0.00 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.02 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.01 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.006 & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.004 \end{bmatrix} \quad (9.12)$$

This matrix was analyzed using the Microsoft Excel Add-In POPTOOLS. The dominant eigenvalue (λ) was 1.257 (r = 0.229 year^{-1}) and the population doubling time was 2.37 years. These values are similar to those produced by the life table analysis, with the population doubling time different by approximately 0.2 years. The left and right eigenvectors (v and w) are given in Table 9.02.

Table 9.02 Age-specific reproductive value (*w*) and stable age distributions (*v*) (proportional) of the Australian sharpnose shark, *Rhizoprionodon taylori*, estimated using a Leslie Matrix (equation 9.12).

Age	*w*	*v*
0	62.9%	4.5%
1	28.5%	9.9%
2	7.4%	10.9%
3	1.1%	11.0%
4	0.1%	10.8%
5	0.0%	10.7%
6	0.0%	10.6%
7	0.0%	10.6%
8	0.0%	10.5%
9	0.0%	10.5%
10	0.0%	0.0%

9.3.2 Stage-based models

In some situations the life history of a species can be divided into discrete segments or stages (e.g., neonate, juvenile, sub-adult, breeding adult, non-breeding adult). In this case a stage-base matrix model can be applied. This type of model can be useful if there is only limited age information for a species, or the time spent in stages is variable. In long-lived species, stage-based models can also simplify the math involved in the calculations. The formulation of the static stage-based transition matrix is similar to that of the Leslie matrix, but the columns represent stages rather than ages, and the survival values are divided between the probability of an individual surviving and moving from one stage to the next (G_i) and the probability of an individual surviving and remaining in the same stage (P_i). There are several approaches to calculating these parameters. In a study of sandbar sharks Cortés (1999) applied a method that used the duration of each stage (d_j) and the stage-specific survival probabilities (p_i):

$$G_i = \frac{p_i^{d_j}\left(1-p_i\right)}{1-p_i^{d_j}}, \tag{9.13}$$

and

$$P_i = \left(\frac{1-p_i^{d_j-1}}{1-p_i^{d_j}}\right)p_i . \tag{9.14}$$

If the stage-specific survival value is not known, it can be estimated as the mean of the age-specific values (survival or mortality, with $S = e^{-Z}$) in each stage. Other authors (e.g., Brewster-Geisz and Miller, 2000; Mollet and Cailliet, 2002) have taken a slightly different approach using the probabil-

ity of survival of an individual in a stage (σ_i) and the fraction of individuals in a stage that move to the next stage (γ_i):

$$G_i = \sigma_i \gamma_i , \tag{9.15}$$

and

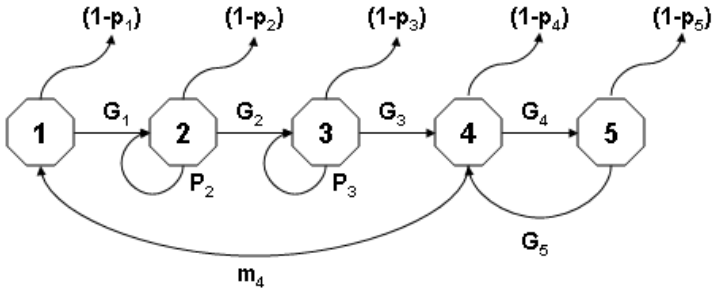
$$P_i = \sigma_i (1 - \gamma_i). \tag{9.16}$$

This method requires an iterative approach to the estimation of the matrix parameters, and more detail can be found in Brewster-Geisz and Miller (2001) or Mollet and Cailliet (2002).

The staged-based transition matrix can take many forms depending on how the stages selected for the population are related. The best way to understand the elements of the stage-based transition matrix is via a life cycle graph. Figure 9.02 shows a life cycle graph for the sandbar shark (*Carcharhinus plumbeus*) with five stages (neonates, juveniles, sub-adults, pregnant adults and resting adults). This life cycle was used by Brewster-Geisz and Miller (2000). The transition matrix for this stage classification as specified by Brewster-Geisz and Miller (2000) is;

$$A = \begin{bmatrix} 0 & 0 & 0 & m_4 & 0 \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 \\ 0 & 0 & G_3 & 0 & G_5 \\ 0 & 0 & 0 & G_4 & 0 \end{bmatrix} \tag{9.17}$$

Figure 9.02 Life cycle graph of the sandbar shark, *Carcharhinus plumbeus*, used to construct the matrix in equation 9.17. Compartments 1 - 5 represent the different life stages (1 – neonate; 2 – juveniles; 3 – sub-adults; 4 – pregnant adults; 5 – resting adults). Parameter values shown correspond to those in equation 9.17. Based on information in Brewster-Geisz and Miller (2000).



Only stage four animals produce young (hence only m_4) on the top line, the transition to all stages up to pregnant adult are one-way, but animals alternate between pregnant and resting stage adults on an annual basis (hence the lack of P_4 and P_5 since they will always move to the other group if the time step is annual), and finally neonates become juveniles after one year (hence there is no P_1 value). Such a transition matrix could be used for many shark populations, but would need to be modified if reproduction was annual, or if the resting adult stage lasted longer than one year. It is not possible to specify all possible combinations of matrices here. Caswell (2001) provides a thorough coverage of how to develop a life cycle graph (which maps out the stages) and the resulting transition matrix.

Like a Leslie matrix the value of γ of the stage-based model is estimated by determining the eigenvalue of the matrix. Similarly, the eigenvectors produce information on the reproductive value and stable age structure, but they are stage-specific rather than stage-specific.

9.3.2.1 Example – sandbar sharks

Brewster-Geisz and Miller (2000) used a stage-based matrix model to examine some management options for the sandbar shark (*Carcharhinus plumbeus*) in the western North Atlantic. The life cycle graph for this species is shown in Figure 9.02 and the matrix formulation is shown in equation 9.17. The analysis examined the results of five scenarios with varying amounts of fishing mortality on the five stages ranging from the current situation (in 1996) to total protection of the neonates and the pregnant females (including the unrealistic assumption of no natural mortality on neonates). They estimated that in the current situation r = -0.124 year^{-1}, indicating that the population was over-fished and declining. The other four scenarios used to explore protection for different stages by eliminating fishing mortality also returned negative values of r. They examined the effect of fishing mortality on r (Figure 9.03) and demonstrated that if fishing mortality at all stages was equal, r = 0 occurred at F = 0.071 year^{-1}. This plot also demonstrates that when no fishing occurs the value of r is approximately 0.07 year^{-1}.

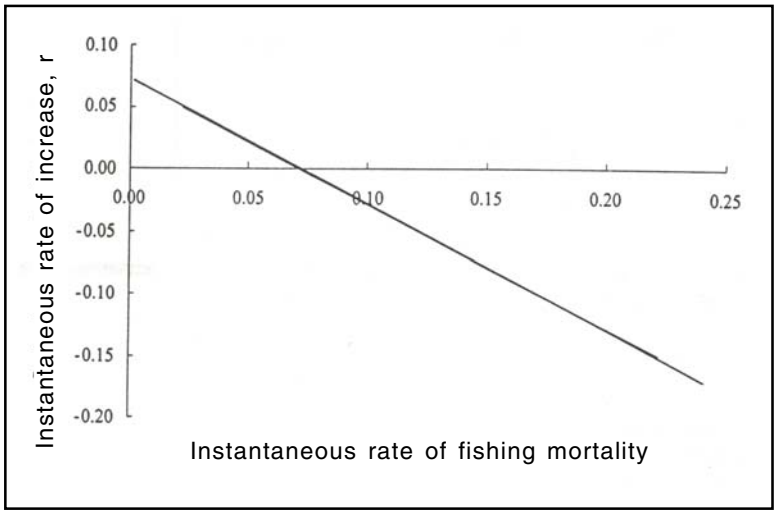


Figure 9.03 The relation between the intrinsic rate of increase (r) and fishing mortality (F). $F_{critical}$ is reached at 0.071. If F is less than $F_{critical}$, the population will increase. If F is greater than $F_{critical}$, the population will decrease. From Brewster-Geisz and Miller (2001).

9.3.3. Elasticities

One piece of information that can be very useful in interpreting the results of matrix models is how much influence can changes in vital rates (reproductive and mortality rates) have on the population growth rate. In absolute terms this is known as the sensitivity, but is normally reported as the elasticity, which is the proportional change. Elasticity is calculated from the elements of the transition matrix (a_{ij}), the population growth rate (λ and the elements of the right and left eigenvectors (v_i, w_i):

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{v_i w_i}{\langle \mathbf{w}, \mathbf{v} \rangle}, \tag{9.18}$$

where (**w,v**) is the scalar product of the two vectors (i.e, (**w,v**)=v_1w_1+v_2w_2+...+v_nw_n). Since elasticities are proportions they sum to give one:

$$\sum_i \sum_j e_i = 1. \tag{9.19}$$

For each column of the matrix, which correspond to individual age or stage classes, elasticity values can also be calculated:

$$E_i = \sum_j e_i \tag{9.20}$$

where E_i is the age or stage elasticity.

Since elasticity will identify the age or stage where the smallest changes in vital rates will produce the biggest change in population growth rate, the researcher has a powerful tool to find where management or conservation action might produce the greatest benefits to the population. For example, Cortés (2002) used elasticity values from a wide range of shark species to show that populations of large, slow-growing, long-lived species were most vulnerable to changes in the survival of the juveniles (as opposed to the adults). Such a result suggests that management arrangements that protect juveniles (e.g., nursery area closures) would provide greater benefit to the population than those that protect adults (e.g., maximum size limit). For a much more detailed discussion of the calculation and interpretation of elasticity values for matrix models consult Caswell (2001).

9.4 CONCLUSIONS AND ADVICE

The static modeling approaches outlined in this chapter provide the researcher with methods to assess the status of a population based solely on life history data. This is particularly useful when there is little or no fishery information available for a population making more complex dynamic modeling approaches inappropriate. However, these simple approaches come with limitations and these must be kept in mind when interpreting the results and applying them to management or conservation. For

example, a life table can provide good information on the intrinsic rate of increase for a population, or the fishing mortality rate at which the population will start to decline. However, it will not provide information on the abundance of the population, its level of population decline or the appropriate quota level to achieve a target biomass. These later types of information are more appropriately determined using the dynamic approaches described in Chapter 10.

The results of the static approaches should also be considered to be conservative in their estimates of population growth rates. This is because both simple life tables and static matrix models do not allow for compensatory effects at low population sizes (e.g., increased growth, reproductive or survival rates). The rebound potential approach of Au and Smith (1997) described in the life table section is an attempt to overcome this limitations. However, the simple framework in which it is implemented means that a number of restrictive assumptions need to be made.

The choice between life tables or matrix models is largely a matter of personal preference. Each of the approaches will provide similar results if used in comparable ways. However, the trend in the fisheries and ecological literature is towards matrix models. Although the math involved in matrix models is more complex the development of software to quickly and easily do the analyses means that these approaches can be easily implemented on a personal computer. In addition the ability to easily calculate elasticity values, and their usefulness in determining management or conservation strategies, provides an incentive to take this approach.

Finally, whichever approach is chosen, it is important to remember that there is a degree of uncertainty and/or variation in the input parameters to any model. For this reason a good demographic analysis will always include a range of scenarios that consider different sets of life history parameters that reflect uncertainty or variation. There are two approaches to this. The first is to construct a number of life tables or matrices that reflect the potential ranges of values. The second approach is to construct a stochastic analysis such as that used by Cortés (1999) for sandbar sharks. With this approach probability distributions for the input parameters are constructed and several hundred random draws from the distributions are made and the life table or matrix solved. The result is probability distributions of the output parameters (e.g., *r*). The first approach is best suited to cases where there is uncertainty in the parameters, and the second is suited to the situation where there is variation in the parameters.

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CHAPTER 10. FISHERY STOCK ASSESSMENT MODELS AND THEIR APPLICATION TO SHARKS

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10.1 INTRODUCTION

Perhaps the most influential, but not necessarily the best, works on shark stock assessment were those of Holden in the 1960s and 1970s. Holden (1977) was one of the first scientists to consider the problem of shark fisheries stock assessment from a general point of view. He correctly pointed out that sharks were different from bony fishes in terms of their biology, but unfortunately he incorrectly concluded that classic fisheries models such as stock production models could not be applied to sharks and rays. Holden dismissed these models and called for new models to be developed. He stated that the assumptions of surplus production models regarding immediate response in the rate of population growth to changes in population abundance and independence of the rate of natural increase from the age composition of the stock do not hold for sharks. These conclusions were based mainly on the time delays caused by the longer reproductive cycles of sharks and their reproductive mode, which in his view would cause a linear and direct stock-recruitment relationship.

Because of this very influential paper, surplus-production models have been mostly ignored for shark stock assessment, and scientists and non-scientists reading Holden's papers have sought new methods and models for dealing with shark fisheries stock assessment. For a while, Holden's thoughts influenced the works of other scientists who opted for the more detailed approach offered by age-structured models (e.g., Wood et al., 1979; Walker, 1992).

The main problem of surplus production models is not that they are inadequate when applied to sharks but *the way* in which they were being applied. A paramount obstacle for the use of *classic* surplus production models in the 1960s and part of the 1970s was the *equilibrium constraint* (see section on fitting models to data below). Back then, due to the lack of readily available computers to perform iterative search algorithms, scientists engaged in surplus production model-fitting were forced to assume that *populations were in equilibrium at all exploitation levels* (i.e., that every catch observed was sustainable) to simplify the process of fitting surplus production models to data.

The dangerous consequences of this assumption are well known and explicitly warned against in fishery text books (Pitcher and Hart, 1982; Hilborn and Walters, 1992). However, the personal computer revolution has helped to overcome the equilibrium constraint through the availability of non-linear optimization routines which are accessible to virtually any fishery scientist in the world today. The diversity of approaches this offers for fitting surplus production models has translated into a new era of popularity for the utilization of what are presently known as *dynamic* surplus production models that have been applied to organisms as slow-growing as whales and sharks (Punt, 1991; Polachek et al., 1993; Prager et al., 1994; Babcock and Pikitch, 2001). Perhaps the most interesting outcome of all this re-appraisal of surplus production models is the view that most of the problems associated with successfully applying them are due to the quality of the fisheries data (Hilborn, 1979; see also section on

data quality below), and the finding that simple surplus production fishery models can sometimes perform better than the more elaborate and biologically detailed age-structured approaches (Ludwig and Walters, 1985, 1989; Ludwig et al., 1988; Punt, 1991).

One of the reasons for the difficulty in applying these models to sharks is that the data available on shark fisheries and our knowledge about shark biological parameters may not be adequate. This is expressed very clearly in the work of Anderson (1990), Anderson and Teshima (1990) and Bonfil (1996). In fisheries science, independently of the species in question, the most common problem is the lack of good and sufficient data and as explained below, the lack of contrast in the data when we have them. Another big problem often overlooked is that the more 'realistic' age-structured models also pose problems in their application. Age-structured data are much more difficult and expensive to obtain. Furthermore, the life cycles of most shark species, even in terms of the basic parameters of age, growth and reproduction, have just started to be unveiled during the last 20 years, and this only in the case of a handful of stocks (see Pratt and Casey (1990) and Cortés (2000) for reviews). In addition, there are some relevant areas of elasmobranch population dynamics that are still largely unknown. For example, empirically derived stock-recruitment relationships have never been documented for any elasmobranch, although a very strong relationship is suspected due to the reproductive strategies of the group (Holden, 1973; Hoff, 1990); the size, structure and spatial dynamics of most stocks of elasmobranchs are almost totally unknown. Inadequate knowledge of migration routes, stock delimitation and movement rates amongst them, can seriously undermine otherwise "solid" assessments and management regimes.

Hoff (1990) favored the use of dynamic surplus-production models for shark stock assessment for a variety of reasons. Punt (1988; 1991) also reported dynamic surplus production models as the most reliable for management of slow-growing resources with limited reproductive potential such as baleen whales, when tested using a simulated fully age-structured population. Similar positive results were reported with a Schaefer model for a swordfish age-structured simulation model (Prager et al., 1994). The results of Bonfil (1996) suggest that surplus production models are good enough for shark biomass assessment but not so much for management parameter estimation. He found that although generally inferior to the Deriso-Schnute model (see below), surplus production models are capable both of estimating biomass benchmarks and obtaining good biomass fits for most of the scenarios analyzed.

The best advice that can be given in regard to the model choice for elasmobranch stock assessment can be found in Chapter 2 (section 2.2.3). Surplus production models can and should be applied to elasmobranch fisheries as they are one of the easiest to implement, but their results should be taken as a first and preliminary assessment. A complete and reliable assessment should not end with surplus production models; delay-difference and fully-age structured models should also be applied.

10.2 SURPLUS PRODUCTION MODELS

These models are among the simplest and most widely used in stock assessment. They are easy to use because they require only two or three types of data. These models are very flexible and have

different variations; the Schaefer, Fox, and Pella-Tomlinson models are some of the best known.

Surplus production models (SPM) are based on the following principles:

Next biomass = last biomass + recruitment + body growth – catch – natural mortality

If there is no catch

Next biomass = last biomass + production – natural mortality

where production is the sum of recruitment and body growth, and

Surplus production = production – natural mortality

Thus

New biomass = last biomass + surplus production – catch

10.2.1 Logistic growth and the Schaefer model

Population growth has been typified in several ways, but most commonly the logistic model of population growth has been found to fit a large number of populations both in nature and in captivity. This model is expressed in the following way (differential equation or continuous model):

$$\frac{dB}{dt} = rB(1-\frac{B}{K}) \qquad (10.1)$$

where B = biomass, K = carrying capacity, and r = intrinsic rate of population increase.

The carrying capacity of the system, K (or B_∞), is the maximum population size that can be achieved. Mortality, age-structure, reproduction, and tissue growth are all captured by a simple parameter called *intrinsic* rate of increase, or intrinsic rate of production, r. In theory, the *intrinsic rate of increase* is fully realized at the lowest population level while *the finite rate* of population growth is highest at the midpoint of K. Figure 10.01 illustrates some of these concepts and shows the trajectories of population growth for two different values of r.

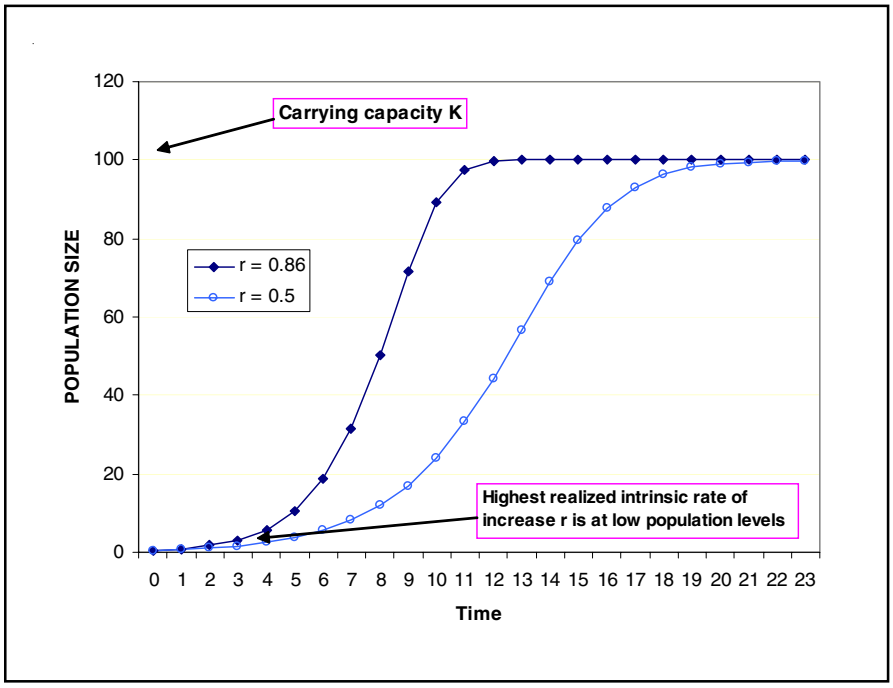

Figure 10.01 Examples of population growth according to the logistic model. Two different r values are exemplified.

The Schaefer model is the most commonly used among SPMs (known also as Biomass Dynamics Models). This model is based precisely on the logistic population growth model. The continuous logistic model explained above can also be written in discrete form in the following way (Hilborn and Walters, 1992):

$$B_{t+1} = B_t + rB_t(1-\frac{B_t}{K}) \qquad (10.2)$$

When catch is included in the above equation we obtain the discrete version of the Schaefer (1954) surplus production model:

$$B_{t+1} = B_t + rB_t(1-\frac{B_t}{K}) - C_t \qquad (10.3)$$

where

$$C_t = qfB_t \qquad (10.4)$$

and C is catch, q is the catchability coefficient, and f is effort. In the Schaefer model above, the middle term is known as surplus production. If surplus production is greater than catch, population size increases; if catch equals surplus production, catch is sustainable and population size remains constant ($B_{t+1} = B_t$); if catch is greater than surplus production, population size declines.

10.2.1.1 Assumptions

The Schaefer model has the following assumptions:

- there are no species interactions
- r is independent of age composition
- no environmental factors affect the population
- r responds instantaneously to changes in B (no time delays)
- q is constant
- there is a single stock unit
- fishing and natural mortality take place simultaneously
- no changes in gear or vessel efficiency have taken place
- catch and effort statistics are accurate

In practice, many of the above assumptions are not met but this does not mean that the method cannot be used. As long as it is used critically, the Schaefer model is a very powerful tool for an initial assessment of a stock.

The management parameters of importance from the Schaefer model are given by:

MSY = r K/4

B_{MSY} = K/2

Optimum effort (f_{MSY}) = r/2q

10.2.2 Fox and Pella-Tomlinson models

There are other SPMs that have been proposed to represent fisheries more "realistically". First is the Fox model (Fox, 1970), which is based not on the logistic population growth model but on the Gompertz growth model. The Fox model equation is:

$$B_{t+1} = B_t + rB_t(1 - \frac{\ln B_t}{\ln K}) - C_t \qquad (10.5)$$

The model is supposed to be more "realistic" because it assumes that the population can never be totally driven to extinction, something that sounds intuitive but is probably wrong in light of the severe depletion of fishery resources in recent years and the well-documented human-caused terrestrial species extinctions.

The management parameters of the Fox model are given by:

$MSY = rKe^{-1}/\ln K$

$B_{MSY} = Ke^{-1}$

$f_{MSY} = r/q \ln K$

Pella and Tomlinson (1969) proposed a generalized model that can take any shape, including that of the Schaefer (m = 2) and Fox (m = 1) models.

$$\frac{dB}{dt} = rB - \frac{rB^m}{K} \qquad (10.6)$$

However, there is a price to be paid for this "improvement" and that is having to estimate an additional parameter (m) to fit the model to the data. This model is not much more useful because despite its "flexibility" the fit will probably be worse than with either the Schaefer or Fox models as there is a known inverse relationship between the number of parameters to be estimated and the performance of the models (see Hilborn and Walters, 1992).

10.2.3 Data requirements

In their simplest form, SPMs have only two data requirements:

- a time series of total catch data (including discards, bycatch, etc.)
- at least one time series of relative abundance data (usually CPUE from the fishery but data from fishery-independent surveys are preferable)

The abundance data can be constructed if we have the effort data corresponding to the time series of catches and if we assume that CPUE is linearly related to abundance. The assessment can greatly benefit if an estimate of the virgin biomass is also available, but this is not essential for applying the model. The longer the time series are and the better the quality of these data (see below), the greater chances of having a good assessment. Modern implementation of SPMs through Bayesian approaches can

incorporate additional heterogeneous information such as estimates of the intrinsic rate of increase of the stock, estimates of historical catches for which no effort or abundance index is available, and others (McAllister and Pikitch, 1998a; Apostolaki et al., 2002; Cortés et al., 2002).

10.2.4 Advantages and disadvantages of Surplus Production Models

These models offer an excellent cost/benefit ratio. Data requirements are modest compared with age-structured models, yet SPMs can yield critical information for assessment and management such as estimates of virgin and current biomass, level of depletion of the population, MSY, optimal effort (f_{opt}). Most importantly, they can be used to make *projections* of the population under several scenarios of management (quotas or efforts) and to evaluate the outcomes of each scenario. This is possible because SPMs incorporate explicitly the time variable unlike demographic analysis and yield per recruit (Y/R) models. Thus they are *dynamic* models that can be used to make *predictions*.

A further advantage (simplicity) but at the same time criticism (lack of biological reality) of SPMs is that they do not include age structure. They assume that all the processes occurring in a population can be captured by the simple processes described above while ignoring the size or age structure of the population and the dynamics of different parts of the population. Another common criticism of SPMs, especially in respect to elasmobranchs, is that they do not incorporate time delays between reproduction and recruitment. While this is true, in practice this seems to be the least of the problems for the application of SPMs to real shark fisheries. Often the shortage and bad quality of the data available for the assessment are more pressing problems. Using Monte Carlo simulation, Bonfil (1996) showed that despite criticisms of these models, SPMs can be useful for certain situations when applied to elasmobranch fisheries data.

10.2.5 Examples of use of Surplus Production Models in shark stock assessment

Aasen (1964) was the first to apply the Schaefer model to a shark fishery and probably the first scientist to perform stock assessment of an elasmobranch species. Although there was a dominant view 40 years ago that these models were not adequate for sharks due to incompatibility between the assumptions of the models and the biology of sharks, they are now widely accepted as applicable although not necessarily recommended as the best. They have been used in the multispecies shark fishery of the east coast of the USA (Otto et al., 1977; Anderson, 1980; McAllister and Pikitch, 1998a; McAllister et al., 2001; Cortés, 2002; Cortés et al., 2002), for the kitefin shark fishery in Portugal (Silva, 1987), the Australian fishery for school and gummy sharks (Xiao, 1995; Walker, 1999) and in the multispecies skate and ray fishery of the Falkland Islands (Agnew et al., 2000).

10.3 YIELD PER RECRUIT MODEL

This model, first developed by Beverton and Holt (1957), provides a steady-state (static) view of the population that allows determination of the catch or yield *relative* to recruitment (catch divided by recruitment, thus the yield per recruit or Y/R name of the technique) that can be obtained from a stock according to different levels of fishing mortality *F* (which is dependent on effort) and age of entry to the

fishery. The method is described in detail by Pitcher and Hart (1982), Megrey and Wespestad (1988), and Quinn and Deriso (1999).

The model describes the population in terms of the biological processes of growth, recruitment and mortality, and treats the exploited population as the sum of its individual members. It has more biological detail than surplus production models reviewed above but is not as powerful and detailed as the fully age-structured models treated below. Also, it is inferior to SPMs in the sense that it is static, assumes that there is no dependence between stock size and recruitment, and cannot provide estimates of absolute biomass or be used for making projections of stock size according to different management strategies. Its main utility is that it indicates if the fishery is catching fish at an age that is too early or too late to obtain the maximum biomass relative to recruitment, and whether the level of fishing mortality is adequate.

10.3.1 Data requirements and assumptions

The calculation of yield per recruit requires the following data:

- at least two mortality rates (Z total mortality; M natural mortality; or F fishing mortality [$F = Z\text{-}M$])
- the parameter k of the von Bertalanffy growth function (VBGF),
- the age of first capture in the fishery
- the age of recruitment to the stock
- the maximum age in the stock

The method has the following assumptions:

- there is a distinct spawning period and all fish recruit at the same time and age (they are both knife-edge processes)
- growth parameters do not change over time, stock size or age
- M is assumed known and constant over all ages and over time and stock size
- F is constant over all ages
- recruitment is constant and can be ignored
- the length-weight relationship has an exponent of 3
- there is complete mixing within the stock

10.3.2 The method

This model is based on three equations:

1. Von Bertalanffy Growth Model (in weight):

$$W_t = W_\infty (1 - e^{-k(t-t_0)})^3 \qquad (10.7)$$

2. Exponential survival model:

$$N_t = R \cdot e^{-M(t_c - t_r)} \cdot e^{-(M+F)(t-t_c)} \tag{10.8}$$

where R is the number of recruits, t_c is age at first capture and t_r is age of recruitment to the stock.

3. General yield equation:

$$Y = \int_{t_c}^{t_1} F \cdot N_t W_t dt \tag{10.9}$$

where Y represents yield (catch).

These three equations can be integrated (not shown here in the interest of space and simplification) to obtain the yield equation of Beverton and Holt (1957):

$$Y = F \cdot R \cdot W_\infty \cdot e^{-M(t_c - t_r)} \cdot \sum_{n=0}^{n=3} \frac{\Omega_n}{F+M+nK} \cdot e^{-nK(t_c - t_0)} \cdot (1 - e^{-(M+F+nk)(t_1 - t_c)}) \tag{10.10}$$

where:

- t_0 is the von Bertalanffy parameter that describes age at zero length
- t_1 is maximum age of fish in stock
- k is the von Bertalanffy growth coefficient
- and the integration constants Ω_0=1, Ω_1=-3, Ω_2=3, Ω_3=-1

Because the level of recruitment is not known, the above equation is usually expressed in relative terms, as yield per recruit:

$$\frac{Y}{R} = F \cdot W_\infty \cdot e^{-M(t_c - t_r)} \cdot \sum_{n=0}^{n=3} \frac{\Omega_n}{F+M+nK} \cdot e^{-nK(t_c - t_0)} \cdot (1 - e^{-(M+F+nK)(t_1 - t_c)}) \tag{10.11}$$

The model predicts the level of yield (catch) that can be obtained depending on the age of entry and maximum age in the stock, and the level of natural and fishing mortality.

This model allows managers to investigate the effects of varying fishing mortality (F) or age of first entry (t_c) on yield. One disadvantage of this model is that the shape of yield is completely determined by growth and mortality. If the stock has a low rate of growth and high M, the yield curve is asymptotical (this wrongly suggests yield does not decrease as you fish harder and harder). Conversely, if the stock has rapid growth rate and low M the yield curve is dome-shaped.

10.3.3 Advantages and disadvantages

The main advantages of the yield per recruit method is that it is relatively simple to implement and does not require historical data on catch and effort. It is a step forward from demographic methods because it tells us—within a relatively simple implementation procedure—if we are exploiting fish at the right age (or size), and also if we are fishing at the right intensity. Using this method we can provide

advice on the best age of entry to the fishery and the adequate level of effort, thus offering information that can potentially translate into direct management recommendations such as changing the mesh size of the gillnet used to catch sharks, or taking a number of boats out of the fishery to reduce fishing mortality.

The main disadvantages are that the method provides no estimate of the absolute biomass of the stock and gives only limited advice on management actions. Similarly to life tables, a disadvantage of this method is that it is not dynamic (there is no time variable) and therefore cannot be used to make predictions, and does not incorporate density-dependent processes like stock-recruitment relationships.

Other disadvantages are that the model unrealistically assumes constant growth and mortality rates; it is more expensive to implement than SPMs as age needs to be frequently determined for large samples of fish; the curve shape is predetermined and inflexible; the model predicts yield even at infinite effort and this is unrealistic; and yield is not expressed in absolute terms so the real magnitude of the catch cannot be known.

Using the Y/R method alone can be misleading as pointed by Grant et al. (1979). These authors suggested that the recommended ten-fold increases in fishing mortality from their Y/R assessment was bad advice as only a two-fold increase could already be reducing the reproductive stock of school sharks to less than half of its original abundance. Using a modified demographic method Au and Smith (1997) showed that the estimates of Y/R obtained by Smith and Abramson (1990) for the leopard shark (*Triakis semifasciata*) were considerably lower after adjusting for the effect of reduction in recruitment due to fishing. Also, Rago et al. (1998) found that the optimum age of entry predicted by the Y/R model would lead to recruitment failure and stock collapse in spiny dogfish (*Squalus acanthias*) because of the late age of maturity in this species. Another problem of the Y/R method is that a poor estimation of growth or mortality can influence very strongly all the conclusions and lead to decisions that could put the stock in jeopardy.

10.3.4 Examples of uses

This method has been used for stock assessment of school sharks by Grant et al. (1979), for little skate by Waring (1984), for leopard shark by Smith and Abramson (1990), for silky sharks by Bonfil (1990), for sandbar sharks by Cortés (1998) and for porbeagle by Campana et al. (1999; 2001). To the knowledge of the author this method has not been used as the main basis for the management of any elasmobranch species.

10.4 DELAY-DIFFERENCE MODEL

The delay-difference model of Deriso (1980) is a clever simplification that allows the inclusion of biological information of the species to be taken into account in a simple way. This model belongs to an intermediate class known as partially age-structured models, which represents a step forward from the rather simple surplus-production models that ignore biological processes like recruitment and individual growth, while avoiding the demanding data requirements of the more sophisticated fully age-structured models. It considers age structure implicitly, not explicitly.

The biological realism of the delay-difference model includes terms for recruitment, natural and fishing mortality, and growth. Yet, this model can be simplified to be fitted to data on catch and effort and an index of abundance, as in the case of surplus production models. Additional requirements are knowledge of the growth in weight of the species and an estimate of natural mortality. An important advantage of this model is that it has a smaller number of model parameters to be estimated in comparison to fully age-structured models. Thus it can be applied to fisheries with limited amounts of data while still offering a more realistic representation of population dynamics.

10.4.1 Deriso's simplifying finding

The delay-difference model was first proposed by Deriso (1980) and further generalized by Schnute (1985). The model incorporates four main types of biological information: body growth, recruitment, survival, and a measure of age structure. The main formula of the model links *present* available biomass (exploitable biomass or that recruited to the gear) to available biomass and population numbers *from the previous year*. The advantage of the model lies on several simplifications that allow the incorporation of important population dynamics processes into a simple equation. However, perhaps its more important characteristic is that the model allows for *time lags* in the dynamics of the stock, such as are found in species with slow growth and late age of entry to the fishery. This ability to take into account time delay is what gives the model its name of "delay-difference" model. Below is a detailed derivation of the delay-difference model taken from Hilborn and Walters (1992). This text should be consulted for further details about this and other models.

The model assumes that body growth of the exploitable stock can be represented by a linear function (the Brody equation):

$$w_a = \alpha + \rho w_{a+1} \qquad (10.12)$$

where w_a is body weight at age a, and alpha and rho are constants. This equation simply states that after a certain age, the typical von Bertalanffy model of growth in weight shown in Figure 10.02 below can be alternatively represented by a linear equation of weight at age a against weight at age a+1.

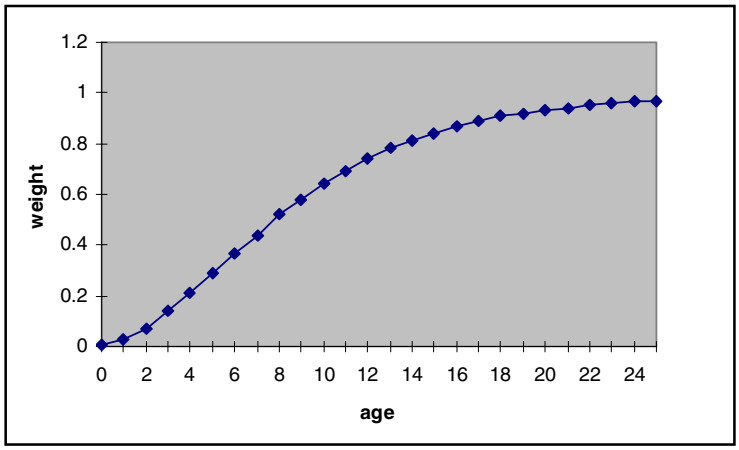

Figure 10.02 Individual growth in weight according to the von Bertalanffy Growth Model.

In order to find the parameters alpha and rho of the Brody equation, we must perform a linear regression as shown in Figure 10.03. This figure shows several possible linear regressions differing in how many points are considered for the regression (different starting points). Which regression we

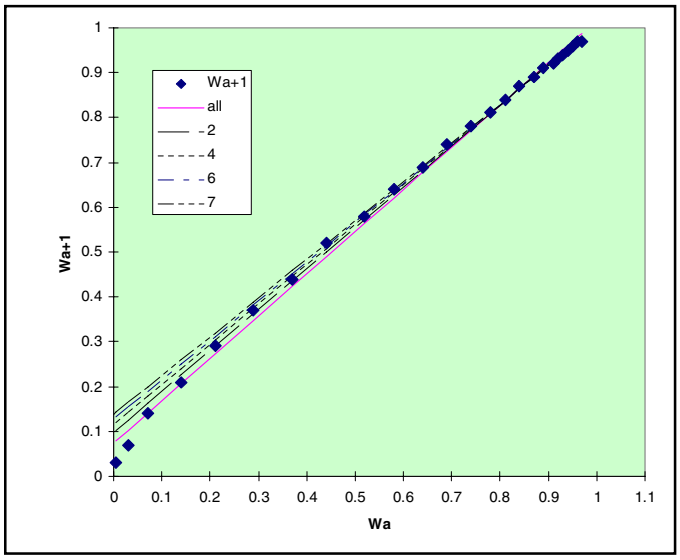

Figure 10.03 Ford-Walford plot of weights at age. Solid diamonds represent the original data points and each straight line is a linear regression using a different starting age (0, 2, 4, 6, and 7).

choose (and therefore which alpha and rho parameters we use in the model) depends on the age of entry to the fishery.

The delay-difference model also assumes that all fish older than age *k* (in this particular model age of entry to the fishery) are vulnerable to fishing and have the same natural mortality *M*.

Another simplification of the model considers that the total survival rate *S* at time *t*

$$S_t = e^{-Z} \tag{10.13}$$

can be decomposed into terms for constant and variable (harvest) survival:

$$S_t = \psi(1-h_t) \tag{10.14}$$

where *Ø* is the natural survival rate and *h* is the harvest rate in year *t*. This assumes that harvest (fishing) takes place in a short time during the beginning or end of the year.

Biomass at age can be represented as numbers at age times average weight at age:

$$\mathrm{B}_a = \mathrm{N}_a \bar{w}_a \tag{10.15}$$

This can be extended for the whole exploited population plus the recruitment R:

$$\mathrm{B}_t = \left[\sum_{a=k}^{a\max} \mathrm{N}_{t,a} \bar{w}_a\right] + w_k \mathrm{R}_t \tag{10.16}$$

remembering that *k* is the age of recruitment (to the gear or fishery). Population numbers N can be written as survivors from last year at age *a*-1, and all the weights at age can be written using the Brody equation, thus arriving at the following formula:

$$B_t = S_{t-1}\left[\alpha \sum_{a=k+1}^{a\max} N_{t-1,a-1} + \rho \sum_{a=k+1}^{a\max} N_{t-1,a-1}\,\bar{w}_{a-1}\right] + w_k R_t \qquad (10.17)$$

Factoring out terms that do not depend on age results in sums over age *k* and older for year *t*-1:

$$B_t = S_{t-1}\alpha N_{t-1} + S_{t-1}\rho B_{t-1} + w_k R_t \qquad (10.18)$$

And total numbers in the population are:

$$N_t = S_{t-1}N_{t-1} + R_t \qquad (10.19)$$

But we can write the term áN$_{t-1}$ of the equation as

$$\alpha N_{t-1} = \alpha S_{t-2}N_{t-2} + \alpha R_{t-2} \qquad (10.20)$$

And also, the term αS$_{t-2}$ N$_{t-2}$ can be expressed in terms of B$_{t-1}$ and N$_{t-2}$ using the equation for B$_t$ above, as:

$$\alpha S_{t-2}N_{t-2} = B_{t-1} - \rho S_{t-2}B_{t-2} - w_k R_{t-1} \qquad (10.21)$$

Combining the last two equations (substituting) and making some more algebraic manipulations we arrive at the delay-difference equation (Schnute, 1985):

$$B_t = (1+\rho)S_{t-1}B_{t-1} - \rho S_{t-1}S_{t-2}B_{t-2} - \rho w_{k-1}S_{t-1}R_{t-1} + w_k R_t \qquad (10.22)$$

This is the original form of the model and it requires seven parameters to predict biomass dynamics and to fit the model to catch and CPUE data:

- ρ and w_k, for the Brody growth equation
- ψ, the natural survival rate (no fishing)
- *a, b* or *a', b'*, for the stock recruitment relationship
- B_0, the stock size at the beginning of the fishery
- R_0, the recruitment at equilibrium (when mortality equals births)
- q, the catchability for the catch equation

Recruitment can be expressed using either the Ricker or the Beverton and Holt models, simplified by assuming that the population was in equilibrium (virgin population) when exploitation began.

For the Ricker recruitment model the equations are:

$$R_{t+1} = S_{t-k+1} e^{(a'-b'S_{t-k+1})} \quad (10.23)$$

$$a' = \ln \frac{(R_0)}{b'} + B_0 b' \quad (10.24)$$

For the Beverton and Holt recruitment model the equations are:

$$R_{t+1} = \frac{aS_{t-k+1}}{b + S_{t-k+1}} \quad (10.25)$$

$$a = R_0 \frac{(b + B_0)}{B_0} \quad (10.26)$$

Other parameters needed to fit the delay-difference model can be estimated externally or internally with some assumptions:

- ρ and w_k estimated directly from growth data
- ψ using external estimates of natural mortality M

This leaves us with only three parameters to be estimated during model fitting by non-linear methods:

- *b* or *b'* for the stock recruitment relationship
- B_0, stock size at the beginning of the fishery
- q, catchability for the catch equation

Thus, the delay-difference model can be simplified by fixing values for the first three parameters listed above and fitted to the catch and effort data by finding the values of the last three parameters using non-linear iterative methods such as those included in spreadsheet software. Remember that the parameter *a* or *a'* of the recruitment model is eliminated by the assumption above**.**

10.4.2 Advantages and disadvantages of the delay-difference model

The advantages of this model can be summarized as:

- The model offers more biological realism than SPMs without the demanding data requirements of fully age-structured models
- It takes into account the time delays due to growth and recruitment
- It can be fitted to simple catch-effort time series of data when information on mortality and growth is available
- Fitting the model to data requires estimation of a lesser number of parameters than fully age-structured models thus simplifying the estimation process and improving performance
- Can be used to estimate stock size and for the calculation of management benchmarks
- Can be used to make predictions of different management scenarios

The main disadvantages of this model are (Hilborn and Walters, 1992):

- They can provide an acceptable fit to the data in terms of goodness-of-fit criteria (see section on model fitting below) while estimating parameter values that are meaningless from the biological point of view (extremely high or low virgin stock sizes, virgin recruitment levels)
- They can sometimes provide very biased estimates of management benchmarks such as optimum fishing effort

10.4.3 Examples of the use of delay-difference models in shark stock assessment

This smart simplification of age-structured population dynamics was initially welcomed with excitement but has been seldom used in practice due to the availability of more sophisticated models that can be easily applied thanks to the powerful computer technology now readily available. The delay-difference model has not been used often for the assessment of shark fisheries, but Monte Carlo simulations executed by Bonfil (1996) showed that it performed better than surplus production models for estimating stock size in shark-like fishes. In addition, this model was used as part of the assessment of the school and gummy shark fisheries of Australia by Walker (1999). Cortés (2002) and Cortés et al. (2002) used a simplified version of the Deriso (1980) delay-difference model known as lagged recruitment, survival and growth model as part of the assessment of small and large coastal sharks, respectively, off the U.S. eastern seaboard.

10.5 VPA AND CATCH-AT-AGE ANALYSIS

This is a family of methods that is based on catch-at-age data. That means that the catch must be broken down into age-groups. These methods are more sophisticated and detailed, and have a higher sense of realism than previously reviewed models. Nevertheless, age-structured models are also extremely data demanding and require a lot of detailed information that is often expensive to obtain.

Age-structured models can be classified into two groups (Hilborn and Walters, 1992): Virtual Population Analysis or VPA, and statistical catch-at-age analysis or CAGEAN. These methods are recursive algorithms that calculate stock size based on catches broken down by each age class. Using these methods it is possible to estimate the magnitude of fishing mortality, levels or recruitment and the numbers at age in the stock for each past year using only catch-at-age and an estimate of natural mortality M.

VPA does the calculations without having a specific statistical underlying assumption. In contrast, the more sophisticated CAGEAN methods depend on formal statistical models and have been developed to the degree that various types of data can be integrated in a statistical framework to be used for the assessment. Thus, data on stock-recruitment (S/R) relationships, CPUE time series, biomass time series, and others can be integrated into a very powerful analysis. The stock synthesis method of Methot (1989) is one of the best examples of a sophisticated CAGEAN model.

10.5.1 Cohorts as the basis of VPA and CAGEAN

A fundamental part of age-structured models is the concept of *cohort*. A cohort comprises all the individuals (fish in this case) that were born in the same year. An example of a human cohort is all the persons that were born in 1960. The cohort of 1960 can be followed through time year after year by looking at individuals that are age 1 in 1961, age 2 in 1962, and so on. The size of the 1960 cohort in the year 2003 consists of all the individuals that were born in 1960 and have survived up to that year. The cohort concept is illustrated in Figure 10.04.

	Birth	Age 1	Age 2	Age 3	Age 4	...	Age 40	Age 41	Age 42	Age 43
1960	$N_{1960,0}$									
1961		$N_{1960,1}$								
1962			$N_{1960,2}$							
1963				$N_{1960,3}$						
1964					$N_{1960,4}$					
...						...				
2000							$N_{1960,40}$			
2001								$N_{1960,41}$		
2002									$N_{1960,42}$	
2003										$N_{1960,43}$

Figure 10.04 Diagrammatic representation of the 1960 cohort of humans (all individuals born in 1960). N represents the numbers of age A alive each year for cohort 1960.

VPA and CAGEAN are recursive recipes (algorithms) that track the history of each cohort in the exploited population back in time from the present to the time each cohort was born or more commonly to the time it recruited to the fishery. In other words, they calculate the number of fish alive in each cohort for each past year, following each cohort through time. Their aim is to reconstruct the entire exploited population in order to estimate fishing mortality and numbers at age for each age class each year.

10.5.2 Virtual Population Analysis

VPA is also known as *cohort analysis* because each cohort is treated separately. The method is based on the following equation:

N alive at beginning of next year = (*N alive at beginning of this year*) – (*catch this year*) – (*natural mortality this year*)

In this particular case recruitment is not considered because we are analyzing only a single cohort.

We can change the above equation to:

N alive at beginning of this year = (*N alive at beginning of next year*) + (*catch this year*) + (*natural mortality this year*)

Assuming that natural mortality M is known and that at some age *x* there are no more fish alive (that is, that all fish in the cohort die after age *x*) we can iteratively calculate the number of fish alive each year, starting from the *oldest* age and *moving backwards* to the youngest.

The basis of the method is the assumption that if we know that this year we have zero fish of the oldest age left alive, and we know how many of them we caught last year (in theory those were the last fish of that age left in the sea after those which died of natural causes) and if we know the instantaneous natural mortality rate, then, for fisheries where the fishing period is short, it can be assumed that there is no natural mortality during the short fishing period so that:

$$N_t = N_{t+1} + C_t + D_t \quad (10.27)$$

where

$$D_t = N_t (1-S) \quad (10.28)$$

so that

$$N_t - D_t = N_{t+1} + C_t \quad (10.29)$$

$$N_t - N_t (1-S) = N_{t+1} + C_t \quad (10.30)$$

$$N_t - N_t + N_t S = N_{t+1} + C_t \quad (10.31)$$

$$N_t S = N_{t+1} + C_t \quad (10.32)$$

$$N_t = (N_{t+1} + C_t) / S \quad (10.33)$$

where N is number of fish, C is catch, D is deaths (numbers dying), t is time (year) and S is the finite survival rate.

The last equation above is the key equation for VPA or cohort analysis, when fishing takes place in a single short period of time during which we can consider M to be negligible. This equation allows the calculation of the numbers last year from the numbers this year, the catch-at-age and natural mortality, but because we assume there were no more fish left of the oldest age this year (we fished them all or they died) we can calculate the numbers last year with only catch and mortality.

10.5.2.1 An illustrative example of the principles of VPA

We will illustrate VPA with a hypothetical example. Consider a shark species that lives only to 10 years (such as *Rhizoprionodon terraenovae*) when we assume that all the individuals die. Consider a situation where this species recruits to a fishery at age three. Furthermore consider that this fishery takes place in only a couple of weeks each year when the fish come to a mating aggregation. The information we need for the cohort analysis is an estimate of M, which for this stock we will consider to be 0.5 (finite rate), and the total catch of fish in each age class for each year. A table with such hypothetical catch data is given in column 3 of Table 10.01 and represents the total numbers in the catch for the cohort of *Rhizoprionodon terraenovae* born in 1980. Using these data and the following equations we can obtain estimates of:

- the population at the end of the fishery each year
- the population just before the fishery each year
- the harvest rate, and
- the instantaneous fishing mortality rate

Year	Age	Catch	Cohort size at start of year	Cohort size before fishery	Harvest rate	Instanteous fishing mortality rate
1990	**10**	**0**	0	-	-	-
1989	**9**	**900**	1,800	900	1.00	Infinite
1988	**8**	**2,480**	8,560	4,280	0.58	0.87
1987	**7**	**6,032**	29,184	14,592	0.41	0.53
1986	**6**	**13,985**	86,338	43,169	0.32	0.39
1985	**5**	**8,183**	189,042	94,521	0.09	0.09
1984	**4**	**7,653**	393,390	196,695	0.04	0.04
1983	**3**	**2,045**	790,870	395,435	0.01	0.01

Table 10.01 Hypothetical example of data (bold font) required and the results of a cohort analysis for a short-lived elasmobranch. Loosely based on the life history of *Rhizoprionodon terraenovae*. See text for explanation on methods to calculate each column.

For this we will need the equation for numbers at the start of the year:

$$N_t = (N_{t+1} + C_t) / s \qquad (10.34)$$

And the following equations:

For numbers alive at the beginning of the fishery:

$$N_t' = N_t S \qquad (10.35)$$

For the harvest rate:

$$h_t = C_t / N_t' \qquad (10.36)$$

And for the instantaneous fishing mortality rate:

$$F_t = - \ln (1-h_t) \qquad (10.37)$$

Table 10.01 shows the results of the calculations for the cohort born in 1980; but other cohorts can be treated in the same way for a full VPA. For the last cohort in the last year of data we assume there are no fish left, they all die after age 10 in 1990. The table is constructed for this cohort using equation (10.34) to calculate cohort size at the beginning of each year (note that fish age 10 in 1990 were age 9 in 1989, etc.). The equations for VPA when fishing takes place during the whole year (continuous fishing) are more complicated and can be found on Hilborn and Walters (1992) and Quinn and Deriso (1999), while Sparre and Venema (1992) introduce length-based VPA.

The above example of cohort analysis includes only one cohort. For a complete VPA, the same method should be applied for all cohorts that have completely ceased to exist, which is all cohorts that are no longer present in the fishery. One remaining problem after doing this is that we still would not have information to do the analysis for incomplete cohorts (those still present in the fishery) and these are usually the most important for managers.

One way to solve the problem of incomplete cohorts is to estimate the fishing mortality rate of cohorts currently being fished and use this to estimate the sizes of the incomplete cohorts. Two ways to estimate the size of current cohorts are to obtain population size estimates from surveys or mark-recapture methods, or most commonly, to assume a value for the current F and estimate previous values from there.

This last case is known as the *terminal F assumption* and comes from the following equation:

$$N_t = \frac{C_t}{(1-e^{-z_t})}\left(\frac{F_t + M}{F_t}\right) \qquad (10.38)$$

There are two ways to estimate the F here, one is from tag-recapture methods, or we can estimate it from effort (f) data while assuming that q is known using F = fq.

The catchability coefficients q for each age can be obtained from the complete cohorts, and assuming q is constant over time we can use that together with effort data to calculate F for each age. Another variation of this approach is known as the "tuned" VPA which first uses the q's from complete cohorts and this is used to derive a new set of q's for the incomplete cohorts.

10.5.2.2 Disadvantages

The problems of VPA are that using the wrong M estimate can lead to severely overestimated or underestimated cohort sizes. More worryingly, when catchability increases as the stock declines in size, using the assumption that the terminal F has not changed has been found to introduce great errors, overestimating the stock size and probably recommending larger catches than can be sustained, which can lead to overfishing of the stock.

Another problem is that to obtain the necessary catch-at-age data it is essential to perform routine ageing of large samples of fish from the catch (which is costly) and if the ages are wrongly estimated this will introduce systematic biases to the assessment.

10.5.2.3 Examples of usage of VPA for shark stock assessment

Smith and Abramson (1990) used backward VPA in combination with Y/R to estimate replacement rates of leopard sharks off California

10.5.3 Catch-at-age analysis

CAGEAN, or statistical catch-at-age analysis, is very similar to VPA with the difference that, in order to deal with the incomplete cohorts, it uses formal statistical methods to estimate the current

abundance of these cohorts. CAGEAN methods also provide a means to estimate natural mortality rate provided that the data have clearly contrasting levels of fishing effort and total mortality rate.

CAGEAN starts by using the catch curve concept (see Chapter 8), to calculate the instantaneous total mortality rate for each age class from the catch at age data. Just in the same way we can build catch curves for the catches at age of one single year, we can apply the same concept to the catches of all cohorts between subsequent years. The equation used for normal catch curves (one single year of data) is a linear regression of the numbers-at-age in the catch (C_a) against age (a), where the slope of the line is the estimate of Z, and the intercept of the Y axis represents the logarithm of the recruitment (R) times the vulnerability to the gear (v):

$$\ln(C_a) = \ln(Rv) - Za \tag{10.39}$$

In order to use the catch equation to estimate mortality within a single cohort we use a modified version of the catch curve with the following equation:

$$\ln(C_{aj}) = \ln(R_j v) - Za \tag{10.40}$$

where j is used to denote a specific cohort. This allows the estimation of the total mortality and the relative recruitment "strength" of each cohort. This method assumes that fishing and natural mortality are constant, and that vulnerability to the fishing gear is constant above a given age. One problem is that these catch curves do not allow us to estimate natural mortality rate or vulnerability, so their usefulness is limited. CAGEAN is a modification of these techniques. A simple introduction to the CAGEAN methods explained below is provided by Hilborn and Walters (1992) and is recommended for beginners; Quinn and Deriso (1999) offer an updated and mathematically and statistically more rigorous treatment of the same topics.

10.5.3.1 Paloheimo method

There are several versions of the CAGEAN method. That of Paloheimo (1980) is the simplest one and the one analyzed here with some detail. The Paloheimo method uses the following equations and some algebra to arrive at its key equation.

We begin with the catch equation, which in this version assumes that fishing mortality acts separately from natural mortality and is responsible for a fraction (F/Z) of the total mortality

$$C = N \frac{F}{F+M}\left[1 - e^{-(F+M)}\right] \tag{10.41}$$

Secondly, the equation below relates numbers at age *a* to recruitment times cumulative fishing and natural mortality for each previous age.

$$N_a = \mathrm{Re}^{-\Sigma F - \Sigma M} \tag{10.42}$$

We also use the following equation which assumes linearity between effort and fishing mortality:

$$F = fq \tag{10.43}$$

where f is effort and q is catchability.

All the above equations combined together and manipulated through algebra give us:

$$\frac{C_a}{f} = \mathrm{Re}^{-q\Sigma f - \Sigma M}\, q \cdot \frac{1-e^{-z}}{Z} \tag{10.44}$$

This equation relates CPUE at age to recruit numbers, catchability, total and natural mortality, and effort. Applying algebra it can be shown that this becomes:

$$\ln\left(\frac{C_a}{f}\right) = \ln(\mathrm{R}q) - q\sum f - \sum M + \ln\left(\frac{1-e^{-z}}{Z}\right) \tag{10.45}$$

The Paloheimo method assumes that M is constant over years and uses a well-known approximation for the last term (which is valid for values of Z that are no larger than 0.7):

$$\ln\left(\frac{1-e^{-z}}{Z}\right) \approx -\frac{Z}{2} \tag{10.46}$$

Then after some algebra we obtain the final Paloheimo equation:

$$\ln\left(\frac{C_{aj}}{f_j}\right) = \ln(\mathrm{R}_{\text{j-a}}q) - q\left(\sum_{k=j-a}^{j-i} f_k + \frac{f_j}{2}\right) - M\left(a - \tfrac{1}{2}\right) \tag{10.47}$$

where *j* = year, *a* = age, and *k* = the number of years that the cohort has been fished.

The above equation is only a linear multiple regression of the form:

$$Y = b_0 + b_1X_1 + b_2X_2 \tag{10.48}$$

Given the needed data (usually catch by age for several ages, and the corresponding effort that produced the catches), this equation can be easily solved with standard multiple regression packages to obtain estimates of *Rq*, *q*, and *M*.

The following simple example (taken from Hilborn and Walters, 1992) shows the application of the Paloheimo method. Table 10.02 presents the required data on catches at age and corresponding efforts for Lake Erie perch.

Age	Catch	Effort
2	103	15.9
3	59	15.4
4	11	13.5
5	3	12.6

Table 10.02 Data on catch at age and corresponding effort for the 1971 cohort of Lake Erie perch (taken from Hilborn and Walters, 1992).

The estimates of the parameters after applying the Paloheimo methods are as follows:

$$\text{Ln}(Rq) = 2.37$$

$$q = -0.22$$

$$M = 4.34$$

The correlations between the parameters are shown in table 10.03.

Parameter correlations

	R_q	q	M
R_q	1		
q	-0.71	1	
M	-0.69	-1	1

Table 10.03 Parameter correlations for the CAGEAN analysis based on the Paloheimo method for the data of table 10.02 (taken from Hilborn and Walters, 1992).

These results are suspicious and suffer from strong parameter correlation. This occurs because of poor data contrast (see section 10.6.4 below); q is negative, which is impossible, while M is extremely high. Notice that to be able to perform this catch-at-age analysis we needed not only the catches at age for each year for this cohort, but also the efforts that were applied to fish them. These efforts are all of the same magnitude and almost constant (very poor contrast in effort), and this is why there is a strong parameter negative correlation between q and M.

If instead we were to simultaneously analyze data for three cohorts of Lake Erie perch using this method (see example in Hilborn and Walters (1992) for further details), we would have to resort to using dummy variables or what is known as an experimental design table, to perform the multiple linear regression. In this case, the equation becomes:

$$Y = b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5 \qquad (10.49)$$

where the first three b's represent the recruitment level of each cohort. The dummy variables $X_{1\text{-}3}$ take the values 1 or 0 depending on which cohort we are analyzing, so that the corresponding b (recruitment) is taken into account or not. The last two terms are the same as before; they are the efforts and the number of years of accumulated natural mortality. If we were to perform the analysis the results would still not be satisfactory because there is still poor data contrast in the effort for this set of data despite the

fact that there are data for three different cohorts and four different years of fishing. It is still impossible to differentiate between the effects of natural and fishing mortality from these data. However, it is possible to obtain good estimates of the recruitment levels because there is good contrast in the relative abundance data (CPUE).

10.5.3.2 Doubleday method

Another and more general approach to the catch-at-age method was put forward by Doubleday (1976). This method does not assume a linear relationship between the variables and is thus more difficult to calculate, requiring non-linear estimation methods. Its advantages are that fishing mortality F is not assumed proportional to effort, so the method can be applied in the absence of effort data. However, this method is not free from the general problem that a good contrast is needed between fishing mortalities for good parameter estimation. The main Doubleday equation is presented below, more details about this method can be found in Hilborn and Walters (1992) and Quinn and Deriso (1999).

$$\ln\left(C_{aj}\right) = \ln(\mathrm{R}_{\mathrm{j\text{-}a}}) - \sum_{k=1}^{a-1} F_{a-k,j-k} - \sum_{k=1}^{a-1} M_{a-k,j-k} + \ln\left(\frac{-F_{aj}}{F_{aj}+M_{aj}}\left[1-e^{-\left(F_{aj}+M_{aj}\right)}\right]\right) \qquad (10.50)$$

10.5.3.3 Other methods

An even more sophisticated and more powerful method is that developed by Fournier and Archibald (1982). Paloheimo and Doubleday derived their models assuming an underlying deterministic process but in nature everything is measured with error and occurs also with natural variability, which can be interpreted as noise. The method of Fornier and Archibald is very flexible and accounts for explicit estimation of errors in:

- C, the catch measurement,
- F, the fishing mortality,
- S/R, the stock recruitment relationship

Their method explicitly accounts for a stock recruitment relationship. This method is very sophisticated both mathematically and statistically so it is not analyzed here, but has the advantage that it can include several types of external information that can help in the estimation of parameters, such as estimates of recruitment levels, fishing mortalities from other studies, and effort data. A further sophistication of this type of analysis was developed by Methot (1989) and is even able to use CPUE, gear selectivity and independent survey biomass data in the estimation of parameters.

10.6 PRINCIPLES OF FITTING MODELS TO DATA

Some of the models used in fisheries stock assessment are very simple but the estimation of their parameters, which implies fitting the models to the data, is not always a simple task. In the case of the surplus production models treated above, there are three main approaches that are commonly employed for the estimation of their parameters.

First, we might assume equilibrium conditions, that is, that all the catches observed so far in the fishery are sustainable. **This is absolutely wrong and must always be avoided**. Equilibrium methods were used decades ago to simplify the computations because of difficulties in calculating parameter values analytically. However, modern computers allow anyone to use any of the other methods mentioned below or even more sophisticated ones and there is no longer any excuse to assume equilibrium. Never use equilibrium methods.

10.6.1 Linear regression

A better option than assuming equilibrium is to use linear regression. Using the case of the Schaefer model as an example, it is shown below that this model can be expressed as a linear equation to which we can then apply standard regression methods to find the values of the parameters and fit the model to our data.

Given the Schaefer model equation for biomass dynamics in a fishery:

$$B_{t+1} = B_t + rB_t(1-\frac{B_t}{K}) - qf_tB_t \qquad (10.51)$$

we have that

$$U_t = \frac{C_t}{f_t} = qB_t \qquad (10.52)$$

and

$$B_t = \frac{U_t}{q} \qquad (10.53)$$

thus, substituting the last equation in the first, we arrive at:

$$\frac{U_{t+1}}{q} = \frac{U_t}{q} + r\frac{U_t}{q}(1-\frac{U_t}{qK}) - f_tU_t \qquad (10.54)$$

Rearranging, dividing by U_t and multiplying by q we obtain:

$$\frac{U_{t+1}}{U_t} - 1 = r - \frac{r}{Kq}U_t - qf_t \qquad (10.55)$$

The above equation is in reality a linear equation of the general form:

$$Y = b_0 + b_1X_1 + b_2X_2 \qquad (10.56)$$

which can be easily solved using the multiple regression facilities available in most spreadsheet software programs.

Although regression methods are easily applied to solve fisheries models, it has been demonstrated that they can give very biased answers (Uhler, 1979). They can also produce obviously

wrong answers, such as negative values of *r* or *q*, which are biologically impossible. The general corollary is that illogical answers only mean bad data!

10.6.2 Time-series fitting

The most recommended method to fit fisheries models to data is time-series fitting. According to Hilborn and Walters (1992), this method was first proposed by Pella and Tomlinson (1969) and implies taking an initial estimate of the stock size at the beginning of the time series of data (catch and CPUE) and using the Schaefer model to predict each point in the entire time series of data. Initial parameters values (guesses) are iteratively adjusted to minimize the difference ($å_t$) between the observed CPUE and the CPUE predicted by the Schaefer model:

$$\varepsilon_t = (\hat{U}_t - U_t)^2 \qquad (10.57)$$

Where *U* (CPUE) is:

$$\hat{U}_t = q\hat{B}_t \qquad (10.58)$$

This means that we have to estimate *r*, *q*, *K*, and the initial biomass size B_0. Usually, the problem of finding the best parameter values (while minimizing the above difference) is solved by using nonlinear estimation procedures (such as those available in spreadsheets).

10.6.3 Introduction to Bayesian estimation

Bayesian estimation is the state-of-the-art and most powerful method for fitting fisheries models to data. It is a very useful method because it allows the incorporation of previous knowledge we might have about the system in question into the estimation process, effectively helping to find solutions that make more sense. The types of additional information that can be incorporated into Bayesian estimation are extremely varied and include items like fishery CPUE, independent survey CPUE, catches, estimates of intrinsic rate of population growth from life-table analyses, biological limits, knowledge from similar stocks, mark-recapture information, and others.

Another advantage is that Bayesian estimation is extremely useful because it tells us a lot about the uncertainty of the parameter estimates. The estimation is based mainly on using previous knowledge to assume a probability distribution for the parameters that will be estimated. This distribution is known as the *prior probability distribution* or just “the prior”. Although relatively new in fisheries stock assessments, Bayesian estimation has rapidly become the most powerful and accepted method to fit models to data in recent years.

Bayes theorem is based on the *conditional probability*, and states that the probability of a parameter or group of parameters given certain data is equal to the product of a) the probability of the data given the parameters and b) the probability of the parameters themselves, all of this divided by the sum over all possible parameter values of the product of a) and b):

$$\Pr\{parameters \mid data\} = \frac{\Pr\{data \mid parameters\} * \Pr\{parameters\}}{\sum_{parameters} \Pr\{data \mid parameters\} * \Pr\{parameters\}} \quad (10.59)$$

The left term of the equation is the posterior probability distribution or "posterior". The right-most terms on the upper and lower part of the equation imply that we have previous knowledge about the shape of the distribution of the parameters. And this is the strength of the method as this is what allows us to include additional "external" information into the estimation process, such as biological or fisheries information we might have at hand.

Depending on the type of external information that we want to incorporate, there are different possible prior distributions we can use for the parameters such as the binomial, normal, uniform, Poisson, multinomial and others. For more details about the types of distributions for different types of data users should consult a statistical text book.

A rudimentary but simple way to implement Bayesian statistics is to calculate the "kernel" which is based on the sum of squares:

$$L(parameters) = SS^{-\frac{t-1}{2}} \quad (10.60)$$

where L is the likelihood of the parameters and SS, the sum of squared differences between the real data and the estimated data points derived from a given set of model parameter values, and t-1 is the degrees of freedom.

$$\Pr(parameters \mid data) = \frac{SS^{-\frac{t-1}{2}}}{\sum_{parameters} SS^{-\frac{t-1}{2}}} \quad (10.61)$$

Bayesian approaches have been recently applied to elasmobranch fisheries by McAllister and Pikitch (1998a,b), Punt and Walker (1998), Babcock and Pikitch (2001), McAllister et al. (2001), and Apostolaki et al. (2001, 2002) among others. Berger (1985), Gelman et al. (1995), and Congdon (2001) provide a comprehensive treatment of Bayesian analysis. The reader is also referred to Hilborn and Walters (1992), Quinn and Deriso (1999) and Haddon (2001) for a more in-depth treatment of parameter estimation issues.

10.6.4 Data quality

An extremely important principle of practical fisheries science identified by Hilborn and Walters (1992) and one often overlooked is that *we cannot understand how a fish stock will respond to exploitation until the stock has been exploited.* A good stock assessment depends as much on having an adequate model to describe the system dynamics as on the quality of the data that the model is fitted to. Data quality does not only mean whether there are biases or errors, but also on how much information is embedded in the data. Historical *variation* in stock size and fishing pressure is needed in the data in

order to estimate the parameters of the model with any degree of reliability. Otherwise the assessment can produce a meaningless set of numbers that do not represent the stock dynamics well.

The most important quality of fisheries data is the degree of *contrast* imbedded in the data. In order to obtain good parameter estimates data must have high contrast. Following with the SPM example, ideally we should have a data point at low stock sizes with low fishing effort (for information about r), a data point at high stock sizes with low fishing effort (to estimate qK) and a data point at high fishing effort to estimate q. This is very difficult to find in a real fishery because of the way most fisheries develop. Typically, low effort at large stock sizes is gradually increased to very high levels that usually lead to low stock sizes. Thus we usually miss having a point of low fishing effort at low stock sizes. This common way in which fisheries develop leads to the most *uninformative* type of data and a typical case known as the "one way trip", in which the data show an increase in effort with time that is accompanied by a declining CPUE (see Figure 10.05). This *lack of contrast* in the data makes for very *uncertain parameter estimates*. In general, the standard deviation of such parameters is as large as, or larger than, the actual parameter values, clearly signaling very unreliable results. Under such circumstances management will be severely handicapped.

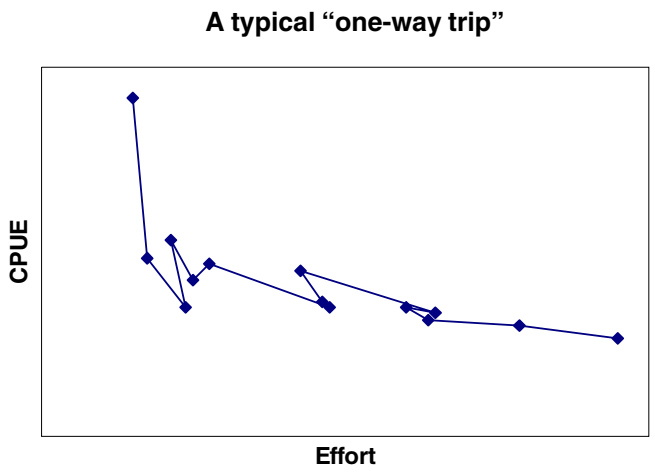

Figure 10.05 Hypothetical example of a "one-way trip" type of data (modified from Hilborn and Walters, 1992).

Data with *better contrast* can be obtained when a fishery shows a period of increased effort followed by a period when effort was reduced gradually such that the stock was allowed to rebuild after heavy exploitation. This case has been termed by Hilborn and Walters (1992) as "moving up and down the isocline". Note from Figure 10.06 how there is a better scatter in the data points instead of all falling along one single line as before. These data have inherently more variation and contrast than the preceding example (the solid diamonds in the figure represent the start and finish points of the time series). Typically, in these cases the model parameters are much more precisely estimated than in a "one-way trip" case, but the slow pace of change in effort in these data still does not generally provide enough contrast for good precision. In cases like the one pictured in the figure, the standard deviation of the

parameters is usually about half or less than the actual parameter estimates and although not good enough it is better than in the previous example.

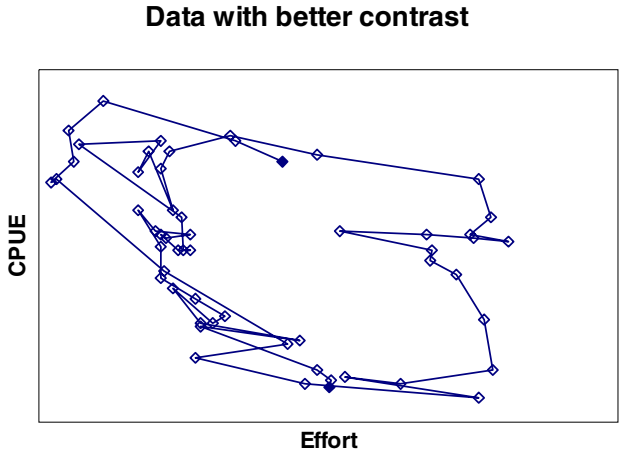

Figure 10.06 Hypothetical example of data with better contrast (modified from Hilborn and Walters, 1992).

Data sets with *high contrast* have strong variations in the data, with relatively rapid changes back and forth between high and low effort. In these cases, parameters can be much more precisely estimated although other factors such as the total number of points in the time series of data and the intrinsic variability of the data also have an influence on the final precision of model parameter estimates.

In summary, when fitting models to fisheries data it is imperative to look at the uncertainty in the parameter estimates, not only at a single "goodness-of-fit" measure such as the sum of squares. It is always advisable to apply different models to the same data set and compare the results between models, trying to validate results or to ask questions about why results might be different and what the implications of this are. In addition, it is important to learn how to use uncertain ("bad") results to try to improve the contrast in the data through carefully thought and well planned management regulations aimed at improving the quality of the data (such as large variations in effort over short periods of time).

10.6.5 The relationship between CPUE and abundance

At the core of most fisheries models that make use of fisheries-dependent CPUE information (and most of them do) there is an important assumption: the abundance of the fish stock (or other aquatic animal) has a direct relationship with CPUE. In other words, these models assume that CPUE is an index of abundance. This can be expressed mathematically for fisheries where the fishing season occurs as a single pulse or over a relatively short part of the year as:

$$C_t = qf_t B_t \longrightarrow U_t = qB_t$$

where U_t is CPUE at year t. According to the last expression, CPUE is directly linked to biomass (abundance) by a constant factor q, known as catchability factor. The above model assumes that there is *proportionality* (a linear relationship) between CPUE and the abundance of the stock. This is a very

dangerous but necessary assumption of most fisheries models, but one that should be questioned and checked for. According to Hilborn and Walters (1992) the relationship between CPUE and abundance can have at least two other forms apart from the linear form. *Hyperdepletion* occurs when the stock abundance decreases at a much slower rate than the CPUE. Thus the CPUE signal tells us that the stock abundance is low when it is still high. If we do not detect that this is a case of hyperdepletion, we would believe that we are overexploiting the stock when in fact the stock might be in a good state. *Hyperstability* happens when the stock abundance falls more rapidly than the CPUE index, thus giving us the opposite impression, that the stock abundance is still high when in fact we might be already dangerously overexploiting the resource.

Hyperdepletion can occur when the species is being exploited only over a relatively small part of its range, as when there are natural refuge areas (such as deeper waters or rougher grounds where the gear cannot fish). In such cases the exploited part of the stock will decrease rapidly but the overall abundance of the entire stock might not. Given that the abundance index (CPUE) is based only on the fishing grounds, it will show a faster decrease than if it was based on fishing over the entire geographical range of the stock.

Hyperstability is a well-known phenomenon in fisheries for highly gregarious or schooling species such as herrings, sardines, anchovies, and tunas. In these fisheries, searching for fish schools is highly efficient and fishing an entire school once located is also relatively quick and efficient, while the remaining schools remain concentrated as the overall abundance of fish goes down.

Possible ways to detect a lack of proportionality between CPUE and effort include mapping and stratification of CPUE and effort data to analyze spatial patterns, and depletion experiments to gain additional information. Overall, hyperstability is far more common in the real world apart from being more dangerous, as it leads to stock collapses. However, a more straightforward, if not easier, way around this is to obtain *fishery-independent indices of stock abundance* (see Chapter 12), either through research cruises or by coordinating efforts with fishermen to perform orchestrated experiments to fish in other areas or other ways than they would usually do, such as following a systematic sampling design. Quinn and Deriso (1999) summarize different ways to model non-linear relationships between CPUE and abundance.

Finally, it should be mentioned that generalized linear models (GLMs) are becoming common practice to standardize fishery-dependent CPUE data. These methods take account of the effect of various factors (such as environmental variables or fishery operational variables) on catch rates.

10.7 CONCLUSIONS AND RECOMMENDATIONS

Fisheries stock assessment in not really a problem of the species or group under analysis but rather a problem of the approach used for the analysis. There are several methods available to perform stock assessment and some of them have been presented here in detail. However, the important message

to take home and the one to keep always in mind is that there are three main rules for good stock assessment:

1. The data drive the analysis, and although we should always try to do the best we can with whatever data we have, only complete and good quality data will provide us with reliable assessments in the long run. Having limited or incorrect data will always provide only limited and uncertain advice no matter which models are used. The main focus and problem for elasmobranch stock assessment is not the model used, but the data that are available. For this reason, fisheries managers should strive to build the necessary systems to collect the appropriate information needed for stock assessment.
2. There is no single "best" model that should be used for fisheries stock assessment. The best assessment is one that uses ALL the models that can be applied depending on available data, and compares the results of all models to detect inconsistencies, coincidences, and patterns. A complete picture of the situation can only be obtained when we question the conclusions from one analysis with those of a different analysis and critically use the different results to gauge our conclusions, improve the data and therefore have the capacity for better assessments in the future.
3. Stock assessment is a neverending and dynamic process. It is one in which we use the models not only to decide how many fish we should take next year or how many fishermen we should allow to fish, but also, and perhaps more importantly, to set goals about the ways in which we obtain our fisheries data, the type of data we are lacking (including biological and ecological information) and that must be obtained from this point onwards in order to improve the quality of our assessments. Fisheries stock assessment must be a feed-back system in order to be successful.

Table 10.04 presents a few examples of real elasmobranch fisheries with a list of their characteristics, the methods used in each case for stock assessment, the status of the fishery and major references. These examples can be reviewed more closely by those interested in more detailed analyses of real elasmobranch fisheries and the practice of their stock assessment and management.

Fishery	*Species*	*Catch level*	*Management System*	*Stock Assessment Methods*	*Status*	*Main References*
Southern Australian shark fishery	*Galeorhinus galeus, Mustelus antarcticus* and other spp	2,800 t/y	Controls on amount of gear (licenses)	Surplus Production, Delay-difference and Age-structured models	Overexploited, under recovering regulations	Walker 1999
Canadian Porbeagle shark fishery	*Lamna nasus*	850 t/y	TAC (250 t), Fishing licenses plus fishing restrictions	Catch curves, catch rate trends, age-structured model	Overexploited, under severe recovering regulations	Campana et al. 1999, 2001
New Zealand shark fisheries	*Galeorhinus galeus, Squalus acanthias, Callorhinchus milii, Mustelus lenticulatus, Raja spp. Hydrolagus spp.* and other 15 spp	17,000 t/y	ITQs and TACs	None, quotas established through ad hoc methods (proportion of past catches)	Recovered after overxploitation or unknown	Francis and Shallard 1999
East coast of US shark fishery	39 species mostly *Carcharhinus*	3,500 t/y	TAC	Bayesian Surplus Production Models	Overexploited, under recovering regulations	MacAllister and Pikitch. 1998a, b; Branstetter 1999
Gulf of Mexico shark fisheries	35 species mostly *Carcharhinus*	12,000 t/y	5 prohibited species and other simple regulations	None	Unknown, likely heavily overexploited	Bonfil 1997, Castillo et al. 1998
Argentinean shark fisheries	*Mustelus schmitii, Galeorhinus galeus, Carcharhinus brachyurus* and other 10 spp	30,000 t/y	None	None	Unknown, likely heavily overexploited	Chiaramonte 1998

Table 10.04 A referenced selection of real shark fisheries, summarizing their main characteristics, the assessment methods in use and the state of management and the resource.

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CHAPTER 11. FISHERY-DEPENDENT SAMPLING: TOTAL CATCH, EFFORT AND CATCH COMPOSITION

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11.1 INTRODUCTION

Fishery-dependent data collection is one of the most valuable tools available to fishery managers. The management plans put into effect based on this type of sampling will only be as good as the data collected. It is critical that managers determine what is the most important data to be collected and implement some system of data recording before signs of overfishing occur. One of the biggest mistakes fishery managers make is waiting until the populations are in peril before initiating some type of management plan. This chapter provides a wealth of information on what type of data should be collected in a shark fishery, why they should be collected and what methods can be used for collection.

11.2 CATCH ESTIMATES

11.2.1 Why and how to collect catch estimate data

Fisheries resource managers must rely on several key factors in determining the status of a fishery. Among these factors are the catch estimates for both target species and any bycatch involved in the fishery, or of all species in a multi-species fishery. Each individual fishery should maintain a continuous database that includes all reported catch, estimates of discard, and estimates of non-reported catch. Catch estimates can be obtained in a variety of ways including fishery observers, logbooks, dockside and shoreside monitoring. Each of these monitoring systems will be discussed in more detail later in this chapter.

Catch estimates are used to illustrate the species composition of individual fisheries and utilization rates, monitor quotas, estimate fishing mortality, and to calculate Catch Per Unit Effort (CPUE). These estimates include not only what is sold at port, but also that which is discarded or utilized as bait at sea and that which is retained for personal consumption or transferral by the vessel's crew. In other words, all fishes retained or discarded should be documented. This type of information becomes extremely important in fisheries where quotas are used as a management tool. Catch estimates allow managers to determine the current status of a fishery and whether the quotas have been met, are being underutilized or have been exceeded. The data produced from catch estimates can also be used to show historical trends in the fishery commonly used to build quota systems, and estimate the population abundance. These numbers can also be integrated into models to predict the outcome of future management plans or what effect current management will have on the stock.

Catch estimates are critical and can be a very contentious shark fishery management issue in countries with well-developed fisheries and fishery management regimes. Catch numbers data often come to fishery managers from vessel captains/owners or shoreside marketers who, understanding that high catch figures might lead to management resulting in reduced future catches, are prone to underreport the actual catches. However, in areas with government-run fisheries, the opposite may be true as fishers and marketers are inclined to demonstrate higher productivity to their superiors. In Individual Transferable Quota fisheries, fishers may overreport their catch in order to ensure a large

individual quota. Since managers who determine the status of a fishery use these data, underreporting or overreporting can result in inappropriate or unfair management measures, such as unreasonably high quotas, and can lead to overfishing, which ultimately negatively affects all stakeholders. It is imperative that every effort be made to monitor the accuracy of all catch estimates.

11.2.2 Catch disposition

In areas where not all the catch is marketed, at-sea monitoring provides the most robust catch data. At sea, fishery observers should accurately record the number of individuals by species, note whether the shark is alive or dead when landed, and record the final disposition of each shark brought aboard a vessel. Disposition is the final fate of the shark, (e.g., saved for market, used for bait, discarded live, discarded dead, discarded after removing fins, etc.). On field data sheets, codes should be made for each possible disposition that are both easy to use and to remember; commonly, initials or letters are used that correspond to each type of disposition.

Disposition estimates for individual species allow fishery managers to better understand what is actually happening in the fishery. For example, in the U.S. Atlantic shark fishery, several hammerhead species are commonly caught but not landed (because their flesh is not marketable). Therefore, the catches of these species do not appear in market or dockside data sets. Disposition data taken by at-sea observers allow fishery managers to acknowledge the cryptic mortality incurred by all species caught and can help detect declines in abundance. At-sea catch estimates often give a very different view of what is actually happening in a fishery than landings (marketed catch) data. However, in areas where the entire catch is brought back to port, landings data accurately depict the scope of total fishing mortality (but not the gear-induced fishing mortality).

11.2.3 Bycatch

Bycatch is a common side effect of directed fisheries, its level depending upon the type of gear employed and amount of effort expended. Sharks commonly are caught as bycatch in a number of directed fisheries such as the oceanic tuna and swordfish longline fisheries; inshore and offshore gillnet fisheries targeting mackerels (Scombridae), herrings (Clupeidae), and other species; and shrimp trawl fisheries. The catch numbers, mortality, and disposition for all of these sharks must be recorded in the same manner as in directed and multi-species fisheries.

11.3 CATCH PER UNIT EFFORT (CPUE)

11.3.1 Definition of CPUE

Catch per unit effort (CPUE) is a ratio commonly used to eliminate temporal and regional trends in fish stock abundance. The “catch” portion of the measure may be expressed as the number or weight of the entire catch, a selected subset of the catch, or a particular species in the catch. The “unit effort” portion of the rate usually refers to the time a uniformly designed and employed piece of fishing gear is deployed in the water. In the absence of uniform gear use, CPUE can be applied on a

coarser scale utilizing whatever effort data is available. Units of effort are dependent on the type of fishing gear used and can use (in increasing levels of finescale reliability) such measures as the numbers of vessels, vessel-days, gillnet or longline sets or number of hook hours, and trawl or gillnet hours. Many aspects of the fishery can be monitored utilizing CPUE analysis, including trends in overall fishery catch rates, catch rates of target vs. bycatch species, catch rates in specific depth strata, seasons or subregions, catch rates of size classes and sexes, and catch rates of specific vessels or types of vessels.

CPUE is a much more powerful tool than catch data alone. A decline in CPUE over a time period is usually a good indication that stocks are declining. However, advancements in fishing gear, improvements in fishing abilities of captains and crews, and changes in fishing grounds, current patterns or weather can influence CPUE trends. Interpretation of CPUE data, therefore, must be undertaken with knowledge of such potentially contributing factors. See Chapter 10 (section 10.6.5) for further discussion of CPUE.

11.3.2 How to collect CPUE data

11.3.2.1 Gillnet fishing gear

The important characteristics of gillnet gear include total net length; mesh size; number of panels; panel length and depth; water depth at deployment; deployed depth in the water column (bottom, midwater or surface set); orientation of the set (parallel or perpendicular to shore or current); and soak time (time the gear is in the water) (Fig. 11.01). The type of information fisheries managers are seeking from CPUE data dictates the catch and unit effort measures used to calculate CPUE. The following are examples of possible CPUE calculations:

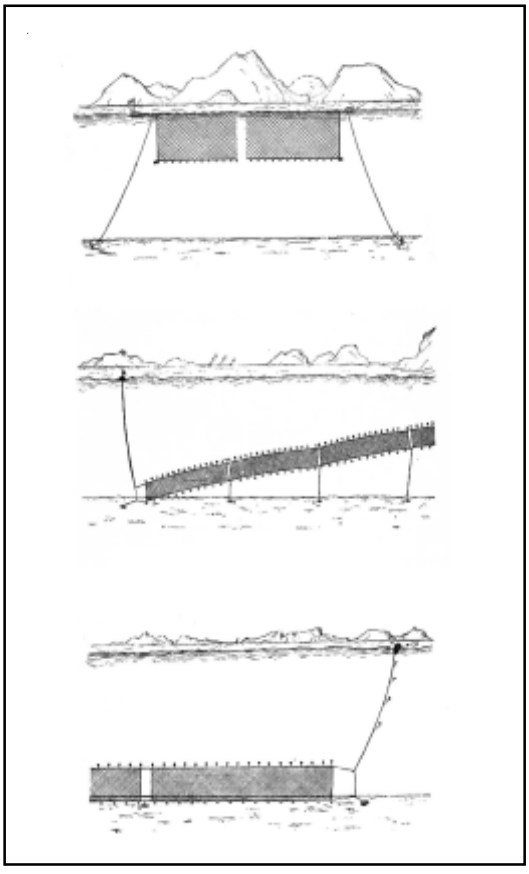


Figure 11.01 Three variations in the placement and design of gillnet fishing gear. The net floats and anchors are all visible (courtesy of NOAA).

CATCH RATE OF FEMALE SHARKS CAUGHT PER PANEL HOUR. For this calculation, we must know the total hours the gear was in the water during the entire fishing period, how many panels were in the water during that time period, and how many female sharks were caught during the time period. Consider a situation in which the total fishing hours was 300, the total panels fished was 5, and total number of female sharks caught was 10. Unit effort is calculated by multiplying

the total hours (300) by the total number of panels (5), resulting in 1500 panel-hours of effort. The female catch (10 sharks) then is divided by the panel-hours (1500), resulting in a CPUE of 0.0067 females per panel-hour. If a CPUE measure is a small number, as in this case, the CPUE's numerator and denominator often are multiplied by an exponent of 10 (e.g., 10, 100, 1000) to produce a larger and more easily expressed CPUE numerator. For example, if our CPUE of 0.0067 female sharks caught per panel-hour is multiplied by 1000, the result is a more readily understood catch rate of 6.7 sharks caught per 1000 panel-hours.

CATCH RATE OF SHARKS VS. OTHER SPECIES IN 100 MM MESH PANELS. Here we need to know the total hours the 100 mm panel gear was in the water during the entire fishing period, the catch of sharks in these panels during that period, and the catch of other species in these panels during the same time period. If 2000 kilogram (kg) of sharks and 4000 kg of bycatch species were captured during 1000 hours of fishing, the calculated CPUE of sharks would be 2.0 kg per hour (2000/1000) of fishing of 100 mm panels and the CPUE of other species would be 4.0 kg per hour of fishing of 100 mm panels (4000/1000).

11.3.2.2 Longline fishing gear

Longline gear characteristics include mainline length; gangion length, number, size and type of hooks; water depth at deployment; where deployed in the water column (bottom, midwater depth or surface set); orientation of the set (parallel or perpendicular to shore or current); and soak time (Fig. 11.02). As with gill nets, the types of catch and unit effort measures used by fisheries managers to calculate CPUE are based on the specific information they are seeking. The following are examples of possible CPUE calculations:

CATCH RATE OF SHARKS TAKEN IN DEPTHS OF 25-50 M. To calculate the catch rate of sharks per hook-hour, one must know the total number of sharks captured while fishing in depths of 25-50 m, the total number of hooks used while fishing in this depth range, and the total time the gear was in the water in this depth range. Assume 12 sharks were caught on 100

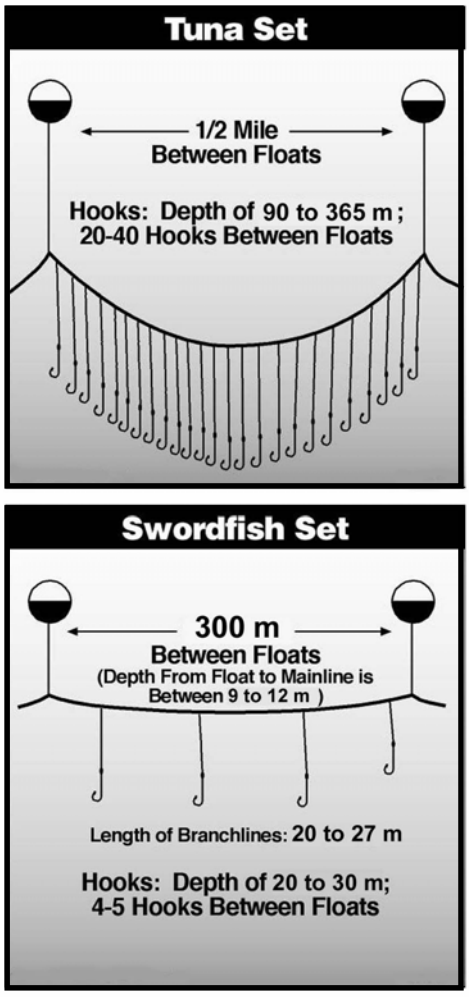


Figure 11.02 Diagram of pelagic longline gear (courtesy of National Marine Fisheries Service).

hooks fishing for 12 hours. The fishing effort, then, is 1200 hook-hours (100 hooks x 12 hours) and the CPUE is 0.01 sharks per hook-hour (12/1200), which also can be expressed (after multiplying by 100/100) as 1.0 shark per 100 hook-hours fishing at depths of 25-50 m. CPUE expressed as catch per hook-hour or as expressed by number of hooks are the preferred measures of expressing longline CPUE; the alternative, catch per set, is less useful because the number of hooks and set time varies from vessel to vessel and from set to set.

CATCH RATE OF SHARKS TAKEN BY AN ARTISANAL FISHING VILLAGE DURING THE MONTH OF JANUARY. Sometimes minimal data is all that is available for calculating CPUE. For instance, consider a situation where the only measure of catch is an artisanal fishing village's monthly sales of fins to a fin dealer. Having obtained that number, a crude CPUE can be calculated even if minimal effort data is available. An estimate of the number of fishing vessels can be derived from vessel counts at the port. Thus, CPUE based on 700 kg of fins originating from 7 vessels fishing in January would yield a CPUE of 100 kg of fins per vessel per month. Effort data might be refined if interviews of fishers revealed that those vessels fished only five days per week throughout the month. That information would produce a new effort of 140 vessel-days (7 vessels x 5 days x 4 weeks) and a more meaningful CPUE of 0.5 kg of fins per vessel-day (700/140). If a count of the fins sold also is available, then an estimate of the number of sharks caught can be made after interviewing fishers to learn the number of fins that are harvested from an individual shark. If four fins are routinely taken from a shark, and the 700 kg of fins represented 1120 fins, then the January catch was 280 sharks (1120/4) and a much refined CPUE of 2.0 sharks per vessel-day (280/140) is generated.

11.3.2.3 Trawl fishing gear

Trawl CPUE is usually determined as the catch per hour of bottom trawling time. Variables that affect trawl CPUE include mesh size; length and width of net; distance between trawl doors; lengths of bridles and foot rope; length and depth of float line; time of trawling; presence of a Turtle Excluder Device (TED), Bycatch Reduction Device (BRD), beam, "tickler chain," or rollers; and cod end mesh size and configuration (Fig. 11.03). Standardization of gear type employed, trawling speed, and time of trawling greatly increases the reliability of generated CPUE's.

Figure 11.03 A shrimp boat rigged with otter trawl gear. Floats, nets, and doors are all visible (courtesy of NOAA).

Non-standardized trawl gear and methodologies can result in considerable variation in CPUE's, making data suspect. (See Chapter 12.)

Figure 11.04 Fishing vessel pulling in a purse seine net. The floats, net, and circular enclosure are all visible (courtesy of NOAA).

11.3.2.4 Purse seine fishing gear

Purse seine nets vary in circumferential length and depth, mesh size, and ability of the fishing crew (Fig. 11.04). CPUE is usually calculated as the number of sharks caught per set, but, as in trawling gear, standardization in gear type greatly facilitates comparisons of CPUE's.

11.4 LANDINGS

11.4.1 Landings reports

Landings reports are one part of the process of estimating total catch and are also used to show how many of each species of shark are brought to port for distribution or sale. There is often quite a difference in the number of sharks caught and the number of sharks actually landed. Historical landings data can be used to correlate increases and decreases in certain species landings to changes in the local market and export demand. Management plans that use quota systems often use only the reported landings against the quota. This is a biased assessment of the actual catch; because many sharks may be discarded at sea, there is commonly underreporting (and occasionally overreporting) of the landed sharks, and sharks are difficult species to identify. A well-designed management plan will utilize both catch and landings data.

11.4.2 Problems associated with species identification

A major shortcoming in using landings data is the common lack of species identification. In many shark fisheries, the sharks are dressed at sea in order to ensure high quality of the flesh. Properly dressing a shark involves removing the head, fins and entrails as soon as possible after being caught (often after bleeding the shark by removing the caudal fin at the caudal peduncle, see Chapter 14) (Fig. 11.05). This makes it nearly impossible to accurately identify sharks to species at landing. If

proper identification is not made at sea, then the landings reports will only reveal the total number of sharks caught and cannot be used to show trends in species abundance. There are a few exceptions to this, including the landings of sharks with telltale external coloration or morphological features such as tiger, leopard, whale, blue, white and mako sharks. Some regional guides to carcasses (called "logs") or to fins may be available.

Figure 11.05 Dressed carcasses ready for sale in the U.S. (courtesy Florida Museum of Natural History).

Carcassed landings also eliminate the ability to record the total size or weight of a shark. Measurements of sharks at the dock after they have been dressed are not accurate. Fishermen use different dressing techniques and so measurements of a carcass will not be a true indication of the size of the shark, but rather the style or ability of the fishermen. However this can be solved by developing length relationships by species and relating interdorsal distance to total length (see Moutopoulos and Stergiou, 2002 for examples of length-length relationships in teleosts). The weight of landed sharks is more easily measured on shore than at sea, but trying to convert from dressed to whole weight can be tricky because conversion factors may vary between fishers and over time. In addition, sex and reproductive maturity cannot be determined after the shark has been dressed. Quantification of bycatch is also lost using landings data, as is information on cryptic mortality (e.g., freshly-caught sharks used as bait at sea) and vitality (alive or dead) of captured sharks.

Landings data are easy to obtain because it is done on land, the sharks are dead, and there is usually more space and equipment available. However, because of the limitations noted above, landings records offer a restricted amount of pertinent information and should be used with discretion.

11.5 FISHING MORTALITY

Fishing mortality is a very important but sometimes underreported aspect of fishery-dependent monitoring. The more than 400 species of modern sharks have evolved from multiple phyletic lines, occupy a wide range of habitats, and engage in a variety of life-styles concordant with their morphological and physiological attributes. Individual species react differently to being hooked or ensnared in a net. The respiratory mode of a species—in particular, whether a species utilizes ram-jet ventilation (and thus must constantly be in motion to respire) or can actively pump water over their gills—is the largest single factor affecting survival time after initial capture in fishing gear, but preexisting physiological stress, ontogenetic stage (size), and soak time are factors as well.

11.5.1 Alive vs. dead at time of capture

The condition, alive or dead, of every shark that is caught, whether targeted or taken as bycatch, should be recorded. This condition does not refer to the final fate of the shark, rather to its status—alive or dead—when initially removed from the fishing gear. There are a number of shark species, notably the tiger (*Galeocerdo cuvier*), blue (*Prionace glauca*), sand tiger (*Carcharias taurus*), and many orectolobiform species, including the nurse shark (*Ginglymostoma cirratum*), that typically survive longer than other sharks when taken on a longline hook or in a gillnet. In some regions these species are considered of low market value and often are returned alive to the sea. By contrast, species like the dusky (*Carcharhinus obscurus*) and hammerhead (*Sphyrna* spp.) sharks have decidedly short survival times when captured in fishing gear. Managers that solely rely on landing data and/or catch estimates without considering the at-vessel fishing mortality of all species may be inclined to overlook the need for management of a significant segment of the fishery. Knowledge of the high fishing mortality these species endure may affect a fishery regulator's choice of management measures. For example, at the time of writing, the dusky shark was prohibited from being landed in the northwest Atlantic waters of the United States. This regulatory measure, which might appear to be a well-considered tool enacted to eliminate fishing mortality, actually is largely ineffective because about 70% of longline-caught dusky sharks are dead by the time the fishing gear is retrieved. This type of management measure, therefore, has a limited effect on conserving the dusky shark population and an alternative strategy aimed at keeping fishers away from dusky concentrations should be considered. See Chapter 13 for further discussion of management measures.

11.6 FISHING AREA

Development of preferred fishing areas is dependent upon vessel size and cruising range, the availability of targeted species and size classes, weather, currents, and bottom configuration. Recording accurate fishing locations associated with catch data allows fishery managers to distinguish geographical variability in catch rates, denote changes in the activities of the fishing fleet, and determine sub-population differences in life history parameters of target and bycatch species. Significant declines in regional catch rates should be examined carefully because such trends often are indicative of localized overfishing.

11.6.1 Recording fishing location

The most specific and preferred way to report fishing location is by recording the latitude and longitude of every set. Usually those coordinates are recorded as gear first enters the water, at the point all gear is deployed and effective fishing has begun, as retrieval of gear begins ending effective fishing, and at the time all gear is returned to the vessel. Total water depth, fishing depth, and time of day also should be recorded at each of these four events, the latter of critical importance in calculating

accurate fishing effort—see section 11.3. Recording the locations and depths at times of release and retrieval is important even when anchored gear such as some longlines and gillnets are employed because these gears often are moved by currents and waves, or they may be picked up intentionally or mistakenly by other vessel operators and dropped off at a different location. Similarly, a single bottom trawl may cover a range of water depths and varying seafloor topography. This information is entered into a database and can be plotted to show all the locations and depths where sets are being made.

11.6.1.1 Different methods for recording location

Most commercial fishing vessels from developed nations have GPS or LORAN systems on board. For those that do not, a hand-held GPS can be used to determine location. Biologists working aboard vessels in regions where such gear is routinely absent must determine the best way to record an equivalent form of this information. For nearshore fisheries, distance from shore and landmarks such as shore structures, islands, rock formations, inlets, or channels can be used to develop an approximate location. In the Maldives, fishers locate their local fishing grounds by counting the number of oar strokes from port (Anderson, 1993). When monitoring fisheries from shore, interviews with fishers may reveal which fishing grounds, reefs or banks were visited on a given trip. If only fishing range of a vessel or fleet is known, a semi-circle originating from the home port can be constructed using that range as the radius.

11.6.2 Catch time series

Catch time series from frequented areas are monitored to determine changes. Prime fishing grounds such as the banks and reefs are exceptionally vulnerable to overfishing because they are easy to find, may host a variety of harvestable species, and may support multiple target fisheries. Fishers exploit such areas until catch rates drop so low that they are forced to move to new locations. Nursery areas, critical regions where young sharks congregate, also are prime fishing sites because of shark abundance and relative ease of capture. These fishing areas are extremely susceptible to fishing pressure and regionally-specific management is required to prevent localized overfishing. Management measures used to alleviate these problems may include area closures, seasonal closures, and regional fishing area quotas (Shotton, 1999).

A detailed analysis of fishing locations utilized by a specific fleet using catch or CPUE time series often shows clear trends. These changes may simply reflect natural temporal variation in shark populations or may be directly attributable to the effects of fishing mortality. They also may be the result of changes in fishing practices, such as moving fishing effort to new target species or different size classes, altering fishing gear, and increases in the fishing ability of fishers. If major changes are observed, further analysis must be undertaken to determine which factors are important. Catch estimates, changes in fishing practices landing reports, market values, and export data are useful clues used in determining the influences of change.

11.7 SPECIES IDENTIFICATION

11.7.1 Importance of accurate species identification

Accurate identification of individual shark species is one of the most important and difficult aspects of fishery-dependent sampling and is integral to good fishery management. Many directed fisheries target a large suite of species and bycatch of sharks in other fisheries often involves multiple species. Many groups, especially the requiem sharks of the genus *Carcharhinus* (Carcharhinidae), some triakids (particularly *Mustelus* spp.), catsharks of the family Scyliorhinidae, and squaloid sharks (spiny dogfishes and their kin) often look very similar to the untrained eye and even experts may have difficulty in identifying some species. The skates and rays (Batoidea) are also difficult to identify and there are many species still awaiting formal scientific description (see Chapter 3). In many areas these difficulties in species identification have lead to aggregated data simply recorded as "shark" (for all chondrichthyans), as "shark" or "ray", or as only slightly narrower categories such as "large shark" and "small shark" (e.g., as "tiburon" and "cazón" in Mexican shark fisheries; Bonfil, 1997). Vernacular names of sharks frequently vary between geographic regions and should not be the only form of identification utilized in data taking. Use of the Latin binomial ("scientific name")—genus and species—eliminates any confusion between regional vernacular names. Every effort should be made to make sure that the total catches of all sharks—be they targeted or bycatch—are correctly identified to species level. In the Maldives, the vernacular name of sharks varies from island to island (Anderson, 1993).

Shark catches need to be reported at the species level to facilitate better fishery management. Lack of species-specific data has forced many countries to report national catches and/or manage their sharks using designated multi-species groups. Japan reports its shark catch in three broad groups, "pelagic", "benthic" and "coastal." These groups are reflective of the fisheries targeting them, namely the tuna longline, trawl, and "other" fisheries, respectively (Nakano, 1999), rather than biological similarity. The United States places 39 species into three groups, "large coastal", "small coastal" and "pelagic." Individual shark species, primarily taken in the pelagic longline, bottom longline and drift gillnet fisheries, are placed into these management groups based on their broad habitat preference and similarity of appearance. As fishing effort increased, it became evident that certain species could not withstand the same fishing pressure as others within a management group, resulting in sharp declines of certain species and revealing the inherent difficulty associated with managing a multi-species fishery. Recording of species-level data and associated advances in understanding of biological attributes of the affected species now allows fishery biologists to fine-tune the management process.

11.7.2 Problems with species identification

Lack of species-specific data collection forces fishery managers to use aggregated shark data in their analyses. This can lead to mismanagement because of the large variation in life history patterns

exhibited by individual shark species. The lack of species-specific reporting is a global epidemic in shark fishery management. According to the United Nations Food and Agriculture Organization (FAO) records (Shotton, 1999), in 1966 15.8% of reported world shark and ray landings were identified to species level, 30.9% to genus and 53.7% to order. Thirty years later, only 8.8% of the world catch was reported to species level, 18.4% to genus and 55.3% to order. Six entire FAO reporting regions, the Atlantic West Central, Eastern Indian Ocean, North Eastern Pacific, Eastern Central Pacific, Western Central Pacific and Southwestern Pacific, did not report any catches to species level in 1996, and the six countries that lead the world in reported chondrichthyan landings (Indonesia, India, U.S.A., Pakistan, Mexico, and Taiwan) did not report any catch at the species level. Of those, only the U.S.A. reported at the genus level.

11.7.3 Materials used for species identification

Prior to the start of a shark fishery or as soon as possible after its start some type of species identification reference guide should be made available to fishers, observers, fish marketers, and any others who will be responsible for recording catch or landing data. Identification guides vary in complexity based on the diversity of species present or captured in a region, the difficulty in distinguishing similar species, the level of education or training of the intended audience, and the resources available to the author producing the guide. See Chapter 3 for a list of some regional identification guides.

These guides are readily usable by trained fishery observers or other working biologists, but consideration should be given to developing a simpler layout for use by fishers and marketers (Fig. 11.06). Most useful for field use are abbreviated, identification-only publications printed in a small format or as laminated cards such as Casey (1964), Schwartz and Burgess (1975), Castro-Aguirre and Perez (1996) and Castro (2000 a,b). Books or large guides are too bulky and too complicated for most fishers and marketers, who are not prone to devote much time to leafing through large volumes in order to identify a species. Lack of literacy is a problem in many regions, as well. An alternative means of increasing the quality of identification is provision of an appropriate-sized poster outlining the key differences among species. Such a poster can be posted on the wall of a cabin or wheelhouse aboard a vessel or in a fish market. If taking a guide or poster to sea is not practical because of limited vessel size, fisher illiteracy, or fiscal restraint, data takers should receive introductory identification training to the shark fauna they will be encountering.

11.7.4 How to collect species-specific data

To facilitate data taking, a unique species code should be assigned to each shark taken in the fishery. Simple combinations of the first letters of the genus and species or the universally accepted vernacular name are easy to remember and to record quickly (Fig. 11.07). Requiring data recorders to write an entire shark name on a data sheet is too time consuming and will result in missing or faulty

SHARKS OF THE GENUS *CARCHARHINUS*

species	inter. dorsal ridge	1st dorsal fin	dorsal fin placement	snout,eyes	notes
longimanus	✓	large, round, whitish tip			white tipped dorsal fin distinguishing characteristic
falciformes	✓		origin well behind rear tip of pectoral fin		inner margin of 2nd dorsal longer than height of fin/last 3 gill slits over pectoral fin
obscurus	✓	curved rear edge of D1	origin over free rear tip of pectoral fin		similiar to perezi, check teeth for distinguishing characteristic
galapagensis	✓	straight rear edge of D1	origin over midpoint of the inner margin of pectoral fin		
perezi	✓		origin over free rear tip of pectoral fin		
signatus	✓		origin over free rear tip of pectoral fin		
altimus	✓		origin of D1 over pectoral axil	snout equal to, or longer than width of mouth	
plumbeus	✓		origin of D1 over pectoral axil	snout shorter than width of mouth	
leucas		large	origin above middle of pectoral fin	snout short, rounded /small eyes	
limbatus		large	origin over midpoint of the inner margin of pectoral fin		
brevipinna			origin over free rear tip of pectoral fin		
acronotus			origin over free rear tip of pectoral fin	snout w/ dusky smudge at tip	

Figure 11.06 Example of a simple layout for species identification (courtesy of Florida Museum of Natural History).

data. As noted above, the use of vernacular names is discouraged unless the name is uniformly used throughout the recording area.

11.8 SIZE

11.8.1 Importance of size structure in shark fisheries

The sizes of all sharks in the catch should be consistently and accurately taken. This can be an arduous task and may be unrealistic for some fisheries. Such data is critical because many species of sharks show dramatic population declines when certain size/age classes are targeted. During the 1940's in Australia intense fishing for adult school sharks lead to severe reductions in abundance and a subsequent change in the fishery. Fishers were forced to move further offshore and further from home in order to catch sub-adult sharks to make up for the loss of the adult population (Walker, 1999). Temporal shifts in the size of the catch can signal overfishing, but this may also be the result of changing fishing practices. The dusky shark in the western North Atlantic, before becoming a prohibited species, was a target of both recreational and commercial fishers. Specimens from all size classes were heavily targeted, which consequently lead to one of the most dramatic population declines in recent history.

11.8.2 Fisheries targeting size classes

Many fishers target specific size classes of sharks, while others are forced to do so because of enacted management regulations such as time/area closures or size limits. Size limits are an efficient way to protect selected age classes from over-fishing, but the size of the sharks being taken in the fishery must be known in order to determine the potential effect of the measure. The regional market demand for sharks often is size specific. In Mexico, for example, sharks are sold as either "cazon" (>150 cm) or "tiburon" (<150 cm) and receive different prices per kilogram (Bonfil, 1997). Prevailing weather patterns also can force fishers to set their gear repetitively on certain fishing grounds, which may lead to an increase in the catch of certain size classes.

Codes for Species Names

Large Coastal Sharks		
Sandbar	*Carcharhinus plumbeus*	CP
Dusky	*Carcharhinus obscurus*	CO
Bignose	*Carcharhinus altimus*	BN
Caribbean Reef	*Carcharhinus perezi*	CS
Blacktip	*Carcharhinus limbatus*	CL
Spinner	*Carcharhinus brevipinna*	CM
Bull	*Carcharhinus leucas*	CB
Tiger	*Galeocerdo cuvier*	GC
Lemon	*Negaprion brevirostris*	NB
Silky	*Carcharhinus falciformis*	CF
Night	*Carcharhinus signatus*	CN
Galapagos	*Carcharhinus galapagensis*	CG
Scalloped Hammerhead	*Sphyrna lewini*	SL
Great Hammerhead	*Sphyrna mokarran*	SM
Smooth Hammerhead	*Sphyrna zygaena*	SZ
Sandtiger	*Carcharias taurus*	OT
Nurse	*Ginglymostoma cirratum*	GN
White	*Carcharodon carcharias*	CC
Small Coastal Sharks		
Bonnethead	*Sphyrna tiburo*	ST
Blacknose	*Carcharhinus acronotus*	CA
Finetooth	*Carcharhinus isodon*	CI
Sharpnose	*Rhizoprionodon terraenovae*	RT
Angel	*Squatina dumerili*	SD
Pelagic Sharks		
Shortfin Mako	*Isurus oxyrinchus*	IO
Longfin Mako	*Isurus paucus*	IP
Bigeye Thresher	*Alopias superciliosus*	AS
Common Thresher	*Alopias vulpinus*	AV
Blue	*Prionace glauca*	PG
Whitetip	*Carcharhinus longimanus*	CW
Big-eyed Six Gill	*Hexanchus vitulus*	HV
Seven Gill	*Heptranchias perlo*	HP
SixGill	*Hexanchus griseus*	HG
Dogfish sharks		
Smooth Dog	*Mustelus canis*	MC
Spiny Dog	*Squalus acanthias*	SA
Roughskin Spiny Dogfish	*Squalus asper*	SR
Florida Smoothhound	*Mustelus norrisi*	MN
Other sharks		
Unidentified	unidentified	unid
Genus	sp.	Genus sp.

Figure11.07 Species codes used in a commercial shark fishery observer program (courtesy Florida Museum of Natural History).

11.8.3 Weight and morphological measure-ments on land and at sea

Recorded weights of landed sharks are also used to show trends and shifts in the fishery. Most fisheries measure the quantity of landed sharks as dressed weight metric tons (dw mt). Landing tonnages often are used as surrogate indicators of catch increases and decreases. This can be very misleading if the sizes and

numbers of sharks being caught are not reported as well. In the absence of numerical data, potential shifts in the size composition of the catch will be missed.

A variety of measurements are taken on sharks, including fork length, total length, precaudal length, first dorsal rear insertion to precaudal pit, eye to eye (for hammerhead species) and other miscellaneous measurements (see Chapter 3). The three most frequently used measurements are fork, total and precaudal length. When only a single measurement can be taken, fork length is the choice of most shark biologists because it provides a consistent measure of body length (see below). All data takers should employ consistent modes and units of measurement; the metric system is preferred internationally. It is not unusual to find the tip of the upper lobe of the tail damaged or missing owing to a previous injury, or as the result of shark-on-shark scavenging prior to retrieval of fishing gear, or the upper lobe cut off by fishers immediately upon being brought onboard. In these cases alternative measurements should be taken. Measuring from the tip of the snout to the precaudal pit, the distinct notch located just anterior to the caudal fin, is a good alternative when the caudal fin is damaged or missing. A measurement from the rear base of the first dorsal to the precaudal pit also is useful, especially if only butchered carcasses (heads, tail, and fins removed) are available. If tail amputation removes the caudal pit, a measurement from the rear margin of the first dorsal fin to the anterior insertion of the second dorsal fin is a good substitute. For each species taken in the fishery, one should take several of the measurements noted above on each of at least 30 individuals in order to develop statistically significant correlations between those measurements. These relationships allow fishery biologists to convert an alternative measurement into a missing desired primary measurement, for example fork, total or precaudal length.

If sharks are landed at market whole, measurements can be made at that time. However, in many fisheries sharks are processed at sea and measurements must be made prior to finning and gutting. In some circumstances, sharks come aboard a vessel or are unloaded too quickly to measure each shark and thus only an estimated length can be made. Estimating lengths should be done only as a last resort, but is sometimes the only option. For example, observers monitoring the U.S. Atlantic directed shark drift gillnet fishery estimate shark lengths (to within 30 cm) while they are still suspended in the net (Carlson and Lee, 2000). A meter stick or other measuring device can be placed on the gunnel where the sharks come aboard the boat as a means of reference.

Obtaining the weight of a whole shark at sea is difficult, time consuming, and often impossible due to logistic considerations. A hanging scale can be used on board for smaller shark species, but this is usually not a viable option for larger sharks. For this reason, most biologists weigh the whole shark or carcass at the dock or simply estimate the weight. A major problem in dockside weighing is that any sharks used for bait or discarded at sea are not weighed. In addition, since only butchered carcasses are landed in many fisheries, whole body weight data is unobtainable. Generating statistically signifi-

cant length-weight curves for major species early in the monitoring process is important because these relationships allow one to convert subsequent length data into biomass estimates. An alternative is to develop relationships between different lengths and between length and weight from fishery independent surveys where all the catch can be accurately measured and weighed. (See Kohler et al. (1995) for length/weight regressions for several species of common sharks.)

11.9 SEX

11.9.1 Segregation

Sexual segregation of sharks based on depth, season, area and sexual maturity is common in some species. The Atlantic sharpnose shark *(Rhizoprionodon terraenovae*) and spiny dogfish (*Squalus acanthias*), common species in the northwest Atlantic, aggregate by sex. Pregnant sharpnose sharks move offshore as a group during gestation and return to the shallows to give birth (Castro, 1983). Catches of spiny dogfish off New England, in which large adults are sought, result in catches composed primarily of females. In the western Australian fishery, gummy sharks also are found in single sex groups. Many fisheries operate at only certain times of the year or in selected locations and thus may have a propensity to target, intentionally or unintentionally, a certain sex or maturity stage. The Mexican artisanal shark fishery, for example, catches a large proportion of neonate and juvenile sharks in its inshore sets (Castillo-Geniz, 1998). Other fisheries target sharks in the same location at different times of the year, resulting in catches of seasonally different sexual maturity groups. The northwest Atlantic bottom longline fishery catches sexually mature sandbar sharks (*Carcharhinus plumbeus*) in the summer and immature sharks in the winter in North Carolina waters (Burgess and Johns, 1999). Sharks generally have a long gestation period, produce few young and reproduce on yearly, biannual, or even triannual basis. Large fishing mortality on one sex or on a particular state of maturity can adversely affect the dynamics of a population. For that reason, it is imperative that representative samples of the sex and maturity composition of the catches are obtained regularly.

11.9.2 Identification of males and females

The sex of a shark is easily identifiable by the presence of claspers in males and their absence in females. In addition, the following information should be recorded whenever possible: for males, clasper size and maturity; and, for females, uterine condition, average ovum diameter, and the sizes and sexes of embryos. These observations should be taken according to the protocols described in Chapter 7.

11.9.3 Reproductive data collection

Reproductive data collection on female sharks is much more labor and time intensive. The ability to collect this data is dependent on the training of data collectors and time considerations. See Chapter 7 for a full discussion of determining maturity stages in female sharks.

If detailed reproductive data is being taken, those involved need to be properly trained. This will be discussed in more detail in the At-Sea vs. Shoreside Sampling section.

11.10 AT-SEA VS. SHORESIDE SAMPLING

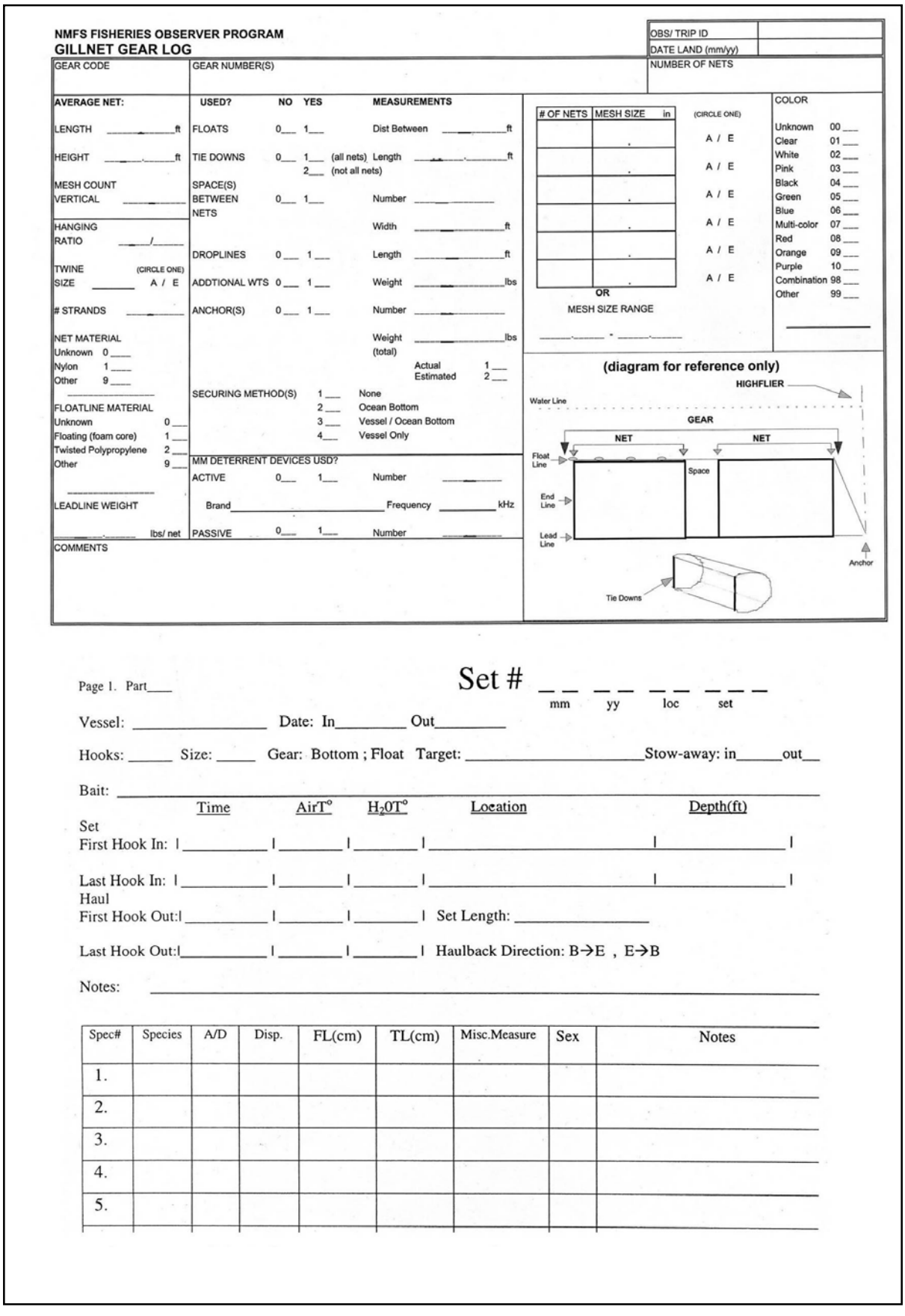
Several methods are utilized in the collection of fisheries and biological data. These include fisheries observers, shore- and dockside sampling, logbooks and surveys. Each have positive and negative aspects, and the decision to use one over the other usually depends upon the size of the vessels in the fishery and the length of fishing trips, which data are desired, and the funding available to support data gathering. The data that are collected will only be as good as the method and people used to collect them. Usually a combination of two or more methods is required for adequate data gathering.

11.10.1 Fisheries observers

Fisheries observer programs are used worldwide to collect fisheries data including biological data, species composition, discards, etc. This is the preferred means of gaining accurate and in-depth data, but it is more costly than other data gathering methods. Observers should be trained in biology and be able to obtain better quality data than fishers. Observers receive training in collection and sampling techniques from fishery professionals involved with and often employed by the fishery organization that manages the fishery. Observer programs tend to be enacted after a fishery has demonstrated a decline, but their use is a wise monitoring strategy in healthy or developing fisheries as well. The amount of data observers collect is dependent on the goals of the management organization. Observers can collect a variety of information, including fishing location and depth; time of sets and haul back; oceanographic data (e.g., water temperature and salinity); type and amount of gear used; species identification; catch vitality; sexes, lengths and weights, and maturity; and biological samples (Fig. 11.08). Observers are extremely beneficial to management programs because of the amount and accuracy of the information they collect. However, observer programs can be expensive, time consuming, and impractical if the boats in the fishery are too small.

11.10.2 Shoreside sampling

Shoreside and dockside sampling is very useful in fisheries where sharks are landed whole, such as recreational and some artisinal fisheries. Unfortunately sharks often are dressed at sea and landed headed and gutted, which can pose significant problems for land-based sampling since species identification, sex, fork and total length, reproductive sampling, and at-vessel vitality cannot be determined. If sharks are landed intact, then a shore-based data collector can produce many of the same data as an at-sea observer. Elicited cooperation with fishing captains can lead to additional data gathering, such as fishing location and depth, type and amount of gear utilized, lengths of sets, etc. If the exact location is known, fishing charts can be used to determine the depth, and water temperatures



NMFS FISHERIES OBSERVER PROGRAM
GILLNET GEAR LOG

OBS/ TRIP ID
DATE LAND (mm/yy)
GEAR CODE
GEAR NUMBER(S)
NUMBER OF NETS

AVERAGE NET:
LENGTH ____ ft
HEIGHT ____ ft
MESH COUNT
VERTICAL ____
HANGING
RATIO ____/____
TWINE (CIRCLE ONE)
SIZE ____ A / E
STRANDS ____
NET MATERIAL
Unknown 0
Nylon 1
Other 9
FLOATLINE MATERIAL
Unknown 0
Floating (foam core) 1
Twisted Polypropylene 2
Other 9
LEADLINE WEIGHT
____ lbs/ net
COMMENTS

USED?	NO	YES	MEASUREMENTS
FLOATS	0	1	Dist Between ____ ft
TIE DOWNS	0	1 (all nets) 2 (not all nets)	Length ____ ft
SPACE(S) BETWEEN NETS	0	1	Number ____ / Width ____ ft
DROPLINES	0	1	Length ____ ft
ADDTIONAL WTS	0	1	Weight ____ lbs
ANCHOR(S)	0	1	Number ____ / Weight (total) ____ lbs
			Actual 1 / Estimated 2
SECURING METHOD(S)		1 None, 2 Ocean Bottom, 3 Vessel / Ocean Bottom, 4 Vessel Only	
MM DETERRENT DEVICES USD?			
ACTIVE	0	1	Number ____ / Brand ____ Frequency ____ kHz
PASSIVE	0	1	Number ____

# OF NETS	MESH SIZE in	(CIRCLE ONE)
		A / E
		A / E
		A / E
		A / E
		A / E
		A / E

OR
MESH SIZE RANGE ____ - ____

COLOR
Unknown 00
Clear 01
White 02
Pink 03
Black 04
Green 05
Blue 06
Multi-color 07
Red 08
Orange 09
Purple 10
Combination 98
Other 99

(diagram for reference only)
HIGHFLIER
Water Line
GEAR
NET
NET
Float Line
Space
End Line
Lead Line
Anchor
Tie Downs

Page 1. Part____

Set # ____ ____ ____ ____ ____
mm yy loc set

Vessel: _____ Date: In_____ Out_____

Hooks: _____ Size: _____ Gear: Bottom ; Float Target: _____Stow-away: in_____out__

Bait: _____

	Time	AirT°	$H_2OT°$	Location	Depth(ft)
Set					
First Hook In:					
Last Hook In:					
Haul					
First Hook Out:				Set Length: _____	
Last Hook Out:				Haulback Direction: B→E , E→B	

Notes: _____

Spec#	Species	A/D	Disp.	FL(cm)	TL(cm)	Misc.Measure	Sex	Notes
1.								
2.								
3.								
4.								
5.								

Figure 11.08 Examples of data sheets used by fisheries observers (courtesy of National Marine Fisheries Service/FLMNH).

can be estimated in some circumstances using existing oceanographic data. There are several ways to conduct shore- or dockside sampling. An example of a data gathering format is shown in Figure 11.09.

1. Samplers can be contacted by boats coming in and meet them ashore as they unload.
2. Samplers can patrol docks/shore every day awaiting boats.
3. In single day fisheries, samplers can be waiting at the dock/shore when all the boats come in at the end of the day.

The number of boats sampled is dependent on what percentage of the fishery each management organization is interested in observing. That percentage most often is determined by the fiscal constraints.

11.10.3 Logbooks

Logbooks are used in many fisheries but data gathered in such a manner is highly variable and can be suspect. Despite this, logbooks are commonly used in stock assessments and as the major data collection source in numerous fisheries. Fishers are required to fill out logbooks while at sea. The following data can be recorded in logbooks: species identification, number caught, sex, size, disposition, gear and amount used, gear modifications, location, time of set and haul back, depth and water temperature (Fig. 11.10). It is widely recognized that fishers do not always record accurate data, underreport their catches, and frequently identify species incorrectly. Fishers busy bringing in and working up their catch are not likely to record accurate data at the expense of fishing productivity. Many fishers do not fill in their data at the time of fishing and recreate data from memory at later dates. Fisher illiteracy is a problem in some regions. Correct species identification is a major issue because most fishermen are not scientifically trained in proper identification techniques. In addition, many fishers dislike any type of management plan and are unwilling to go out of their way to collect data. Finally, there is no quality control in logbook data gathering, with no on-board monitoring of logbook entry. However, this type of data collection is inexpensive and is often the only method available if funding is lacking or if vessels are too small to take observers. Some estimates of the accuracy of logbook data may be available when limited observer data are also available from the same fishery. This can be done by comparing the observers record of various parameters to those in the logbook records.

11.10.4 Telephone and dockside sampling

Telephone or dockside surveys often used to monitor recreational fishers involve either calling or going to the docks and interviewing fishermen about their trips as they come back in. Surveyors usually ask questions about the species targeted and catch composition, type and amount of gear employed, gear modifications and lengths, and size of the vessel. This is a very basic type of data collection and there are real problems associated with this type of sampling. Interviews are often done several days after a trip, which results in fisher memory lapses and poor data quality. As in logbook

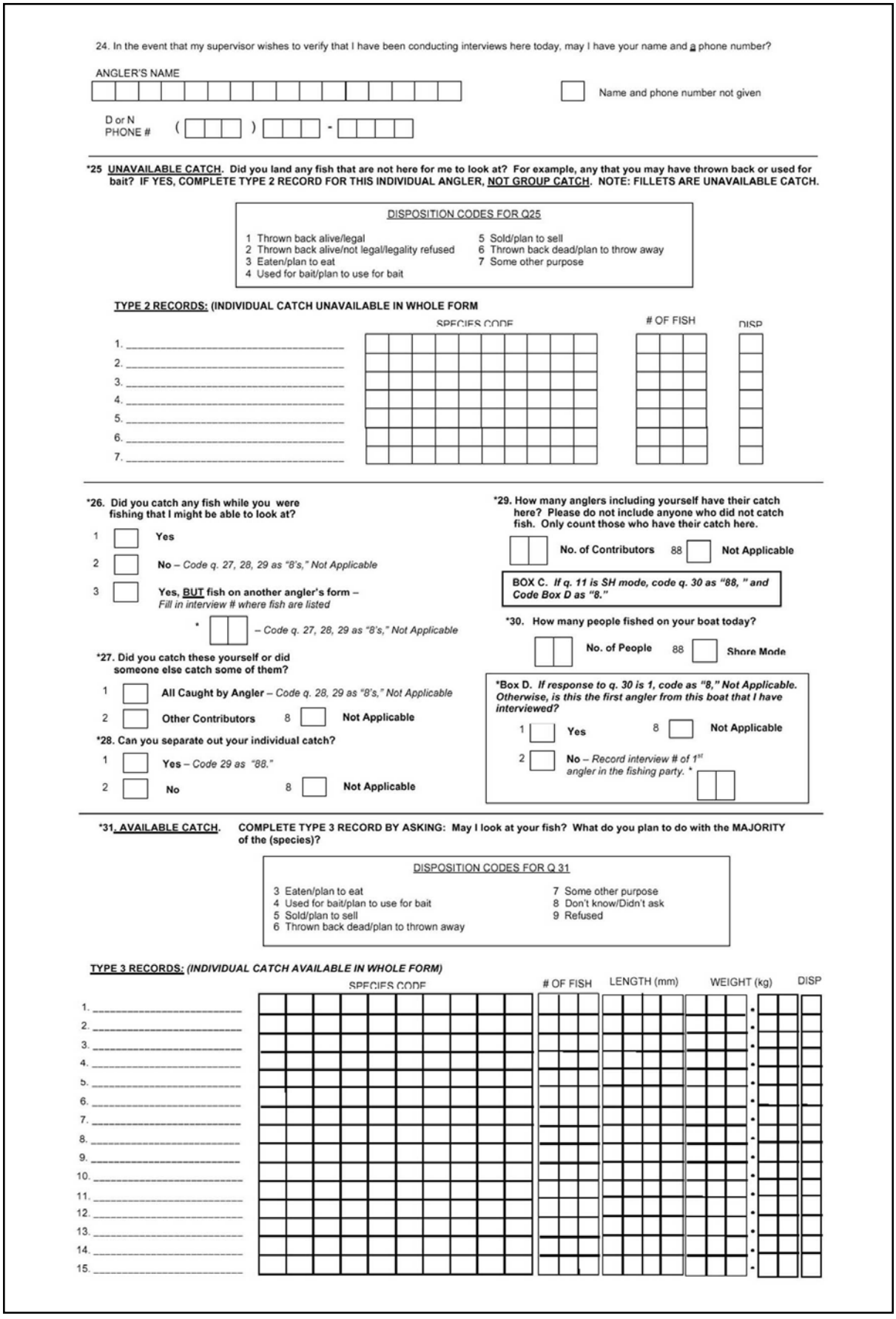


Figure 11.09 Examples of a shoreside survey data collection sheet (courtesy of National Marine Fisheries Service).

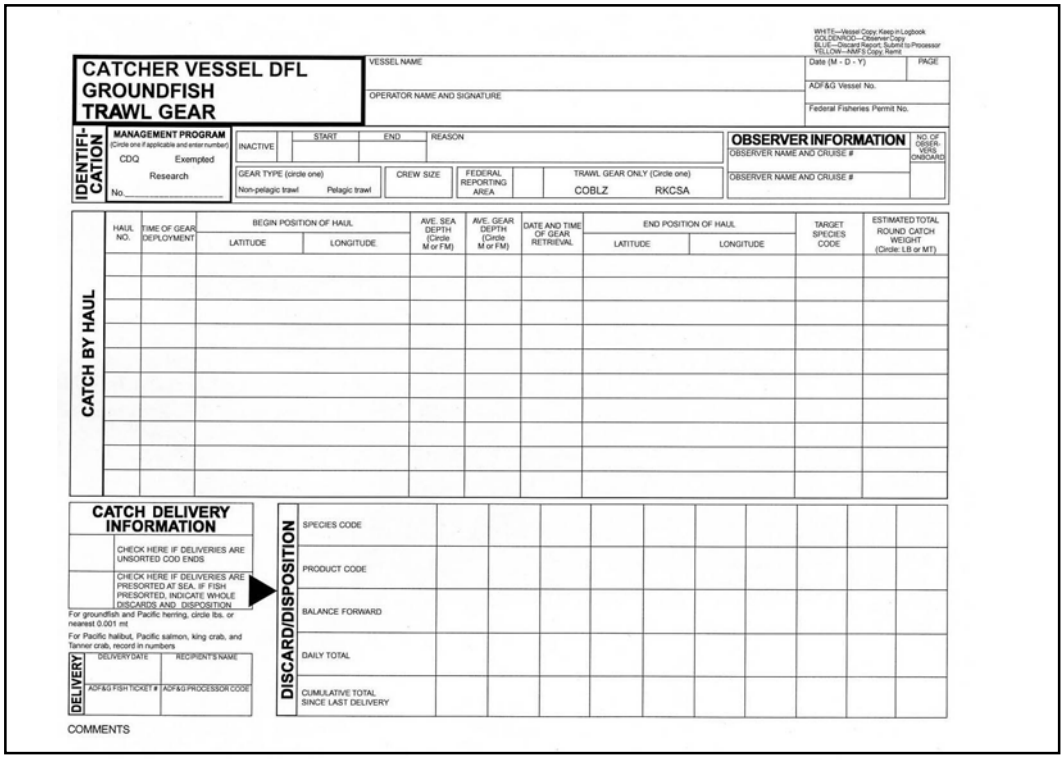


Figure 11.10 Example of a logbook used to collect data by fishers while at sea (courtesy of National Marine Fisheries Service/FLMNH).

data, this type of data gathering is relatively inexpensive and provides an alternative to more costly methodologies.

11.11 CONCLUSION

The use of fishery-dependent data is a vital component of the fishery management process. This chapter has provided the tools necessary for managers from different areas to determine what type of data should be collected, and how to collect it. The methods used will vary depending on locality, experience and the types of management plans utilized. In all cases the collection of even the simplest data set will help eliminate the threat of overfishing and subsequent population collapses.

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CHAPTER 12. FISHERY-INDEPENDENT SAMPLING: SURVEY TECHNIQUES AND DATA ANALYSES

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12.1 INTRODUCTION

Fishery-independent estimates of abundance form the cornerstone of many stock assessments for teleost and shellfish species. The advantages of such abundance indices are well described in Hilborn and Walters (1992) and in greater detail by Gunderson (1993), Doubleday and Rivard (1981), and Smith (1990). Fishery-independent surveys provide valuable measures of relative abundance, rates of population change, and size and sex composition for a wide range of species. As these measures are obtained from scientific sampling or within an experimental design, they are less subject to the unknown and often confounding factors that complicate the interpretation of fishery-dependent indices of stock status. Such generalizations, however, do not apply entirely to elasmobranchs.

For a variety of reasons, fishery-independent surveys for elasmobranchs are more difficult to interpret (Simpfendorfer et al., 2002) than surveys for teleosts and shellfish. Perhaps the most important reasons are the average size of individuals and the need to use passive sampling gear (also called "fixed" or "static"). Large elasmobranchs often have swimming speeds that exceed the towing speed of active fishing gear and therefore, have low probabilities of capture in mobile gear (perhaps with the exception of purse seines). In the context of survey design, indices of abundance based on passive gear are challenging because the "zone of influence" depends on both environmental factors and the behavior of the animal. To be captured, fish must swim to the gear and become entangled or hooked. In the latter case, fish must also be hungry and encounter a baited hook. This chapter will explore these issues, suggest possible methods for design and analysis, and highlight the benefits of fishery-independent surveys. Emphasis is placed on gears that have actually been used in such surveys (trawls, longlines, and gillnets) rather than potential, but as yet unproven, gear (purse seines, traps) or other technologies (such as acoustics, optical systems, or automated underwater vehicles).

12.1.1 Utility of surveys

Whether one is initiating a new survey or using an existing survey, the first order question must be "For what area, species and populations can I make valid inferences?" The scope of inference can be defined rigorously, but initially it has more value as a conceptual tool for evaluating survey utility. Surveys are circumscribed by physical boundaries and if one is fortunate, the species of interest will reside within those boundaries. Otherwise the survey will only allow valid inference about the fraction of the population that is present in the sampling area during the time of the survey (e.g., Carlson and Brusher, 1999). If the fraction of the population in the sampling area is unknown, then other methods, such as population models or empirical smoothing methods, may allow inferences to be made about the entire population. Thus fishery-independent surveys strike a balance between the ability to make inferences about one or more populations versus the usage of a specific area by one or more species. An overview of the different uses of fishery-independent surveys for elasmobranchs is provided in Table 12.1.

There are two primary uses of fishery-independent surveys. The first use is to generate an estimate of population abundance. For such an estimate to be valid, the survey index (**I**) must be strictly

Use	Comment
Estimate Relative Density	Can be used to infer trends over time and calibrate numerical population models but the target population and area must be defined. Otherwise inferences are restricted to population available to area sampled.
Define mating, spawning and nursery areas	Useful for monitoring trends in important localized habitats.
Biological attributes of population	Inferences regarding size composition, growth rates, sex ratio, maturity status, fecundity, etc., can be extended to whole population if samples are representative.
Seasonal presence/absence	Same restrictions as for relative density, but in this case the information is qualitative.
Relative selectivity of commercial gear	Establish sampling properties of commercial gear and facilitate interpretation of relative biases.
Evaluate alternative fishing methods	Assist in development of fishery management measures.
Tag release programs	Essential information for defining stock structure, possible migration patterns and rates, validating growth rates, and so forth.

Table 12.1 Uses of fishery-independent surveys for elasmobranchs.

proportional to stock abundance **P** or expressible as a monotonically increasing function of true stock size, e.g., $\mathbf{I = aP}$ or $\mathbf{I = aP^b}$. The second use of fishery-independent surveys is to examine attributes of the sampled population (such as size frequency, maturity, sex ratios, age). These attributes have value in understanding the basic species biology and in developing life history models. If the attributes of the sampled population are representative of the population as a whole, then the survey results can be used to infer the expected effects of exploitation. In turn, the size and sex composition of the sample may be sufficient to estimate the likely magnitude of harvest rates on the population (Rago et al., 1998).

Derived indices of abundance are used to calibrate various population models for teleosts but have had less applicability for elasmobranchs for a number of reasons. Many of their life history characteristics confound the interpretation of such data. Elasmobranchs are often long-lived and difficult to age. Many shark species approach their maximum size at relatively young age and live many years near their asymptotic size. For these species, body size provides little information about age, making it difficult to distinguish

cohorts. Larger elasmobranch species can be highly migratory, aggregating on prey species or in response to environmental factors that are difficult to detect a priori. Under these circumstances, fishery-independent surveys that encounter such clusters may produce widely varying indices over time (see Warren, 1997; McAllister, 1998). When variations in estimates of relative abundance are inconsistent with the biology of the species, variations in survey catchability may be responsible. In many instances, indices derived from surveys must be processed with other statistical techniques (see sections 12.4.1 and 12.4.2) to take account of unplanned sources of variation.

Survey requirements for elasmobranchs fall in between those for most fish species and those for marine mammals. Owing to their larger size, fast swimming speeds, pelagic behavior, and in many cases, scarcity, many shark species are infrequently captured by trawl survey gear. At this time, the only feasible alternatives to trawls are various types of fixed gear. Surveys for marine mammals rely primarily on the visual sighting of surfacing animals, or in the case of pinnipeds (Ver Hoef and Frost, 2003), visual or photographic surveys of seasonal aggregations on known terrestrial habitats (e.g., haul-out sites). Line transect methodologies may be used effectively for these species (Burnham et al., 1980; Palka and Hammond, 2001). In the long run, it may be possible to develop methodologies that combine acoustics, pattern recognition, and line transect techniques to assess large-sized elasmobranch species. Even if possible from a technological standpoint, these approaches will require significant advances in sampling theory to define the scope of inference. In the meantime, the principles outlined in this chapter can be used to develop useful estimates of stock abundance and biological attributes for elasmobranch species.

12.2 BASIC THEORY

Relevant theory for the design and analysis of fishery-independent surveys draws heavily from traditional sampling theory (Cochran, 1963; Thompson, 2002). As Morrison et al. (2001) note, estimating the abundance of animal populations is an atypical problem. The most important distinction between sampling theory designed for human populations and animal populations is the loose definition of the sampling frame. Far from being a statistical nuance, the sampling frame is a critical issue in fishery-independent surveys.

The sampling frame is defined as a list, or total set, of sampling units (Mendenhall et al., 1971). The total number of sampling units is the total area of the population domain divided by the average size of the sampling unit. For human populations the sampling frame might consist of a list of residents, a list of households, or list of firms. In turn, each resident, household or firm would constitute a sampling unit. In the case of fisheries surveys the sampling unit is the site for deployment of the gear. For active fishing gear, the area of the site is defined as the footprint of the gear. Depending upon the species and its response to the advancing gear, the footprint is defined as the product of the length of the tow times the effective width of the gear. For species that respond to visual cues, the width of the gear may be as large at the distance between the trawl doors; for others, it may only be the distance between the wings of the net. These considerations alone can induce the sampling frame to vary by a factor of two. The sampling

frame is modified further by areas that cannot be sampled within the population domain. Rocky bottom, shallow water, interference with passive gear (e.g., lobster traps, gill nets) and wrecks all act to reduce the total area that can actually be sampled. The sampling frame may also be reduced if the fish that frequent such areas are never available to capture elsewhere.

The ambiguity of defining the number of sampling units for active gear is small relative to the problems of defining the effective area of passive gear. For gill nets and hook gear, the footprint must be defined in terms of the zone of influence. Conceptually this is the area over which there is a reasonable expectation that an animal could encounter the gear. This will be a function of the environmental conditions, the average swimming speed of the species, and the duration of the set. All things being equal, the encounter rate with the gear should increase with the average swimming speed of the animals and the duration of the set. For hook gear, the encounter expectation is also conditioned on the presence of a baited hook and a feeding response.

Design-based surveys assume that each sampling unit has an equal probability of being included in the sample (Smith, 1996). A random sample is obtained by selecting one or more sampling units from the sampling frame. Let $\mathbf{y_i}$ denote a response variable that is measured from sampling unit i, (e.g., the number of sharks per longline set). The mean is estimated as the sum of the observations divided by the number of samples, $\bar{y} = \sum_{i=1}^{n} y_i / n$. The variance is estimated as the sum of the squared differences between each observation and the mean divided by the sample size minus one, $s^2 = \sum_{i=1}^{n} (y_i - \bar{y})^2 / (n-1)$. In most fisheries surveys, the variance tends to be unacceptably large relative to the mean (Pennington, 1983), highlighting the need to reduce the variance in some way.

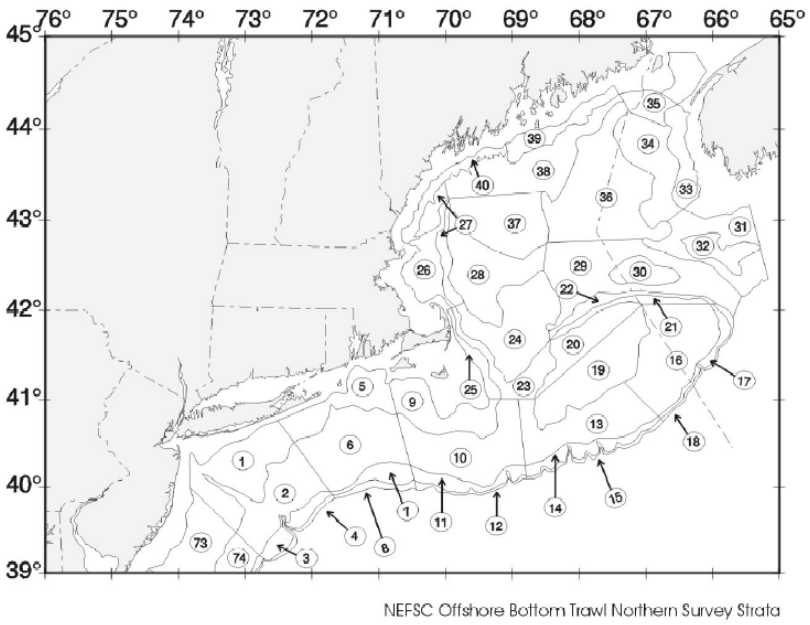

Figure 12.1 Example strata definition for bottom trawl surveys conducted by the Northeast Fisheries Science Center, NOAA Fisheries, Woods Hole, MA.

12.2.1 Survey design

One of the primary methods of reducing the variance of the estimate is to stratify the sampling frame into sets of sampling units with more homogeneous properties (Fig. 12.1). The overall variance is estimated as a weighted average of the within-stratum variances. If the strata have been defined appropriately, the stratified estimate of the variance will be smaller than that obtained from a simple random sample. Combining the notation in Cochran (1963) with the fisheries orientation in Gunderson (1993) we can illustrate the general principles of design-based estimation and extend it to model-based estimation. The details of these derivations become very complicated and the reader should consult standard statistical texts for further details. In what follows, the objectives are to provide an intuitive understanding of the underlying concepts, identify relevant literature, and illustrate the need to carefully weigh the utility of fishery-independent surveys.

We begin with some basic definitions. Let L denote the total number of stratum and let h denote the stratum index, such that h =1, 2,…, L. The total number of samples taken over all strata (n) can be written as $n = Sn_h$, where n_h is the number of samples taken in each stratum h. The sampling frame is defined as $N = SA_h / a_h$, where A_h is the area for stratum h and a_h is the size of the sampling unit in stratum h. The maximum number of sampling units in stratum h is defined as $N_h = A_h / a_h$. A weighting factor, defined as the fraction of sampling units in stratum h, is denoted as $W_h = N_h/N$. In most fisheries-independent surveys the fraction of the sampling frame that is sampled is very small and can generally be ignored. Under these conditions the stratified mean $\bar{y}_{st}$ and variance $Var(\bar{y}_{st})$ are estimated as

$$\bar{y}_{st} = \sum_{h=1}^{L} W_h \bar{y}_h \qquad (12.1)$$

and

$$Var(\bar{y}_{st}) = \sum_{h}^{L} W_h^2 \frac{s_h^2}{n_h} \qquad (12.2)$$

where

$$s_h^2 = \sum_{i=1}^{n_h} \frac{\left(y_{h,i} - \bar{y}_h\right)^2}{n_h - 1}$$

The above formulation allows the size of the sampling unit to vary with stratum. If the sampling units vary with each sample, then the sampling frame would be approximated as the total area of the stratum divided by the average area of the sampling unit within the stratum, $N_h \sim A_h / \bar{a}_h$. Such a situation could occur in a trawl survey if the footprint of the trawl varied significantly with each tow in the stratum. The stratum-specific area swept per tow would then be defined as $\bar{a}_h = \sum_{i=1}^{n_h} a_{h,i} / n_h$.

Equation 12.2 illustrates two ways in which the overall variance of the mean can be reduced. Since the within stratum variances are weighted inversely by the number of samples per strata (n_h), allocation of additional samples to strata with the highest variances can be an important strategy. Since the

variance increases with the mean in almost every fishery example, the allocation of additional sampling units to high density strata makes intuitive sense. The second way that variances can be reduced is through choice of stratum boundaries. The strong association between the mean and variance suggests that defining stratum boundaries according to density zones will act to reduce the variance within strata to minimal values. Selection of strata and allocation of samples is not simply a mathematical problem. Biological information on habitat and oceanographic features must be considered before an algorithmic approach. Moreover, most fishery-independent surveys are designed to estimate relative abundance for more than one species. In such cases, it is unlikely that a single stratification or allocation scheme is optimal for every species.

Overall cost represents one of the most important factors in the design of a survey. Samples are expensive to collect and it is generally desirable to minimize the variance of a survey subject to a total cost constraint. Strategies, such as Neyman allocation (Cochran, 1963, p. 97; Mendenhall et al., 1971, pp. 64-73) can be used to define appropriate sample allocations wherein the optimal number of samples is proportional to the product of total sampling units within stratum *h* and the standard error, and inversely proportional to the square root of sampling cost in stratum *h*. The costs of collecting additional information on the biological attributes of the species are generally small relative to the costs of deploying vessels and crew. Hence it is desirable to collect as much information as feasible on individual specimens. “Feasibility” to collect such information is generally controlled by the average time between adjacent stations.

A significant fraction of the total sampling effort should be allocated to continuous experimentation and quality control measures. The former measures are important during the early years of a survey when the penalty for altering a design is small relative to the gains in precision. As the number of survey years increases, the gains in precision must be progressively greater because the costs of discarding historical information increase. Quality assurance/control (QA/QC) measures include ongoing verification of gear performance, evaluation of fixed stations, and comparisons with other vessels and gears. Some of these measures, such as fixed stations, can be incorporated in the overall survey design via partial replacement designs (Warren, 1994). Rather than viewed as a burden, QA/QC measures should be evaluated with respect to the question, “Can I afford to redo this study?”

Stratified random designs are one of many designs that might be implemented for evaluation of elasmobranch species. Systematic surveys are worthy competitors and have desirable properties inasmuch as they may provide better support for kriging methods. The important caveat for such studies is that strictly speaking, a design-based variance is not estimable (Cochran, 1963; Gunderson, 1993). Other authors cautiously advocate systematic designs, noting that their desirable properties can outweigh the problems of variance estimation (Levy and Lemeshow, 1991; Hilborn and Walters, 1992; Morrison et al., 2001).

Gear	Advantages	Disadvantages
Trawl	Design assumptions easier to satisify Multispecies perspective	—Size selectivity —Species selectivity —Requires large vessel and high costs —Limited utility for pelagic habitats —Limited utility in rocky, coral reef, and complex bottom areas —Vessel effects may reduce catchability
Gill Net	—Relatively inexpensive —Can use smaller vessels —Wider range of bottom types —Benthic and pelagic zones	—Size limitations based on mesh selectivity —Domain of influence difficult to specify —Day vs night and turbidity differences —Movement required
Hook Gear	—Effective —Relatively inexpensive —Can use smaller vessels —Wide range of habitats —Benthic and pelagic zones	—Movement required —Must detect bait, encounter and consume baited hook —Competition with other fish for hooks —Once hooked, potential predation by larger fish —Loss of bait reduces effective sampling time

Table 12.2 Gear-specific design considerations for primary gear used in fishery-independent surveys of elasmobranchs.

12.3 IMPLEMENTATION

Although many types of gear can catch or detect elasmobranchs, three basic gear types define the range of applicable fishery independent methods (Table 12.2). Trawls (Rago et al., 1998; Graham et al., 2001), hook gear (Musick et al., 1993), and gill nets (Nakano and Nagasawa, 1996) have all been used to define abundance metrics. Other gear, such as traps and purse seines, may be useful for specialized surveys, but no examples of routine surveys are known. Similarly, routine use of acoustic surveys is hampered by the lack of a swim bladder in elasmobranchs, difficulties in identifying species, fast swimming ability relative to the survey vessel, and the relatively low density of individuals. Surveys based on explosives or poisons, are both ecologically unacceptable and unlikely to be effective in ocean environments.

12.3.1 Gear types

The ability to implement a valid survey design ultimately depends on the performance of the sampling gear and the ability to satisfy the assumptions of the survey design. All sampling gears are biased and no study can fully meet all of the assumptions of a design-based survey. The relevant question however, is the magnitude of these violations and their influence on the bias and precision of the survey. Table 12.3 summarizes some of the critical assumptions and potential tests for fishery independent surveys. Many of these issues can be addressed through simulation studies wherein the validity of conclusions is conditioned on the realism of the simulation (Punt et al., 2002).

Problem	Recommendation
Gear saturation	• Evaluate set duration or tow duration • Alternative hook spacing
Zone of influence	• Record environmental variables • Video monitoring • Field experiments
Scaling of catch rates	• Evaluate catch rates for various lengths of nets or longlines, and tow duration for trawl nets
Fixed vs. random stations	• Partial replacement design
Gear avoidance	• Compare day vs. night differences
Vessel effects	• Use acoustics to evaluate potential dispersal of fish during deployment
Size selectivity	• Multiple mesh size panels in gillnets • Alternative hook and bait sizes, and types
Simple random vs. stratified vs. systematic sampling designs	• Compute design effects for reduction in variance • Consider all species unless survey specifically targets a single species

Table 12.3 Recommended measures for survey programs to reduce bias and improve precision. The following list is indicative, but not exhaustive.

In general, no single type of gear is equally effective for all life stages of a single species, much less so for multiple species. As a simple example, catch rates of selected shark species from Northeast Fisheries Science Center autumn and spring research vessel bottom trawl surveys during 1967-2003 are summarized in Table 12.4. Except for smooth dogfish, the average percentage of positive tows was less than 5%. Larger sharks were caught less frequently and average numbers per positive tow were low. Maximum observed sizes were less than 2 m and no trends are immediately apparent for the larger species. If trawl data were the only source of information for these species, it would be difficult to draw any conclusions regarding stock status.

As a consequence, it is helpful to examine several types of gear and gear configurations when designing a survey program. In a survey based on longlines, it would be useful to test for differences between sizes of hooks, types and sizes of bait, spacing of hooks, duration of sets and so forth, even after a standard protocol had been established. Reserving some of the sampling effort for ongoing experimentation can be an effective strategy for improving fishery-independent surveys.

Gear bias is just one violation of an assumption in a survey design. Most fishery scientists have a good intuitive concept of what constitutes a valid random sample. In practice, they could agree on the inclusion or exclusion of a particular sample within a survey design. However, as the number of samples and complexity of the design increases, the basis for agreement on the validity of an overall survey is likely to diminish. As a simple example, suppose that a study demonstrates an optimal soak time of six hours and that a 24-hour soak time in an area of high shark abundance is generally too long, resulting in either gear saturation or loss of bait. Should a 10-hour set be rejected as unrepresentative? Real world con-

Survey	Statistic	Angel	Black-nose	Dusky	Sandbar	Chain Dogfish	Bonnet-head	Smooth Dogfish
Fall 1967-2002 (13100 stations sampled over 36 years)	Total number of positive tows	262	2	25	123	125	2	2172
	Number of years with positive tows	36	2	5	30	33	1	35
	Average number per positive tow	1.51	1.00	1.24	1.31	2.38	1.00	7.46
	Maximum size (cm) captured	126	102	211	186	47	99	150
Spring, 1968-2003 (12209 stations sampled over 36 years)	Total number of positive tows	190	1	39	53	493	2	706
	Number years with positive tows	35	1	16	20	36	2	36
	Average number per positive tow	2.39	1.00	3.44	2.09	2.59	1.00	24.45
	Maximum size (cm) captured	123	105	212	168	50	88	140

Table 12.4 Summary of fishery-independent catch statistics for selected shark species caught during fall (1967-2002) and spring (1968-2003) bottom trawl surveys from Cape Hatteras to the Gulf of Maine conducted by the Northeast Fisheries Science Center, NMFS, 1967-2003.

straints on deployment, retrieval and processing of samples rarely allow for resetting gear, and rejection of samples will typically reduce the utility of already sparse sampling designs.

As another example, consider the interactions between the duration of a survey and the movement patterns of the resource. Fishery-independent surveys typically attempt to provide snapshots of the population at a particular time. However, if the normal movements of a species are large relative to the spatial distribution of the survey, it may be difficult to distinguish changes in abundance from variations in seasonal migration or foraging patterns. For example, finfish bottom trawl surveys conducted during the spring and autumn by the Northeast Fisheries Science Center typically occur over an eight-week period

and proceed from Cape Hatteras to the Gulf of Maine. For less mobile species, the duration of the survey is a negligible source of bias, but for highly migratory species the bias effect could be significant. Walsh (1997) provides an excellent review of the performance characteristics of active and static gear. This thorough review gives a clear exposition of the major factors influencing the capture rates and relevant technology that can be used to better understand gear performance. A useful companion article by Millar and Fryer (1999) describes modern techniques for comparing the relative fishing power of various gear types. The general statistical methodology of Millar and Fryer conceivably could be used to generate adjustment factors for size composition estimates from survey data. Together these articles provide a useful foundation for selecting, deploying, and analyzing the basic survey gear types used in fishery-independent surveys for elasmobranchs.

12.4 STATISTICAL ESTIMATION AND PRECISION

Assuming that a reasonable sampling design can be developed and implemented, the next step is to analyze the results. Realized means and variances can be estimated using equations 12.1 and 12.2, but studies rarely go exactly as planned. Gear and vessels fail, storms curtail sampling and may alter fish distributions, non-target species may fill nets or longlines, and emergencies may prevent execution of a full design. Such restrictions on randomization will generally necessitate consideration of alternative analytical approaches, imputation methods for missing strata, or post-stratification of the original design. The statistical literature is not unanimous on how such issues should be addressed, except to acknowledge that restrictions on randomization reduce the scope for inference by uncertain magnitudes.

One of the ongoing problems in fishery-independent surveys is the overdispersion of population variances. Excessively high catches in a single realization of a survey design can bias means upward and imply low precision (Kappenman, 1999). Alternatively, low number of sample units within a stratum may underestimate the true variance. Model-based estimation methods have been proposed by a number of authors (e.g., Pennington, 1983). Others have noted that model-based estimators are preferable when the assumed model is true but undesirable when the model is not true (Myers and Pepin, 1990; Syrjala, 2000). As an alternative to model-based confidence intervals and design-based estimators that rely on asymptotic variance estimators, Smith (1996a, b) was the first to demonstrate the properties of bootstrap estimation in fisheries surveys. His results suggested that percentile confidence limits could be developed from complex surveys.

Model-based estimators encompass a broad range of methodologies. In general they are characterized by an assumption that the catches are derived from a particular distribution (e.g., Poisson, log normal, negative binomial—Taylor, 1953; Power and Moser, 1999). Compound distributions such as the delta distribution can be useful for evaluating abundance measures. Pennington's (1983) work on this distribution has been influential in stimulating methodological research (Myers and Pepin, 1990; Syrjala, 2000). Cortés (2002) recently assessed four coastal shark populations, utilizing nine fishery-independent time series (trawls, gill nets, longlines). He modeled these time series with a Generalized Linear Model

(GLM) as a two-stage process in which presence/absence is considered a binomial process, and positive catches are treated as a Poisson process. Similar methods have been applied to migratory bird populations (Link and Sauer, 1998).

12.4.1 Smoothing procedures

Model-based estimation can be viewed as a general class of smoothing procedures in which the results of a survey design are interpreted as realizations of a complex, but continuous underlying function. Moving averages constitute perhaps the simplest such procedure, wherein time series of observations are expressed as simple averages of adjacent observations. The moving average process can be extended to include locally weighted regression methods with robust treatment of residuals. This approach goes by the acronym, LOWESS or "locally weighted regression scatter plot smoothing" (Chambers et al., 1983). Figure 12.2 depicts the use of LOWESS in illustrating temporal changes in the abundance of mature female spiny dogfish off the northeast U.S. coast. The LOWESS smoothing separates the major signal from the noise of year to year sampling variability.

Auto-regressive, integrated moving average (ARIMA) models (Pennington, 1985) employ a more formal approach to smoothing by explicitly accounting for the correlated error structure. These techniques have been applied rather infrequently in fisheries, perhaps due to their rather demanding and hard-to-test assumptions. When the number of years in a data set is small, it may be difficult to test the assumption of stationarity and estimate the autocorrelation precisely.

Spatial correlation between observations underlies the geostatistical modeling approaches that have been applied to some fish stocks (see Petitgas, 2002). One of the useful features of these approaches is the ability to approximate the precision of non-random surveys. Generalized linear models

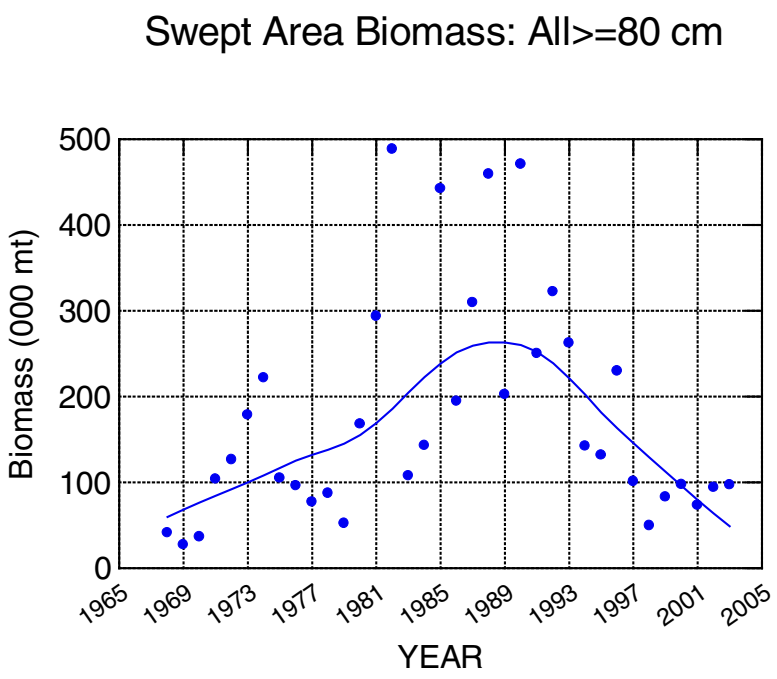

Figure 12.2 Swept area biomass estimates of spiny dogfish biomass (000 mt) in spring research vessel bottom trawl surveys (1968-2003) for dogfish greater than 80 cm, both sexes combined. Line represents LOWESS smooth with tension factor = 0.5.

(GLM) and Generalized Additive Models (GAM) are distinct from geostatistical models but share a common objective of describing the underlying structure of the data in terms of one or more explanatory variables. Swartzman et al. (1995) successfully applied GAM models to walleye pollock populations.

Variation in abundance indices are a function of the true variation in the temporal and spatial distribution of the resource, sampling error from the statistical design, and measurement error associated with gear performance. Changes across years provide a measure of the true change in abundance and variations in the catchability of the resource. It was noted earlier that when variations in estimates of relative abundance are inconsistent with the biology of the species, variations in survey catchability may be responsible. There are several ways in which such variations can be addressed but none of them are entirely satisfactory.

The ratio of changes in average catch rates across years can be used as an aggregate measure of population change, if the factors that influence the average catch rate remain the same over time. Otherwise the rate of population change is confounded with changes in the fraction of the stock in the sampling frame, variations in the zone of influence of the gear, and other factors. Ways of considering these other factors are outlined below.

12.4.2 Influence of covariates

One of the major advantages of model-based estimation is that the model parameters can be expressed as functions of explanatory variables. The importance of various explanatory variables can then be evaluated in the context of their reduction of the variance in the observations. Cortés (2002) demonstrates the utility of this approach wherein model parameters were expressed as functions of a set of variables (time of day, depth, temperature and so forth.). Baum et al. (2003) successfully applied a zero-truncated negative binomial GLM in analyzing shark landings recorded in commercial fisheries logbooks from the U.S. pelagic longline fleet. By adjusting for the effects of various covariates, Baum et al. (2003) were able to identify population trends apart from variations in extraneous variables. Ver Hoef and Frost (2003) demonstrated the utility of hierarchical Bayesian models for the assessment of trends in seal populations; application of such models to elasmobranch longline surveys should be a productive area of future research.

Perry and Smith (1994) developed a nonparametric method to examine the degree of association between catch rates and environmental factors. One of the most useful features of their approach is the explicit incorporation of the sampling design into the measure of association. Shepherd et al. (2002) applied this approach to the analysis of spiny dogfish catch rates in Canadian trawl surveys.

12.4.3 Data structures

Efforts to collect fishery-independent data are wasted unless similar efforts are made to develop and maintain databases. All of the statistical methods described above rely on a proper data structure. Here our emphasis is on the development of modern relational databases. Such databases are required not only to support complex statistical models, but also to support questions that have not yet been asked and

techniques that have not yet been developed. Properly structured relational databases have the potential to meet these challenges; poorly structured and maintained databases have much lower chances.

Guidance on data collection and handling procedures may be found in a number of sources. The general principle is to collect and check as much data as possible while at sea, subject of course, to safety considerations and the overall constraints of the mission. Recent advances in at-sea data collection technologies utilizing electronic measuring boards, scales, sample custody processing, and integration of environmental data, can greatly improve the speed and quality of survey data. The Fisheries Scientific Computing System at the Northeast Fisheries Science Center is one example of an integrated data acquisition system. (See http://www.nefsc.noaa.gov/nefsc/publications/crd/crd0117/symposium/benigni-mchugh-shields-stepka_presentation/index_files/v3_document.htm for additional details.)

Data should be summarized in a relational database such as Oracle, Access or other commercially available products. At least four table types should be considered. For economy, denote these tables as the STATION, CATCH, LENGTH, and BIOLOGY tables, respectively. The STATION table should summarize the attributes of the sampling station. This table should include the design attributes (strata, station number), date, time, location, gear performance measures, and environmental data. The STATION table should also include information on the vessels used, gear deployed, type of station (random vs. fixed). Using one or more key fields from this table, other tables can be developed to summarize the total number and weight of all species (CATCH table), the length, weight, maturity status, and sex of each measured fish (LENGTH) and finally one or more BIOLOGY tables to identify attributes of individual fish. Table fields may include age, stomach volume and/or contents, tag release number, special treatments (e.g., tetracycline injection) and so on. Collectively, the relational database provides a compact way of summarizing the voluminous data from individual surveys. More importantly, it provides a standardized, long-term system for archiving data for elasmobranch populations.

The costs of collecting additional environmental information while at sea are minor compared to the overall survey costs. Post-hoc analyses of capture rates are likely to be necessary for all but the most abundant species. Collection of environmental data may be especially important for these types of analyses. Collection of various environmental variables at the sampling site is standard in most surveys. However, the relevant conditions that affect capture rates may occur on larger spatial scales (e.g., proximity to frontal zones) or longer temporal scales (e.g., rate of warming of shelf waters). This type of information is more difficult to incorporate as a standard data table, but the efforts may allow a much more coherent interpretation of the data.

A related issue is the acquisition of data on gear performance. For mobile gear, various forms of electronic data acquisition allow scientists to evaluate gear configuration and contact time, each of which is critical for judging the quality of a sample. For passive gear, the requirements are less rigorous but equally useful. The recent analyses by Baum et al. (2003) of commercial longline data for shark populations relied heavily on detailed, set-specific data records.

The archival importance of fishery-independent survey data cannot be overemphasized. In some cases, the value of long-term data has only recently been summarized (Jackson et al., 2001; Hoey et al., 2002; Baum et al., 2003). Some surveys may be difficult to interpret when viewed in isolation but clear when compared with one or more other surveys. Thus it is important for governments, universities, and other groups that collect fishery-independent survey data to recognize the enduring responsibility of maintaining these data for the world's managers, scientists, and harvesters alike. While these arguments are true for all surveys, they are particularly relevant for large-bodied species whose abundances have declined on a worldwide basis (Myers and Worm, 2003).

Data should be routinely audited with specialized software that attempts to identify infeasible codes and improbable biological attributes such as excessive maximum sizes or unlikely combinations of lengths and weights. (As an example, additional details on the procedures used at the Northeast Fisheries Science Center may be obtained by contacting scientists via the following web site: http://www.nefsc.noaa.gov/esb/survey.htm.) Standardized summarization programs are useful for ensuring that appropriate statistical methods are used and for verifying the selection criteria employed. Most fishery research institutions have developed standardized summarization programs for fishery-independent data. Examples include the SURVAN program used at the Northeast Fisheries Science Center (Kramer, 2001) and SPlus software for bootstrapping surveys developed by Stephen Smith (DFO, Bedford Institute of Oceanography, Nova Scotia). Information on a sophisticated, commercially available survey analysis system, known as SUDAAN, may be found at http://www.rti.org/sudaan/home.cfm. The "Fideas" computer program by Swartzman et al. (2002) combines features of database management systems, geographic information systems, higher level programming languages, and web browsers into a general software tool for analyzing fishery-independent survey data. The Environmental Analysis System (EASy; Tsontos and Kiefer, 2003) is an advanced, PC-based Geographical Information System designed for the storage, dissemination, integration, analysis and dynamic display of spatially referenced series of diverse oceanographic and biogeographic data. It can be found at http://www.runeasy.com.

12.5 CONCLUSIONS

Fishery-independent surveys fulfill a wide range of objectives and are a valuable component of any stock assessment program. They fulfill an important role in the monitoring and assessment of the world's elasmobranch species. Long-term data sets have undeniable value for detecting changes in abundance. As the length of time series increases, the ability to confirm the validity of historical data is diminished. Through rigid adherence to standard protocols and appropriate documentation, fishery-independent surveys help ensure that such data can be evaluated at a later time. Properly designed surveys have enduring value. For example, Graham et al. (2001) compared trawl survey data collected in 1996-97 with data from earlier surveys in 1976-77. Despite the gap between survey periods, Graham et al. were able to demonstrate significant declines in abundance of multiple elasmobranch species after 20 years of intensive fishing.

This chapter provides only an introduction to the many challenges for designing multispecies fishery-independent surveys for elasmobranchs. Additional details on the statistical methods may be found in statistics text books (Cochran, 1963; Mendenhall et al., 1973; Levy and Lemeshow, 1991; Thompson, 2002) and in various applied fields. Given the biology of elasmobranches, useful approaches may be found not only in fisheries (Gunderson, 1993) but also in wildlife (Seber, 1973; Morrison et al., 2001), forestry (Schreuder et al., 1993) and even sociology (Kish, 1987). While it is yet unclear that sustainable fisheries can be developed for large elasmobranchs (Walker, 1998), fishery-independent surveys provide essential information necessary for sound management.

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CHAPTER 13. MANAGEMENT MEASURES

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13.1 INTRODUCTION

Fisheries management can be viewed as an assemblage of restrictions on fishing or, alternatively, viewed with positive connotations as bestowing use rights for harvesting fish to an individual, company, group or community. With use rights go the obligation to apply those rights in a responsible manner.

In allocating fishing rights, clear objectives need to be set for a fishery. These objectives will relate to sustainable use of the resource, provision of food and other products, economic return to the community, welfare of fishing communities, biodiversity conservation, and maintenance of the structure and function of ecosystems. The mix of objectives for any fishery will inevitably change with community attitudes and with stage of development depending on whether the fishery is evolving from a traditional to an artisan fishery or from an artisan to an industrial fishery. Compromises are inevitable to address competing social, political, legal, economic and biological objectives.

Fisheries impacting populations of chondrichthyan animals (sharks, rays and chimaeras) require careful management. Where excess fishing capacity occurs, mechanisms need to be established to reduce capacity to levels commensurate with the biological productivities of the species taken to ensure sustainable and rational use of the resources. Similarly, where bycatch species are depleted or threatened, then steps need to be taken to manage and, if necessary, provide special protection to those species for biodiversity conservation. Critical habitats need to be protected and, where affected by fishing or other human activities, restored. At a broader level, trophic interactions and the effects of fishing need to be understood and, if necessary, managed to ensure that the resilience of ecosystems are not impaired.

The present chapter briefly characterizes fisheries impacting populations of chondrichthyan species and identifies those features of their biology that can cause their populations to be sensitive to the effects of fishing. It outlines the elements of fishing mortality and how these need to be understood when considering gear restrictions or constructing more environmentally benign gear for conservation and management of this group of animals. The chapter develops a method for rapid assessment of risk for identifying species most in need of precautionary management. It also describes the outcomes of complex political processes culminating in the International Plan of Action for the Conservation and Management of Sharks and describes the jurisdictional and institutional frameworks required for administration, consultation, monitoring, research, assessment, and surveillance in fisheries. The tools of fisheries management are presented here in the framework of use rights and restrictions imposed through technical measures. For chondrichthyan animals, special attention is required to protect newborn and young juveniles and maternal animals for species that have nursery, pupping and mating grounds, or migration lanes. The advantages of prescribing in law the form in which these animals can be landed are also discussed.

The terminology adopted mostly follows the Code of Conduct for Responsible Fisheries developed under the auspices of the Food and Agriculture Organisation of the United Nations (Anonymous, 1995). The term "catch susceptibility" is adapted from the scientific literature (Stobutzki et al., 2001; Stobutzki et al., 2002) for the purpose of the present chapter. In addition, a distinction is made between the terms "fishing area closure" and "marine protected area." This distinction is made to distinguish area closures designed to meet fishery-management objectives of ensuring sustainable use of a resource, biodiversity conservation, amelioration of ecological impacts of fishing, and reduction of interference with other human activities (e.g., shipping and recreation) from area closures designed to meet other community objectives. The concept of fishing area closure, which is an essential management tool for managing animals of low productivity such as chondrichthyans, is extended to promote to the concept of "regional fisheries management."

13.2 FISHERIES, BIOLOGY AND ASSESSMENT OF CHONDRICHTHYAN SPECIES

13.2.1 Fisheries impacting chondrichthyan species

The harvest of animals for products from shark and other chondrichthyan species pre-dates recorded history. Every part of these animals has been used for some purpose. Depending on region of the world, shark meat is important food consumed fresh, dried, salted or smoked. The demand for fins of sharks has grown rapidly in recent years such that they are now among the world's most expensive fishery products. Similarly, the demand is rising for shark cartilage and other products for medicinal purposes. In some fisheries, only the meat is retained, while the rest of the animal is discarded. In other fisheries, only the fins, or liver or skin is retained; few fisheries utilize all parts of the animals.

The number of shark species targeted is small compared with the number of species of teleosts and many of the invertebrate phyla harvested. This has resulted in a lack of studies of sharks and inappropriate stock assessment techniques being applied to these animals. Most of the shark catch is taken by fishers targeting teleost species, which results in most of the catch reported as unidentified shark or mixed fish or not reported at all. In addition, sharks can be difficult to identify down to species level, particularly given the need to behead and eviscerate sharks at sea to reduce spoilage rates of the meat and the fishers' preference to remove fins at sea. Taxonomic problems need to be resolved, particularly for batoids, before effective monitoring, research and management can be achieved. This lack of species identification for catches and lack of information on fishing effort means basic data for fishery stock assessment are currently available for only a few species (Walker, 1998).

Although the overall number of species harvested is relatively small, sharks are captured with a wide variety of types of fishing gear and vessels. Sharks are mostly taken by gillnet, hook or trawl in

industrial and artisanal fisheries. Small amounts are taken in traditional and recreational fisheries (including game fishers and divers) and bather protection programs by beach gillnet and drumline fishing. There are several fisheries directed at one or a small number of species of sharks, but most sharks are taken in multi-species fisheries where the fishers tend to target more highly valued teleosts. In some fisheries, part or the entire shark catch is discarded. Shark fisheries can be classified as "coastal hook and gillnet fisheries", "demersal trawl bycatch fisheries", "deepwater bycatch fisheries", "pelagic bycatch fisheries" (primarily bycatch in tuna longline and purse seine fisheries), and "fresh-water fisheries" (Anonymous, 2000).

Coastal hook and gillnet fisheries operate in regions of the continental shelf. Construction of the fishing gear depends on topography of the fishing grounds and on the available species mix of shark, chimaerid and teleost species. Much of the artisanal catch is taken by bottom-set longlines and by bottom-set gillnets, mostly constructed of monofilament webbing with some constructed of multi-filament webbing. These gears take a variety of shark species and teleost species. In regions of narrow continental shelves, where deep waters off the continental shelf are readily accessible, or, in regions of broader continental shelves, the artisanal fleet uses surface-set longlines and driftnets to target pelagic sharks (Anonymous, 2000).

In demersal trawl bycatch fisheries, demersal trawl fisheries are impacting stocks of dogfishes (*Squaliformes*), angel sharks (*Squatiniformes*), rays (batoids), and chimaeras (holocephalans). As in the high seas fisheries, much of the trawl bycatch of sharks and rays is discarded dead and often not reported. Fishery-independent surveys in several parts of the world show that many species of these groups have exhibited marked declines in abundance.

In deepwater bycatch fisheries, like many of the teleost species studied from the deeper and colder waters of the continental slopes, the deepwater dogfishes (notably genera *Centrophorus*, *Centroscymnus*, *Etmopterus*, *Dalatias*, and *Deania*) have particularly low productivity. The continental slopes are usually steep and the total area of associated seabed is small compared with the areas on top of the continental shelves and on the abyssal plains of the oceans. As some species of dogfish are confined to particular depth ranges on these slopes, the total area occupied by some of these species is small. Expansion of demersal trawl fisheries into progressively deeper water to target dogfish and high valued teleosts on the continental slopes in some regions of the world is placing several species at high risk of severe depletion. Already demersal trawling occurs on the continental slopes at depths exceeding 1000 m. Part of the catch is targeted or is bycatch taken by gillnets and hooks (Walker, 1998).

In pelagic shark bycatch fisheries, longline, purse seine and driftnet fisheries targeting tunas and tuna-like species on the high seas and in the Exclusive Economic Zones through bilateral access

agreements take significant bycatch of sharks. Blue shark (*Prionace glauca*) is the main species caught and other species caught widely in lower quantities include *Isurus oxyrinchus*, *Alopias supercilious*, *Carcharhinus falciformis, Carcharhinus longimanus*, and *Lamna nasus* (Bonfil, 1994; Anonymous, 2000).

Shark species occurring in freshwater habitats are among some of the most threatened species. There are several reasons why these species are more vulnerable than those inhabiting marine waters. The amount of freshwater in rivers and lakes is small compared with the amount of seawater on Earth. The tropical rivers and lakes where freshwater species occur are mostly in developing countries with large and expanding human populations. These areas are more accessible to exploitation than marine waters. Freshwater habitats are also less stable than marine habitats in terms of water temperature, dissolved oxygen, clarity and water flow, and these factors are gradually being changed through deforestation. Contamination of the water with toxicants from mining and agriculture, physical modifications to the waterways through dam construction and irrigation, and inevitable changes to the flora and fauna in freshwater habitats are likely to alter them beyond the tolerance of some shark species. Several species of sharks and rays have declined such that they are now extremely rare (Compagno, 1984; Compagno and Cook, 1995).

13.2.2 Biological characterization of chondrichthyan species

Populations of shark and other chondrichthyan species tend to have lower reproductive rates and lower natural-mortality rates than populations of teleost and invertebrate species. Consequently, for many chondrichthyan species, only a small proportion of the population can be removed annually if the catches and populations are to remain sustainable. Such populations are said to have low biological productivity.

Harvested populations of these animals therefore require careful management and monitoring. Managers need to take a somewhat more precautionary approach to the management of fisheries taking sharks than they might to the management of fisheries based on teleost or invertebrate species. Late maturity, low fecundity, and parturition cycles often exceeding one year provide for close stock-recruitment relationships, with relatively little interannual variability in response to environmental variation, and for long stock recovery periods in response to overfishing.

There are directed fisheries for sharks in various parts of the world, but most species of shark are captured in multi-species fisheries directed at more productive and usually more highly valued teleost species. Harvest strategies designed to optimize economic and social benefits from these multi-species fisheries inevitably deplete the less productive shark and other chondrichthyan species unless strategies for reducing the catch of the less productive species can be developed and implemented. As fishing effort increases, characteristic and predictable changes occur in the fish assemblages. The

number of large animals decline or disappear from the assemblage and are replaced by smaller animals. This results in a gradual drift towards shorter-lived, faster-growing species. This is accompanied by an initial increase and later a decrease in the number of species in the exploitable population although the number of fish actually appearing in the catch can increase to a maximum level.

In multi-species fisheries where the main target species are teleosts, sharks landed as non-target species (byproduct) or caught and discarded (bycatch) might require special management to prevent severe depletion. Some species of shark are apex predators and naturally have comparatively small population sizes. Whereas some species have very wide geographic distributions, others have very restricted ranges falling within the full range of a fishery or the range of other anthropogenic influences. Some species have complex spatial stock structures, with critical habitats such as nursery, parturition and mating areas, and migration lanes, which might need special protection (Walker, 1998).

The magnitude of change in many of the world's fisheries has not been well appreciated because most of the change occurred during the early developmental stages of the fisheries before surveys began, and subsequent fisheries management has only been effective at stabilising fish stocks at low levels. Recent meta-analysis of large survey data sets from throughout the world indicates industrialized fisheries typically reduce community biomass by 80% during the first 15 years of exploitation, which inevitably leads to marked changes in coastal ecosystem structure and function. The analyses suggest that the global ocean has lost more than 90% of large predatory fish (Myers and Worm, 2003). This paints a bleak picture for the world's fish fauna and marine ecosystems in general, but given the biological characteristics of the chondrichthyan fauna, it can be expected that this group of animals is among the most severely affected. This is exacerbated in the open ocean for large predatory sharks, which, along with tunas, billfishes and sea turtles, tend to aggregate at distinct diversity hotspots associated with coral reefs, shelf breaks and sea mounts. These animals appear to be particularly vulnerable to targeting in latitudes 20-30° N and S where tropical and temperate species overlap (Worm et al., 2003).

The failure to manage for sustainability at rational levels is primarily due to socio-political pressure for short-term gain in harvests and due to intrinsic uncertainty in predicting the harvest that can cause stock collapse. There is, nevertheless, a growing awareness of the need for a more holistic approach by considering multispecies interactions and influences of the physical environment to achieve sustainability through adaptive management (Botsford et al., 1997).

This requires an ecosystem approach to fisheries management, which integrates information from a wide range of disciplines and applies mathematical models to synthesize multiple processes at a wide range of spatial and temporal scales. Greater use of fishing area closures and moratoria can reduce risk to sustainability through application of the precautionary principle. Harvest refuges effec-

tively protect a proportion of the exploited population and reduce uncertain assumptions about relationships between fishing effort, catch and biomass (Botsford et al., 1997). Exposing an entire population to exploitation without a sound understanding of the dynamics of the fishery can risk depletion, whereas fishing area closures can serve as a hedge against inevitable uncertainty (Lauck et al., 1998). However, such areas are insufficient protection alone because they are not isolated from all critical impacts; scales of fundamental processes, such as population replenishment, are much larger than the areas can encompass. Fishing area closures need to be complemented by other management and conservation measures outside the closures (Allison et al., 1998).

An ecosystem approach to fisheries management requires management over broad regions and across fisheries, and away from single-species and single-fishery management that characterizes past and present practices. The approach involves monitoring all species impacted by the effects of fishing and requires better understanding of the dynamics of fish movement and species interactions through food chains. Whereas complex models and comprehensive long-term monitoring data sets are required to reduce uncertainty, it is essential in the short-term to develop rapid assessment methods based on simpler data sets and judgement that can provide for interim management of species and ecosystems at risk.

13.2.3 Fishing mortality

In fishery models, fishing mortality rate for a harvested population is usually expressed as the product of the two quantities: fishing effort and catchability. Fishing effort can be quantified as the number of fishing vessels in a fleet, a measure of the amount of fishing gear deployed, amount of fishing time, or some other variable that is a mix of these variables. Catchability is the proportion of the exploited population taken by one unit of fishing effort and has a value in the range 0–1 for any age or size of fish. It is the product of three parameters, each of which also has a value 0–1. The three parameters comprising catchability are availability, encounterability, and selectivity; i.e.,

$$catchability = availability \times encounterability \times selectivity.$$

Availability is the proportion of the habitat area of a population fished by the fleet. A population with a habitat area extending well beyond the range of the fishing fleet has a low availability value. Conversely, a population with a habitat area that falls entirely inside the range of the fishery has a high availability value of one, unless parts of the habitat area are inaccessible to the fishing fleet.

Encounterability is the proportion of that part of the population available to fishery encountered by one unit of fishing effort. For any species, encounterability depends on construction of the fishing gear and on the biological characteristics of that species. Pelagic and semipelagic species that actively swim in the water column are more likely than less active species to encounter passive gears such as gillnets or longlines with baited hooks. These actively swimming species therefore have a higher

encounterability to these gears than the less active species. For active gears such as demersal trawl, bottom-dwelling, sluggish species, such as angel sharks (*Squatiniformes*) and batoids have a higher probability of capture and therefore higher encounterability than the more powerful swimming species, such as the whaler and hammerhead sharks (*Carcharhiniformes*) and mackerel sharks (*Lamniformes*). Sixgill and sevengill sharks (*Hexanchiformes*), sawsharks (Pristiophoriformes), dogfishes (Squaliformes), catsharks, wobbegong and carpet sharks (Orectolobiformes) and horn sharks (Heterodontiformes) probably exhibit intermediate trawl encounterability.

Selectivity is the proportion of the animals encountering the fishing gear that is captured by the fishing gear. For any fishing gear, selectivity gives rise to a range of complex dynamics that relate features of the fishing gear to size of animals captured. Selectivity by trawl nets for size of chondrichthyan animals is not well understood, and hook-size selectivity for size of animal is weak. For gillnets, however, sharks of different sizes are not equally vulnerable to capture. Small animals swim through gillnets but become progressively more vulnerable to capture as they grow. After reaching the length of maximum vulnerability they then become progressively less vulnerable with further growth as they deflect from the meshes of the nets (Kirkwood and Walker, 1986). These size-selectivity effects are stronger for fusiform-shaped sharks than for more dorsoventrally-flattened species or for species with protruding structures such the heads of hammerhead sharks, the rostral teeth of pristiophorid sawsharks and pristid sawfishes, and the dorsal spines of squalid and heterodontid sharks and chimaerids. When captured by gillnet or hook, fast swimming species, dependent on ram-jet ventilation of their gills for respiration tend to die more quickly than bottom-dwelling species when caught. Bottom-dwelling species with spiracles to aid gill ventilation are better able to pass water over their gills after capture by gillnets and can struggle vigorously to either escape or become more tightly enmeshed in the gear. Species that can struggle vigorously after capture in gillnets tend to have narrower selectivity ranges than species that struggle less. Hence, for some species, careful regulation of mesh-size can be used to ensure that the sharks captured are large enough to avoid growth overfishing and small enough to facilitate escapement of large breeding animals to avoid recruitment overfishing (Walker, 1998).

The concept of catchability is usually applied to target and byproduct species where most of the animals captured are retained. So as to broaden the concept to include bycatch, the term “catch susceptibility” (Stobutzki et al., 2002) and the term “post-capture mortality” are adopted here to allow for survival of part of the catch released. The parameters catch susceptibility and post-capture mortality both have values in the range 0–1 and are related to each other and to catchability by the equation

catch susceptibility = *catchability* x *post-capture mortality*,

which can hence be further expanded to provide the equation

catch susceptibility = *availability* x *encounterability* x *selectivity* x *post-capture mortality*.

Post-capture mortality is the proportion of the animals that die as a result of being caught in or of encountering the fishing gear. Animals of target and byproduct species that are mostly retained have a post-capture mortality value approaching one. This can be less if some are discarded because of their size or breeding condition. Post-capture mortality for discarded species can vary markedly. In addition to handling by fishers, the fishing gear and biological characteristics can contribute to various kinds of mortality referred to as unaccounted fishing mortality or as collateral mortality. Dead sharks not tightly enmeshed can drop out of gillnets and contribute to unaccounted fishing mortality through drop-out mortality. Sharks eaten by other fish or mammals after capture in the gear contributes to unaccounted fishing mortality through predation mortality. Dead sharks either partly or totally decomposed or eaten by invertebrates and vertebrates when fishing gear is left in the water for extended periods also contribute to unaccounted fishing mortality. Also, lost gillnets contribute to unaccounted fishing mortality through ghost fishing mortality until they are rolled into a ball by tidal flow. Post-capture mortality from normal handling by fishers is low for heterodontid and orectolobid sharks but high for carcharhinids.

13.2.4 Rapid assessment for evaluation of risk

Stock assessment of chondrichthyan species that incorporates time series of catch and indices of relative abundance, includes biological parameters, and accounts for fishing gear selectivity has been undertaken for only a few species, such as *Mustelus antarcticus* (Walker, 1994; Walker, 1998) and *Galeorhinus galeus* harvested off southern Australia. The assessments of *G. galeus* also incorporate spatiality (Punt et al., 2000) and evaluation of risk in a Bayesian framework (Punt and Walker, 1998; Punt et al., 2000). Such assessments require large data sets from long-term fishery monitoring and from extensive biological and gear selectivity studies (see Chapter 10). Because of their comparatively low biological productivity and, for many species, because of their high catch susceptibility, most chondrichthyan species require management action long before sufficient data are available to undertake full stock assessment. It is therefore necessary to apply rapid assessment techniques for evaluation of risk from the effects of fishing.

A rapid assessment approach for evaluating risk to chondrichthyan species was applied to species caught as bycatch in a tropical prawn fishery in northern Australia (Stobutzki et al., 2002). This method ranks the relative sustainability of each species on the basis of its "susceptibility" and "recovery" (Stobutzki et al., 2001; Stobutzki et al., 2002), which are assessed on the basis of the biological attributes of the species. A similar approach is proposed here for sharks and other chondrichthyans, but the approach alters the terminology and the method of quantification of the various parameters used to be more compatible with more comprehensive fishery assessment methods.

The alternative method proposed here provides a framework for considering a species' ecological risk, risk of depletion, or risk of extinction. For this method, the terms catch susceptibility and biological productivity are used in place of susceptibility and recovery to represent parameters associated with fishing mortality and population growth, respectively.

Species of high biological productivity can be viewed as having rapid population turnover, whereas species of low biological productivity can be viewed as having slow population turnover. For an unexploited population to remain in equilibrium, there has to be a balance between the natural mortality rate reducing numbers and the reproductive rate increasing numbers. Otherwise, over time, if the reproductive rate exceeded the natural mortality rate, the population would grow to infinity; conversely, if the natural mortality rate exceeded the reproductive rate, the population would go extinct. Low reproductive rate and low natural mortality rate are associated with low biological productivity, whereas high reproductive rate and high natural mortality rate are associated with high biological productivity. It follows, therefore, that either reproductive rate or natural mortality rate can serve as a proxy for biological productivity for rapid assessment.

Other expressions of biological productivity include the "intrinsic rate of population growth" parameter formulated variously in biomass dynamics models (Schaefer, 1957; Schnute, 1985), demographic models (Lotka, 1922), and various adaptations of these models for sharks (Au and Smith, 1997; Xiao and Walker, 2000). Using a particular formulation of a demographic model to allow for density-dependent change in natural mortality (Au and Smith, 1997), one study classed 26 Pacific shark species on the basis of the "intrinsic rate of population growth" (referred to by the authors as "rebound potential") (Smith et al., 1998). In addition, intrinsic rate of population growth is related to inter-generation period and reproductive output per generation (Heron, 1972). Application of biomass dynamics models requires time series of catch and relative abundance data, and demographic analysis combines available parameter estimates for natural mortality rate and reproduction. Required information for this purpose on chondrichthyan reproduction for a population includes the maternity ogive (proportion of the female population contributing to annual recruitment expressed as a function of length or age), fecundity expressed as a function of maternal length or age, and sex ratio of progeny. If the maternity ogive and fecundity are expressed as a function of length, then the relationship between length and age is also required for the application of demographic models.

Using natural mortality rate as a proxy for biological productivity requires some caution, as the natural mortality rate is likely to be density-dependent and age-dependent. Also, fishing is likely to remove the oldest animals from the population and reduce the maximum age detected in a sample of animals collected for ageing purposes. Notwithstanding these potential biases, rough estimates of natural mortality or maximum age can be used for broad categorization of risk. The instantaneous

mortality rate, Z, can be approximately related to maximum age, t_{max}, by the equation $\ln(0.01) = -Z\, t_{max}$, where 0.01 represents survival of 1% of the animals reaching maximum age (Hoenig, 1983). Because natural mortality rate is much higher for the young age classes than the older age classes, as demonstrated from modelling shark populations (Walker, 1994; Punt and Walker, 1998), this equation is reformulated here for application to chondrichthyans by considering only that part of the population of age greater than 2 years. Assuming that mortality is constant for all age classes, calculations of instantaneous total mortality rate for 1% of 2-year-old animals to survive to ages 8, 16 and 24 years are 0.77, 0.33 and 0.21, respectively. If total mortality is divided evenly between natural mortality and fishing mortality, a condition sometimes assumed for a population in equilibrium producing the maximum sustainable yield (Thompson, 1992; Au and Smith, 1997), natural mortality rates for 2-year-old animals surviving to these ages approximate to 0.38, 0.16 and 0.10, respectively. These values are used as a basis for arbitrary categorization of chondrichthyan species for risk (Table 13.1). For example, based on published instantaneous natural mortality rates, *Galeorhinus galeus* (Punt and Walker, 1998; Smith et al., 1998), *Carcharodon carcharias*, *Carcharias taurus*, *Carcharhinus plumbeus* and *C. obscurus* (Smith et al., 1998) can be classed at high risk. Similarly *Mustelus antarcticus* (Walker, 1994), *M. californicus*, *M. henlei* and *Sphyrna tiburo* (Smith et al., 1998) can be classed at medium risk, and *Rhizoprionodon terraenovae* can be classed at low risk (Smith et al., 1998).

Parameter	Values for three arbitrary categories of risk		
	Low (L)	Medium (M)	High (H)
Total mortality (y^{-1})	>0.76	0.32–0.76	0.00–0.31
Natural mortality (y^{-1})	>0.38	0.16–0.38	0.00–0.15
Maximum age (y)	0–8	9–16	>16
Availability	0.00–0.33	0.34–0.66	0.67–1.00
Encounterability	0.00–0.33	0.34–0.66	0.67–1.00
Selectivity	0.00–0.33	0.34–0.66	0.67–1.00
Post-capture mortality	0.00–0.33	0.34–0.66	0.67–1.00
Catch susceptibility	0.00–0.33	0.34–0.66	0.67–1.00

Table 13.1 Values of various parameters for three arbitrary categories of risk

Catch susceptibility and each of its four components (availability, encounterability, selectivity, and post-capture mortality) can also be arbitrarily divided into three categories of risk. This is achieved here by evenly dividing the possible value range of 0.00–1.00 into the three ranges 0.00–0.33, 0.34–0.66 and 0.67–1.00 and designated low (L), medium (M) and high (H), respectively. For each fishing method adopted in the fisheries of south-eastern Australia, for example, it is possible to categorize encounterability, selectivity and post-capture mortality into one of the three categories on the basis of chondrichthyan taxonomic order (Table 13.2) by considering the animals' biological characteristics. This means that the only parameter to be determined for any particular species is "availability," which for rapid assessment can be estimated as the ratio of the area fished within the spatial range of that species divided by the entire area inhabited by the species. By adopting the upper limit values for the three ranges of 0.33, 0.66 and 1.00 for low, medium and high risk, respectively, then catch susceptibility can also be categorized as low, medium or high risk. For example for a fishing method where mortality is high, then catch susceptibility is low. This is calculated as catch susceptibility = 0.33 x 1.00 x 1.00 = 0.33 (i.e.., catch susceptibility = LHHH=L)

Taxonomic order	Common name	Envounterability				Selectivity			Discard post-harvest mortality				
		trawl/ seine	Gillnet	Hook	trap/ pot	trawl/ seine	Gillnet 6-6½ in	Hook	Trap pot	Trawl seine	Gillnet 6-6½ in	Hook	Trap/ pot
Pelagic and semipelagic species													
Carcharhiniformes	Whaler and hammerhead shark	L	L	L	L	H	M	H	L	H	H	M	H
Lamniformes	Mackerel and thresher sharks	L	L	M	L	H	M	H	L	H	H	M	H
Demersal species													
Carcharhiniformes	Whaler and hammerhead shards	L	H	H	L	H	M	H	L	H	M	L	H
Squatiniformes	Angel sharks	H	L	L	L	H	L	H	M	M	L	L	L
Pristiophoriformes	Sawsharks	M	H	M	L	H	H	H	M	H	H	L	M
Squaliformes	Dogfishes	M	H	H	L	H	L	H	H	M	M	L	L
Hexanchiformes	Sixgill and sevengill sharks	L	H	H	L	H	M	H	H	H	H	M	H
Orectolobiformes	Catsharks, wobbegongs, carpet sharks	M	H	H	M	H	M	H	H	M	L	L	L
Heterondontiformes	Horn sharks	M	H	M	L	H	M	H	H	M	L	L	L
Pristiformes	Sawfishes	H	L	L	L	H	H	H	H	H	L	L	L
Rhinobatiformes	Shovelnose and guitar rays	H	L	L	L	H	L	H	H	H	L	L	L
Torpediniformes	Electric rays	H	L	L	L	H	L	H	H	H	L	L	L
Rakofpr,es	Skates	H	L	L	L	H	L	H	H	H	L	L	L
Myliobatiformes	Eagle and devil rays and stingrays	H	L	L	L	H	L	H	H	H	L	L	L
Holocephaliformes	Chimaeras	M	L	L	L	H	M	H	H	H	H	M	L

Footnote: The values presented in this table are based on species found in southeastern Australia, but they should be applicable to most regions of the world, except " selectivity" of gillnets, which is presented here for 6-6½ inch mesh and is likely to vary regionally depending on size of animals for each species in the region.

Table 13.2 Catch susceptibility of chondrichthyan animals to demersal fishing gear. Catch susceptibility is defined as "availability" x "encounterability" x "selelectivity" x "post-capture mortality"; "availability" is the ratio of area of range of specimens divided by the area of the range of the fishery; "catch susceptibility", "availability", "vulnerability", "selectivity", and "discard post-harvest mortality" all have values ranging 0-1, for risk assessment these are categorized as L (low, 0.00-0.33), M (medium 0.34-0.66), and H (high, 0.67-1.00).

13.3 FRAMEWORKS FOR FISHERIES MANAGEMENT

13.3.1 International developments

Growing widespread concern during the past decade about expanding fisheries for sharks and for the potential impacts of fishing on their populations and those of rays and chimaeras led to initiatives to implement better management of these animals. During the mid-1990s, submissions were presented to the Convention for International Trade in Endangered Species of Wild Fauna and Flora (CITES) seeking restrictions on the trade of products from sharks as a means of controlling the harvest of these animals. In response to requests from CITES, the Food and Agricultural Organization of the United Nations (FAO) subsequently initiated a worldwide process that led to development of the International Plan of Action for the Conservation and Management of Sharks (IPOA-Sharks). The IPOA-Sharks was endorsed by the FAO Committee of Fisheries and its 80 or so member nations during 15–19 February 1999. The IPOA-Sharks provides guidelines to member nations for development of National Plans of Action for the Conservation and Management of Sharks (NPOA-Sharks) and for coordination of shark management at global, regional, and sub-regional levels under the auspices of FAO. The IPOA-Sharks forms part of the Code of Conduct for Responsible Fisheries and defines "sharks" to include sharks, rays and chimaeras.

Through the IPOA-Sharks and other international developments, the scope of fisheries management for these animals is expanding beyond the focus of sustainable use of the resource to take account of the need for biodiversity conservation and maintenance of ecosystem structure and function. There is also growing emphasis on bycatch reduction and on ethical issues associated with full utilization of dead sharks and the handling and processing of these animals (Anonymous, 2000).

13.3.2 Jurisdictional and institutional frameworks

Fisheries management presupposes a minimum set of institutional arrangements and recurrent activities at local, sub-national, national, sub-regional, regional and global levels. Entities engaged in fisheries management require appropriate policy, and legal and institutional frameworks to adopt measures for the long-term conservation and sustainable use of shark fishery resources. Conservation and management measures need to be based on the best scientific evidence available. Effective coordination of implementation of fisheries management at a national level through development of shark plans and ongoing shark assessments requires a structure, a definition of roles, agreed processes, and mobilization of resources. All relevant fishing sectors, fishing communities, non-government organizations, and other interested parties should be consulted as part of the decision-making process. Creation of public awareness of the need for the management of shark resources and participation in the management process by those affected should be promoted.

To be effective, management of fisheries has to be concerned with whole stock units over the entire area of distribution of the species harvested. The best scientific evidence available should be

used to determine the area of distribution of the resource and the area through which a fish in the stock migrates during its life cycle. Where a stock falls entirely within the Exclusive Economic Zone (EEZ) of a single nation then that resource can be managed under the single jurisdiction of that nation. On the other hand, where a stock is distributed in the EEZs of more than one nation or in the high seas, complex jurisdictional arrangements are required. Shared or transboundary straddling stocks need to be managed through bilateral and multilateral arrangements or Regional Fisheries Management Organizations (RFMOs) (Anonymous, 2000).

All nations are free to harvest fish in the high seas and regulation is beyond the control of any individual country. Straddling and highly migratory fish stocks are managed cooperatively under a United Nations treaty. This treaty is the Agreement for the Implementation of the United Nations Convention on the Law of the Sea of 10 December 1982 Relating to the Convention and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks. It is more briefly termed the UN Fish Stocks Agreement. Ratification of the Agreement by nations provides rights and obligations to those nations and prescribes fisheries management principles for the long-term conservation and sustainable use of straddling and highly migratory fish stocks. The Agreement provides a framework for cooperation between fishing nations, including through RFMOs. Also, it provides rights to member nations of RFMOs to board and inspect fishing vessels on the high seas to check compliance with regionally agreed conservation and management measures. Nations signing the Agreement accept the principles of the Agreement. The UN Fish Stocks Agreement depends on "Flag State responsibility," which is a principle of international law. The national law applying to a vessel on the high seas is the law of the country whose flag the vessel is entitled to carry. If there is any infringement of rules, the Flag State of the vessel concerned is responsible for undertaking investigation and appropriate enforcement action.

13.4 USE RIGHTS

Granting use rights bestows property rights whereby an individual, company, or defined group or community can own fish after the fish have been captured. Once captured the fish become private property. Before they are captured, the fish are private property only if the water body holding the fish is private property. Within a country's EEZ, fish in the water are usually deemed the property of the citizens of that country and said to be state property. Nevertheless, a state can legislate to privatize fish in the water and thereby grant ownership to an individual, company, or defined group or community. Where the fish in the water are owned in common by a defined group or community, the fish are said to be common property. For example, where a government legislates to bestow ownership of fish in a specific body of water to people traditionally using that fish resource, the fish in the water become the common property of those people. However, the fish of an entire nation are often referred to as common property. Here the group or community is defined as including all citizens of a nation; the term common property is equated to state property (Charles, 2002).

Through fisheries management, use rights can be implemented under any of private property, state property or common property. In addition, the United Nations Fish Stocks Agreement (Article 10) provides facility to prescribe use rights in waters outside the EEZs of nations on the high seas where the fish in the water are deemed "non-property" (Charles, 2002). Fishery managers need to ensure that no vessel is allowed to capture sharks or take sharks as bycatch unless authorized in a manner consistent with international law for the high seas or in conformity with national or sub-national legislation within areas of national or sub-national jurisdiction.

The FAO World Fisheries Conference in Rome during 1983 recognized that open access to non-managed fisheries resulted in competition for limited resources, overcapitalization, and depletion of stocks. It was considered that fishers should have clearly defined fishing rights and that catches should not exceed the productivity of the resource. One approach to allocate rights for the capacity to fish is through input controls such as license allocation. Another approach is to allocate rights for specified shares of the resource through output controls in the form of catch quotas (King, 1995).

13.4.1 Territorial use rights

Rights can be assigned to individuals or communities to fish in certain locations based on long-standing tradition of use (customary usage). This approach is variously termed Territorial Use Rights in Fishing (TURFs) and Customary Marine Tenure (CMT). A feature of these systems is the local solution of usage issues. Many fishing communities informally regulate their fishing effort, based on their observations of fish abundance and their interpretation of their indicators of abundance over time (Charles, 2002).

Territorial management is highly effective where it is supervised by the fishing community itself or by its elected leaders. Many TURF and CMT systems have declined as traditional fisheries commercialize. Nevertheless, several countries of Oceania, such as Solomon Islands, Fiji and Samoa, have moved to re-establish these systems. Customary fishing ground boundaries based on oral claims are being formalized in legislation (Charles, 2002). Japan, for example, has integrated ancient local systems of management into fisheries planning at all levels of local, regional and national government (Pinkerton, 2002). A challenge for countries is to support traditional approaches to management and to integrate them into regional and national management systems through co-management agreements. There is evidence of customary usage of sharks and rays in Canada, northern Australia (Last and Stevens, 1994), Solomon Islands (Sant and Hayes, 1996), and New Zealand (Francis, 1998). However, there are no examples where territorial use rights have been formally granted specifically for the harvest of chondrichthyan animals in recognition of traditional usage.

13.4.2 Limited entry

Limited entry is a common management tool whereby the management agency issues a limited number of licenses to take fish. This creates a use right to participate in a particular fishery. License limitation is the restriction of fishing rights to those fishers, fishing units, or fishing vessels licensed in a fishery.

Several types of fishing licenses are used for fisheries management throughout the world. A "personal license" authorizes a particular fisher to deploy fishing gear for catching fish, but requires the licensed fisher to be present at the site of fishing operations. A "vessel license" authorizes a particular vessel to deploy fishing gear for catching fish, but requires operations to be made from the licensed vessel. A "fishery access license" authorizes the holder, or a person nominated by the holder, to deploy fishing gear for catching fish from any nominated vessel. A "gear license" authorizes the use of a particular item of fishing gear for catching fish by the holder, or a person nominated by the holder, from any nominated vessel. Special conditions or endorsements on such licenses can be used to nominate one or more fisheries, species, gears, catch levels, or effort levels authorized.

Licenses are either non-transferable or transferable. Non-transferable licenses are auctioned or issued at the discretion of the licensing authority through a Minister of State. Development of merit criteria as guidelines for issuing non-transferable licences by licensing authorities are usually criticized as discriminatory. Allocation of non-transferable licenses according to merit inevitably leads to dissatisfaction and pressure from holders to make the licenses transferable. Transferable licenses are exchanged by mutual financial agreement between the seller and buyer (usually within guidelines prescribed by the licensing authority). Once transferable, licenses acquire a value related to earnings that might be acquired from possessing the license. Debts associated with the purchase of transferable licenses create an incentive to increase the catch to service the loans, which create a need to reduce the number of licenses or entitlements associated with each license. If there is the need to reduce the number of licenses in a fishery, the licensing authority can withhold non-transferable licenses, but has to buy back transferable licenses from license holders at market price.

Annual license fees collected by the licensing authority can be used to recoup management, surveillance, research and fishery monitoring costs, and collect a resource rent on behalf of the community. Personal licenses can be effective in artisanal and recreational fisheries, but fishery access or vessel licences are favored in industrial fisheries where costly assets are required and there is a need to exchange fishing masters or skippers on a vessel to ensure its economic viability. All four types of license have been variously applied in fisheries either targeting sharks or taking sharks as byproduct or bycatch.

Limited entry caps the number of operators in a fishery, but is rarely sufficient to manage a fishery. Once license limitation is implemented, improved skill of the operators and technological innovation inevitably increase the fishing power of the vessels in the fleet. Limited entry is best implemented during the early phase of the development of a fishery, before the catching power of the fleet is excessive. It is difficult to reduce the number of licenses once there is overcapacity in the fleet. Whereas limited entry is a reasonable mechanism for assigning use rights, it must be implemented as part of a management portfolio.

13.4.3 Quantitative input rights (effort rights)

Input controls designed to limit or reduce fishing mortality requires some form of restrictive licensing, which limits the number of fishing vessels engaged in a particular fishery, and some measure for limiting the fishing effort of the licensed vessels. Where overfishing occurs and the fleet is too large, there is a need to reduce the number of licensed vessels or reduce the fishing efficiency of the vessels. Furthermore, where license limitation is established, incremental technological advances in vessel and fishing gear design and improvements in fish-finding equipment and navigation aids are likely to cause the effective fishing capacity of a fleet to increase with time. In addition, if the licenses are transferable and acquire progressively higher value, economic forces will cause inactive vessels with their associated latent effort to become activated and increase the total effort applied by the entire fleet. Hence, with any input control system, increasing efficiency and increasing effort create an ongoing need to reduce the number of vessels or efficiency of each vessel. Overcapacity of a fleet can be reduced in several ways: removing vessels, reducing fishing time of the vessels, limiting the amount or size of gear that a vessel can carry, or reducing efficiency of fishing effort.

Removing vessels from the fleet requires rescinding licenses. This involves removing the rights from some vessels to operate in a fleet. Just systems applied for this purpose are referred to as Buy-Back Schemes or Decommissioning Schemes where funds are made available by government, the industry itself or some other stakeholder group to purchase licenses as a means to removing vessels from the fishery. A feature with these schemes is that the least efficient operators have the highest economic incentive to sell their licenses. Whereas this improves the overall economic efficiency of the fleet, it can result in a large number of vessels being removed with very little change in overall fishing mortality.

Reducing vessels' fishing time can be implemented by imposing limits on the number of days or times of the day vessels can operate. Extended closed seasons, closed days of the week, or closed times of day are unpopular with fishers as it reduces flexibility and creates incentives to operate under adverse weather conditions. Closed days of the week are seen as inequitable as it impacts greatest on larger vessels that undertake extended periods at sea. Closed periods disrupt market supply of fish and employment patterns.

Fishing capacity of a fleet can be restricted by limiting the size of vessel and engine power and thereby restrict the ability of vessels to tow fishing gear such as demersal trawls. For most other fishing methods, however, the relationship between the size of the gear and the size of the vessel or power of the engine is not so clear. Nevertheless, fishing capacity of a fleet can be restricted by limiting the size of vessels and thereby restricting the number of fishing days by weather conditions. This can cause problems of safety for fishers if there are strong economic incentives to operate under hazardous conditions.

Fishing gear can be limited in type, size and number. Gillnets can be restricted by controlling the length and height of the nets, the mesh-size of the webbing, and hanging ratio for the construction of the nets. Longlines can be restricted by controlling the length (or volume) of mainline and the number of hooks that can be used during each operation. Restrictions might also be placed on hook-size and presence or absence of a wire trace between the hook and the snood, and on the use of automatic baiting and setting machines. Trawl nets can be limited to a maximum length of headline.

Gear regulations tend to restrict the efficiency and cost of catching fish for each operator. Gear restrictions are often implemented where there are the social objectives of providing employment and food to a large number of traditional and artisan fishers. Hence, gear restrictions are minimized where there is the economic management goal for reducing the number of operators and improving economic efficiency, but can be adopted as a means to maintenance of fishing communities and equity of incomes among participants (Pope, 2002).

Some of the benefits of limits on the quantity of fixed gear used, such as gillnets, can be offset by the gear being in the water for extended periods. Legislating for vessels not to leave the gear unattended discourages the practice of returning to port while the gear remains set at sea. This practice leads to cryptic fishing mortality from predation mortality and ghost fishing mortality if the nets are lost.

Meeting the biological objective of reducing fishing mortality by reducing vessel efficiency is incompatible with the economic objective of improving economic efficiency of the fleet. Similarly, meeting the biological objective by reducing vessel numbers is incompatible with the social objective of providing employment for fishing communities.

There are many general vessel and fishing regulations that apply across fisheries, but few have been implemented specifically for chondrichthyan species. Within the European Union, every country has agreed to a maximum gross tonnage of vessels and maximum engine power. The limits are set for each fishery, fishery sector, and, in some cases, fish stock (Pawson and Vince, 1999).

During the late 1980s and the 1990s, a complex system of quantitative rights was adopted for the shark fishery of southern Australia. Depending on historic catches by a vessel, vessel licenses

were endorsed to use various length of gillnets. These gear holdings were not transferable except for a short period when a small proportion of the licenses could be amalgamated to allow for an increase in gear holdings. After amalgamation, the maximum gear holding was 6000 meters long, but this was subsequently reduced to 4200 meters (Walker, 1999). This type of effort rights was taken a step further in the shark fishery of Western Australia. Here time-gear units were allocated where a time-gear unit authorized the use of a particular length of gillnet for one month of the year (Simpfendorfer, 1999).

13.4.4 Quantitative output rights (catch quotas)

Also referred to as output control, limitation of catch can take the form of a global catch quota, individual quotas as non-transferable individual quotas or individual transferable quotas (ITQs) with a total allowable catch (TAC), bag limits or trip limits.

A global catch quota, alternatively referred to as a competitive TAC, is the maximum catch allowed from a resource by the entire fleet for a year or season. Under this system, individual fishers compete for catch until the fleet reaches the overall limit and the fishery is then closed. Such a system requires rapid collation of catch statistics to be effective. Individual fishers feel compelled to operate under hazardous weather conditions and to capitalize in vessels and gear to attain a competitive edge. This can result in progressively shorter seasons, which disrupt employment patterns and market supplies.

Bag limits are a simpler form of catch limit where the number of animals a person or vessel can retain. Bag limits are usually applied on a daily basis for recreational fishers where an individual is permitted to land up to a specified catch weight or a prescribed number of carcasses. Limiting the number of carcasses can create an incentive to retain the largest animals and discard small animals, which might be dead and hence contributing to cryptic fishing mortality.

Trip limits may be applied on a trip or daily basis for fishers who do not hold a license to operate in the fishery. Trip limits may be designed to avoid wastage by allowing non-licensed operators to land byproduct catch. However, the trip limit needs to be sufficiently low so as not to encourage targeting by non-licensed operators. Trip limits may be applied also in a fishery to discourage “derby fishing” and to spread the take of a quota over a long period of time.

Individual non-transferable quotas are where each operator has a prescribed catch, which is usually fixed as a specified proportion of the TAC. This avoids the competitive element, but does not allow the operator the opportunity to increase catch by personal choice.

Individual Transferable Quotas (ITQs) are where each operator has a prescribed catch of one or more units of catch. The ITQs can be traded freely, or traded between specified operators. Operators can hold one or more ITQs, depending on the number they choose to buy. By prescribing an ITQ

or non-transferable quota as a proportion of the TAC, the catch allowed under each ITQ varies depending on the TAC, which can be set annually or some other period. The facility to trade ITQs allows less efficient operators to sell all or part of their quota to more efficient operators at the market price of the quota. A substantial enforcement effort is required to ensure that individual quotas are not exceeded. Individual catch quotas create an incentive to under-report catches and a temptation to sell to black market buyers. In addition, management by individual quotas can encourage operators to discard that part of the catch that potentially receives a low price (maybe damaged, small or large animals) and replace them with animals that would receive a higher price. This practice is referred to as high grading.

TACs for some species of fish are expressed as the number of fish, but they are usually expressed as weight. Although they should ideally relate to the catch, for administrative convenience they are limits on landings. Components of TACs are often used as a basis for resource allocation between different user groups, such as between recreational users and commercial users or between sectors or regions of the commercial users. This also occurs in internationally shared fisheries where allocations are negotiated between countries.

Various types of TACs are administered for shark resources. For management of the United States Atlantic Shark Fishery, 39 species of sharks are categorized into four groups: “large coastal”, “small coastal”, “pelagic”, and “prohibited” for the commercial sectors of the fishery. Apart from the prohibited group, each group has a separate TAC, reviewed periodically. In the absence of limited entry in the fishery, the commercial catches have regularly exceeded the TACs. In addition, there is a commercial trip limit of 4000 pounds weight for the large coastal group and a recreational fishing bag limit of two sharks per boat per day plus two Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) per person per day or trip (Branstetter, 1999). New Zealand and Australia have set TACs for key individual species of shark and have ITQs (Francis, 1998; Walker, 1999).

13.5 TECHNICAL MEASURES

13.5.1 Regulation of fishing gear

Ideal fishing gear achieves many things simultaneously. It is efficient at capturing target species while avoiding small animals to minimize growth overfishing and avoiding large breeding animals to minimize recruitment overfishing of the species. It has negligible direct or indirect impact on bycatch species, habitats, and substrates, and it causes minimal damage to animals captured and in no way diminishes the food quality of the animals caught.

Regulation of fishing gear can be used for control of fishing mortality, of impacts on habitats and ecosystems, and of the food quality of fish retained. Regulation of fishing gear should not be used as a way of controlling the fishing effort component of fishing mortality, but rather as a way of control-

ling the catch susceptibility component of fishing mortality. This can be achieved by variously controlling one or more of the four components of catch susceptibility—availability, encounterability, selectivity, and post-capture mortality. Availability can be controlled through the fishing area closure to the use of specific gears, whereas encounterability, selectivity and post-capture mortality can be controlled or influenced through regulation of the construction of the gear or the way it is used.

Fishing gears are classified as passive or active. This classification is based on the behaviour of the target species in relation to the gear. Passive gears include gillnets, trammel nets, longlines, handlines, jigs, droplines, troll lines, pots and fish traps. Active gears include spears, harpoons, dredges, demersal trawls, mid-water trawls, Danish seine nets, Scottish seine nets, beach seines, and purse seines. Table 13.3 provides an evaluation of different fishing gears for selectivity and ecosystem effects of fishing. The values presented are from evaluation across many fisheries, but specific values for a particular fishery, particularly as it might relate to chondrichthyan species, can be altered depending on regulation of the fishing gear (Bjordal, 2002).

Fishing gear	Size selection	Species selection	Bycatch mortality	Ghost fishing	Habitat effects	Energy efficiency	Catch quality	Ecosystem effect index
Gillnets	8	4	5	1	7	8	5	5.4
Trammel nets	2	3	5	3	7	8	5	4.7
Handlining	4	4	6	10	9	9	9	7.3
Longlining	6	5	6	9	8	8	8	7.1
Pots	7	7	9	3	8	8	9	7.3
Traps	5	5	8	8	9	9	9	7.6
Spear, harpoon	8	9	5	10	10	8	9	8.4
Pelagic trawl	4	7	3	9	9	4	8	6.3
Demersal trawl	4	4	6	9	2	2	6	4.7
Beam trawl	4	4	6	9	2	1	6	4.6
Shrimp trawl	1	1	7	9	4	2	6	4.3
Seine net	5	5	6	9	4	5	8	6.0
Purse seine	-	7	5	9	9	8	8	7.7
Beach seine	2	2	5	9	6	9	9	6.1

Table 13.3 Estimates of ecosystem effects of fishing for different fishing gears. Ranking is a scale from 1 (non-favorable) to 10 (highly favorable) for different ecosystem-related factors; ecosystem effect index is the mean of the other seven factors (reproduced from Bjordal, 2002).

Fishery managers need to ensure that fishing methods and practices in a fishery are consistent with the code of conduct for responsible fishing. Those methods that are not should be phased out and replaced with acceptable methods and practices (Anonymous, 1995; Anonymous, 2000).

The type of fishing gear used and the species of shark taken as bycatch determines which techniques and equipment are appropriate for minimizing bycatch. For trawl nets, there is evidence that catches of sharks have been reduced when fitted with turtle exclusion devices, suggesting there might be advantages investigating alternative devices designed specifically to exclude sharks. Also, there is scope to reduce bycatch of sharks in gillnets by regulating mesh size and possibly the breaking strain of the webbing filaments. Many species of sharks remain alive on hooks for extended periods and can be released alive. There might be scope to improve survival of sharks by prohibiting the use of wire traces used to attach hooks to the snoods on a longline and by regulating for reduced breaking strains of the snoods. Wire traces reduce the probability of hooks being bitten off the snoods by sharks. Regulation of hook size may provide a means of eliminating or reducing the catch of smaller, younger individuals in a shark populations (Dowd, 2003). Minimum mesh sizes or square mesh panels in codends of trawl nets are applied widely, but are not selected specifically for chondrichthyan species. Selection of appropriate trawl codend mesh size and shape might have some benefit in allowing neonate and small juvenile sharks to escape.

Regulation of mesh size is a highly effective measure for shark management. Careful selection of mid-sized mesh allows small animals to pass through the meshes and large animals, notably breeding and other mature animals, to escape (Kirkwood and Walker, 1986). Adoption of a predominantly 6-inch mesh size during 1975 has been the key to success in sustainable use of the gummy shark (*Mustelus antarcticus*) stocks in Bass Strait. In this fishery, not only does the gear selectivity allow escapement of small and large animals, but the fishers operate in areas inhabited by mid-sized animals, which tend to be away from the inshore areas inhabited by pre-recruits and breeding females (Walker, 1998). In Western Australia, mesh sizes, number of meshes deep, and length for the construction of shark gillnets are also controlled. These vary between different zones (Simpfendorfer, 1999).

13.5.2 Area and time restrictions

Closures involve restricting all or particular methods of fishing in selected areas, and the closures can be permanent, temporary, seasonal, daily or part of the day. Spatial and temporal closures are frequently applied to meet specific fishery-management objectives, but they are also used to meet other community objectives. Other objectives for closures include protecting marine, estuarine, and freshwater biota, items of special cultural value, or geologic interest. In addition, areas might be set aside for specific purposes such as navigation, aquaculture, or mining. The various purposes of clo-

sures have produced confusion and debate over terminology. So for the purpose of this chapter, a distinction is made between closures designed to meet fisheries management objectives and closures designed to meet other community objectives. The two terms adopted are “fishing area closure” and “marine protected area”.

These terms are not meant to be mutually exclusive, but rather to provide a means for distinguishing between addressing fisheries management objectives as they relate to sustainable use, biodiversity conservation, and protection of ecosystem structure and function from the effects of fishing and addressing other community objectives. The fishery manager needs the flexibility of prescribing management boundaries and varying rules between zones. At the simplest level, this might be prohibiting angling from a jetty to avoid injury to bathers. At a more complex level, this might be zoning a broad region of thousands of square kilometers to meet a range of fishery and ecological objectives through a complex system of licensing use rights, gear restrictions, and area closures across several fisheries. For example, gear restrictions across a complex of zones might be designed to provide high sustainable yields from target species of high biological productivity, while simultaneously minimizing impacts on bycatch species of low biological productivity. Where marine protected areas are proposed within broad fishing areas, the astute fishery manager will endeavor to influence the positioning of the boundaries that are compatible with fisheries objectives or at least gain some benefit for a fishery. Examples of how marine protected areas and fishing area closures can benefit sustainable use of target species and biodiversity conservation of chondrichthyan animals are presented in the following section.

13.5.2.1 Marine Protected Areas

A Marine Protected Area (MPA) is defined by the World Conservation Union (IUCN) as “any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment” (Anonymous, 1988). An MPA can be a large or small area and the overall objectives for an MPA can be specific or broad. Large MPAs with broad objectives are often divided into geographically smaller zones and designated for multiple use. Depending upon the objectives, an MPA, or a zone within an MPA, might be designated for one or more uses. MPAs are usually declared from judgement using qualitative information, as quantitative evaluation is costly and long time series of environmental or community-monitoring data are rarely available. Selected areas are usually judged as being unique or having high conservation value. An example of a unique area declared an MPA is the stromatolite assemblage of Shark Bay, Western Australia. Corner Inlet in Victoria, Australia, on the other hand, was declared an MPA in 1983 because it was judged to have several high conservation values. These values include the presence of international migratory birds, soft substrate biotic communities, mangrove stands, and *Posidonia* sea grass meadows (Plummer et

al., 2003). In Australia and South Africa, for example, networks of MPAs are presently being established to protect representative areas of a range of habitat types.

MPAs with single or multiple zones have been declared throughout the world for providing various levels of protection and for a variety of uses. A preservation zone or wilderness zone usually provides the highest level of protection through very limited access. A cultural zone is designed to provide protection to special items of cultural value and sites of historic, cultural or religious significance. Items of cultural value include shipwrecks, archaeological relics, submerged aboriginal middens, and fossils. Zones, which allow for access, but for minimal disturbance, include education, science, experimental, and recreation zones. An education zone is usually a relatively safe diving or intertidal area that can be visited for training and educational purposes. A scientific zone is an area where authorized researchers can undertake the study of particular species or ecology of marine communities. Other types of zones, such as recreational zones or traditional fishing zones, allow for exploitative activities. A recreational zone might allow for diving and photography but no fishing, or might allow for recreational fishing activities. A traditional fishing zone recognizes traditional fishing rights of a community or group of individuals and allows for ongoing subsistence fishing.

MPAs are highly suitable for management of chondrichthyan species known to aggregate, where they are vulnerable to capture or disturbance by human activities (Bonfil, 1999). There are several examples from various parts of the world where these have been applied for sharks and rays. In New South Wales, Australia, the grey nurse shark (*Carcharias taurus*) is fully protected, but, to avoid unintentional kill in the coastal waters from longline fishing, a system of 10 sanctuary areas was established during December 2002. Each sanctuary extends 200 meters out from an island or a section of coast with buffer zones extending a further 800 meters. Fishing is prohibited, and new controls on scuba diving include bans on night diving, feeding, touching, harassing or chasing sharks, and on use of electronic shark repelling devices and electric scooters in these areas. In the Florida Keys National Marine Sanctuary, nurse shark (*Ginglymostoma cirratum*) mating aggregations at the Dry Tortuga Island group were recently given added protection by implementing a seasonal closure to boat traffic (Bonfil, 1999; Stevens 2002). The Ningaloo Reef Marine Park in northern Western Australia on the edge of the Indian Ocean provides protection to whale shark (*Rhincodon typus*) when these animals aggregate in this region from late March to early May. The number of divers and hours that divers and boats can approach these animals is restricted. Touching the animals or use of camera-flash lights is prohibited (Tricas et al., 1997). The Kinabatangan wildlife sanctuary in Sabah, East Malaysia, includes about 27,000 hectares of tropical forest and the lower reaches of the Kinabatangan River and provides some protection (although some artisanal fishers operate there) to several rare freshwater elasmobranch species. These include the river speartooth shark (*Glyphis sp.*), giant freshwater stingray (*Himantura chaophraya*), and greattooth sawfish (*Pristis microdon*) (Payne and Andau, 2002).

13.5.2.2 Fishing area closure

Fishing area closure is defined here as closing an area to all or selected fishing gears for continuous or selected time periods to limit fishing mortality on all or particular length or age classes of one or more fish species, or to reduce gear impacts on habitats or other uses. Fishing area closures can be applied to target, byproduct, or bycatch species. MPAs can also limit fishing mortality, but areas closed to meet fisheries management objectives are not normally referred to as MPAs, marine parks, reserves or sanctuaries. In MPAs, more than fishing mortality and impact of fishing gear are controlled.

Fishing area closure as a fisheries management tool is applied to meet specific fisheries objectives. One important objective is to protect aggregations of small (pre-recruit) animals to allow these animals to grow and thereby improve yield per recruit and avoid growth overfishing. Another important objective is to protect aggregations of breeding or mature animals to enhance survival of the largest animals, which produce the highest number of offspring, and thereby avoid recruitment overfishing.

Fishing area closure will be used much more extensively in the future and there are several reasons why it has been applied conservatively in the past. The first is that fisheries managers have tended to focus attention on abundant species with high biological productivity, whereas closures are a more essential management tool for managing less abundant species with low biological productivity. A second reason is that setting boundaries for closures requires extensive data sets to provide detailed information on distribution and biological condition of fish and often these data sets have not been available. A third reason is that fishery managers have been reluctant to prescribe in law complex demarcation boundaries because they have been difficult to enforce and fishers have been often uncertain of their navigational position at sea in relation to demarcation boundaries.

There have been several developments in recent years to facilitate greater application of fishing area closures in the future. One of these developments is the growing awareness in the community that chondrichthyan species are among the least biologically productive animals and need special conservation and management attention. In addition, three important technological developments in recent years make fishing area closures a more practicable fisheries management tool. The first development is that of Geoglobal Positioning Systems (GPS), which enables the navigational position of a vessel to be known continuous with high precision. The second and third developments are linked to GPS. The second development is that of Geographic Information Systems, which allow for better management, analysis, and visual display of spatial data. This innovation is providing facility to better understand the spatial and temporal distributions of species and habitats and to better evaluate the significance of various areas. The third development is that of Vessel Monitoring Systems (VMS), which overcomes the need for deployment of high-cost vessels at sea for surveillance purposes. VMS

allows the navigational positions of vessels at sea to be electronically monitored using satellite communication systems. As costs of VMS decline so too will the surveillance cost for effective enforcement of fishing area closures.

Two types of fishing area closures have been implemented in the shark fishery of southern Australia since the 1950s. Closure to shark longline fishing in nursery areas of school shark (*Galeorhinus galeus*) in the inshore waters of northern and south-eastern Tasmania were first adopted during 1954 and extended during the 1960s. In 1990, fishing gear regulation was extended to included gillnets used for targeting sharks (>150 mm mesh-size) and gillnets for recreational and commercial fishing to target other species (60–70 mm mesh-size) in some of these areas. These closures were designed to prevent targeting pregnant females entering shallow waters for parturition, as well as to reduce the incidental kill of neonate and small juvenile animals (Williams and Schaap, 1992). In addition, closed seasons during October or November (months immediately prior to parturition) were adopted across the entire fishery during 1953–67. During 1994, the use of gillnets were prohibited during the period from 8 October to 22 November for the area west of the South Australia–Victoria border and during the period from 11 November to 25 December for the area east of the border. These rolling closures were designed to protect pregnant animals as they migrated from the western region of the fishery to the nursery areas in the eastern region for parturition (Walker, 1999).

Other examples of fishing area closures for sharks, include large areas being closed to gillnet and longline fishing for sharks in Western Australia to protect breeding animals of *Carcharhinus obscurus* and *C. plumbeus* (Simpfendorfer, 1999). Also, although not specifically designed for chondrichthyan species, many nations designate coastal waters for artisanal fisheries and those further offshore for industrial fleets. This is designed for social reasons, but it does provide some limitation on fishing mortality in coastal waters.

The most promising approach to fisheries management is to take a more regional approach to fisheries management and adopt greater use of fishing area closures. There are numerous examples where fishing area closures have been applied in the past, but they have tended to be small in inshore areas.

13.5.2.3 Regional fisheries management

Regional fisheries management is defined here as integrated management of a broad region of waters across species and fisheries. Management is through allocation of use rights and application of fishing area closures and other technical measures. It is designed to efficiently harvest resources in specified areas and to meet the triple goals of sustainable use with high yields, biodiversity conservation, and maintenance of ecosystem resilience. Open and closed areas are selected to minimize impacts on pre-recruit and breeding and other mature animals of target species, on species of low biological productivity, and on habitats, particularly critical habitats.

A regional approach to fisheries management through the judicial use of fishing area closures is required to avoid depletion of the populations of species with low biological productivity impacted by the fishing gear used to target species of high biological productivity. Maximum benefits from fishing area closures can be attained by aligning refuge areas for species of high catch susceptibility and low biological productivity (low reproductive rates and low natural mortality rates) with areas containing critical habitats, and pre-recruit and breeding animals of the target species. Whilst some trade-offs are inevitable, where practicable, the fishing area closures should not be so large that there are insufficient fishing grounds open to efficiently harvest high-valued target species to ensure high sustainable yields.

Regional fisheries management requires an exhaustive information base. Extensive data sets on monitoring distribution, abundance and fishing mortality, and on critical habitats and population biology are not only required for intensive management of target species, but for all byproduct and bycatch species. The positions of the boundaries of the fishing area closures need to be flexible so they can be updated as improved information is acquired. Through improved information and an adaptive management approach, the goal is to optimize yields across species, biodiversity conservation and ecosystem maintenance.

The low biological productivity of many chondrichthyan species is likely to have a major influence on the selection of the boundaries of area closures and will provide an impetus to adopt the regional fisheries management approach. Also, species found in temperate regions tend to have lower productivity than those found in tropical regions, and those found in cold deepwater on the continental slope tend to have lower biological productivity than those found in the warmer waters on the continental shelf in temperate regions. The recent depletion of the deepwater squalids and chimaerids on the continental slopes of the Earth's temperate regions, such as southern Australia (Graham et al., 2001), has created a need to establish substantial refuge areas for these species.

Multispecies modelling tools for evaluation of alternative spatial policy options are emerging. Such models need to account for trophic interactions with important top-down impacts of predators on prey and dispersal responses of harvested species and redistribution of fishing effort in response to trophic cascades. Determination of appropriate sizes and effectiveness of closed areas are highly dependent on predator-prey relationships and movement rates of harvested species. In general, a few large closed fishing areas are likely to be more effective than a large number of small ones. Local protection can be negated by fishing effort concentrated at the boundaries of closed fishing areas or at nearby sites where the presence of prey species can rapidly attract highly mobile predator species out of the closed areas (Walters et al.,1999). Importantly, the perimeter-to-area ratio decreases as size of closed area increases. Closed area boundaries can be minimized by having large closed fishing areas, and by placing the closed fishing areas adjacent to land or in bays and inlets (Walters, 2000).

Closure of fishing areas can have unintended consequences caused by the redistribution of effort from those areas, particularly if the fisheries are principally managed by TACs and ITQs. Whereas TACs and ITQs control the catch of quota species, which are usually target or byproduct species, they do not control bycatch species. Hence, redistributed effort from closed areas might have undesirable effects on bycatch species. An alternative potential management alternative to TACs with ITQs is to adopt a total allowable effort with ITQs specified as "transferable effort quotas" (Walters and Bonfil, 1999). These quotas could be allocated according to a carefully prescribed distributional pattern, but would be dependent on VMS for surveillance.

13.5.3 Product form

Products from sharks and other chondrichthyans when landed by fishers, transported, sold, or exported occur in many forms. These forms include whole animal, carcass, tissue or processed product. The carcass form can be beheaded and eviscerated carcass with skin on and fins on, be-headed and eviscerated carcass with skin on and fins off, or beheaded and eviscerated carcass with skin off and fins off. Tissues, body parts, or product can be in the form of filleted meat only, heads only, jaws only, head cartilage, vertebral column, powdered cartilage, skin only, fins only, whole livers only, or liver oil.

This wide range of product forms creates difficulties identifying the species or measuring these animals when they are brought ashore. This creates ambiguity in the official catch statistics. Monitoring sex composition of the catch is not possible if the pelvic fines and claspers of males are removed. Monitoring length-frequency composition and enforcing size limits usually involves measuring partial length, which can be uncertain if all fins and the tail are removed.

Fishers should not be forced to land sharks whole, because sharks need to be gutted and gilled as soon as practicable after capture to avoid degrading the quality of the meat and other products. Species, sex and partial length of a shark can be determined ashore if sharks are beheaded and eviscerated at sea, and landed in the product form as carcasses with fins, skin, claspers and, where applicable, dorsal spines attached. Leaving the head attached, with the gills removed, is an option where species identification from the carcass with fins attached is uncertain. If there is a requirement for species identification for marketing or trade purposes, field guides based on fins and other body parts will need to be prepared. There may also be advantages in establishing regulations to ensure that shark products (carcasses, meat, fins, skins, heads, vertebral columns, livers, liver oil and jaws) are clearly labelled with species name. If sharks are not required by law to be landed in a standard product form, statistics forms may require provision for reporting the product form of the sharks, in addition to reporting weight of catch. This also applies to data from landing sites, processing plants and markets, and applies to trade data. All trade products should be specified by species and as frozen or dried. Without these provisions catch weights will be ambiguous.

If more than one product form occurs it is necessary to have appropriate weight conversion factors to produce a single set of standard statistics. Similarly, if it is necessary to adopt more than one standard length measurement, the data should be converted to a single standardized length, ideally total length or fork length.

To standardize the statistics for chondrichthyan species, Australia has adopted the following wording in its National Plan of Action for the Conservation and Management of Sharks (Anonymous, 2002).

- Fishers should be required to report shark weights for the form in which they are landed and, where practical, all sharks be landed in the carcass form where a carcass is defined as a beheaded and gutted shark with all fins and, for males, the claspers attached. Leaving the claspers intact enables monitoring the sex of sharks after landing ashore.
- Fishers should be required to report chimaera weights for the form in which they are landed. Where practical, all chimaeras should be landed in the carcass form where a carcass is defined as a beheaded and gutted chimaera with all fins and, for males, the claspers attached, except for the pectoral fins and belly flaps which are removed.
- The issue of standard reporting of rays needs to be addressed. There is a growing practice of retaining the outer margins of the discs (pectoral fins) of the animal and discarding the rest of the animal for several large-sized species. This involves removing a relatively small proportion of the animal and might be regarded as wasteful and analogous to finning.
- Official statistics of catch weights should be published as standard carcass weights and, where reported by fishers in a different form, the weights are converted to the standard carcass form.

13.5.4 Size limits

Size limits can be legal minimum sizes or legal maximum sizes. They can be an effective management measure where the animals are landed from the fishing gear live and in condition where the survival rate of released animals is high. Conversely, size limits are ineffective measures where the animals are landed dead or in poor condition and the survival rate of released animals is low. Hence, they are effective for many species that survive release from hooks, seine nets, and fish traps, but are not effective for many species released after capture by gillnets and trawls where survival rates are low.

Legal minimum sizes can be used to avoid growth overfishing. Growth overfishing occurs where the yield from a fishery is sub-optimal; many of the animals are caught when they are small and

at an age such that the yield from the fishery is lower than the potential yield had the animals been given time to grow and increase their mass.

Legal maximum sizes can be used to avoid recruitment overfishing. This is potentially useful for those many species of sharks where the proportion of the females in breeding condition each year increases with size and fecundity increases with maternal size. Where reproductive rates increase with size, the contribution to recruitment is likely to be much higher for large animals than for small animals. Hence, there can be stock benefits in releasing large animals live. A legal maximum size is likely to be of higher value for females than for males.

In addition, there is usually a strong correlation between mercury concentrations in shark meat and size of shark (Forrester et al., 1972; Walker, 1976). Where the concentrations in large animals exceed food standards, legal maximum sizes have occasionally been used as a means of reducing the number of sharks with high mercury concentrations from reaching the consumer (Walker, 1980).

Fishers recognize the benefit of releasing undersized animals and usually endorse legal minimum sizes. They are prepared to release undersized animals on the understanding that they can be recaptured at a later time and benefit from a mass gain. On the other hand, they are less likely to support legal maximum sizes. Large animals have a higher market value and fishers are aware of the uncertainty of survival of large animals released. It is therefore preferable to apply alternative management measures to protect large animals.

Legal minimum sizes and legal maximum sizes are usually expressed as legal minimum lengths and legal maximum lengths, respectively. Because most sharks are beheaded when the animals are landed, length needs to be prescribed as a partial length rather than a total length. The longest reliable partial length that can be taken from a beheaded and eviscerated carcass is from the last gill slit to the distal end of the caudal fin. The last gill slit closely coincides with the anterior edge of the pectoral fin, or, where the fins are removed, the cartilage from the pectoral girdle is usually intact. Where the caudal fin is removed, then the base of the caudal fin should be adopted.

In Australia, a legal maximum length was applied for school shark (*Galeorhinus galeus*) in Victoria, during 1972–85 as a way of reducing the average mercury concentration in shark meat reaching the consumer (Walker, 1999). Similarly, a maximum weight of 18 kg for trimmed carcass applies to all sharks in Western Australia (Simpfendorfer, 1999). Legal minimum lengths for sharks have been applied in southeastern Australia for school shark (*Galeorhinus galeus*) and gummy shark (*Mustelus antarcticus*) since 1949 (Walker, 1999).

13.6 SPECIAL PROTECTION OF THREATENED SPECIES

Naturally rare species and species with poor conservation status may require special protection or management through such measures as a prohibition on catch, injury and interference. Where

such species are inevitably killed, injured or disturbed accidentally, consideration should be given to establishing sanctuaries through fishing area closures or MPAs.

There are no internationally agreed definitions of "threatened" or "endangered with extinction", but some countries have adopted classifications such as "endangered", "threatened" and "depleted", which have legal status in their jurisdictions. The most widely accepted classification for the conservation status of chondrichthyan species is the IUCN Red List, which classifies species as "critically endangered", "endangered", "vulnerable", "lower risk", and "data deficient". The first three of these are grouped as "threatened" species. Criteria for classifying species include rate of population depletion (percentage decline over three generations), overall population size, and geographic area and extent of fragmentation within the distributional range of the species (Anonymous, 1994; Hilton–Taylor, 2000). Chondrichthyan species first appeared on the IUCN Red List in 1996 (Hudson and Mace, 1996). Later, during 2000, when the list was last updated by the IUCN Shark Specialist Group, 40 chondrichthyan species were listed as threatened worldwide and an additional five species were listed within isolated local populations. More recently, 31 chondrichthyan species have been identified as becoming extinct at particular localities and one regionally extinct (Dulvy et al., 2003).

Some species are classed as threatened on the basis of extreme rarity. These include all the river sharks (*Glyphis* spp.), all freshwater sawfish (*Pristis* spp.) and several other freshwater batoids. Others species are classified as threatened because their populations have been depleted by the effects of fishing. These include several species of angel shark (*Squatina* spp.) and batoid species severely impacted by trawl fisheries. Species that have naturally small populations and have been depleted, include the whale shark (*Rhincodon typus*), basking shark (*Cetorhinus maximus*), grey nurse shark (*Carcharias taurus*), and white shark (*Carcharodon carcharias*) (Anonymous, in press; Camhi et al., 1998).

Various initiatives to protect endangered species have been taken in various parts of the world. Fishing for whale sharks is banned in the Maldives. The number of divers and hours that divers and boats can approach these animals is restricted in Ningaloo Reef Marine Park to minimize disturbance. White shark is now protected in South Africa, Namibia, Australia, USA, Maldives and Malta. In addition to declaring full protection for this species, Australia has developed species recovery plans for the white shark and grey nurse shark. Several additional steps have been taken to reduce the accidental kill, injury or disturbance of these animals. Ten grey nurse shark sanctuaries were recently declared in New South Wales waters, and there is a total ban on the use of shark fishing gear and the use of mammal blood or oils for attracting sharks in all Victorian waters. There are legislative requirements to report all interactions with white sharks and codes of practice are being developed for ecotourist activities.

13.7 PRODUCT CERTIFICATION AND ECOLABELLING

Product certification and ecolabelling can be applied in support of fisheries management. Product certification is a measure mandated by governments to ensure that only legally harvested and reported fish landings can be traded and sold on domestic and international markets. Product certification is an extension to normal fisheries management activities. Where there are problems regulating access, such as on the high seas, product certification schemes provide a means of reducing illegal, unreported, and unregulated fishing. Ecolabelling programs can create market-based incentives for better management of fisheries by creating consumer demand for seafood products from well-managed stocks by tapping the growing public demand for environmentally preferable products. Criteria used for the accreditation process are a compromise between the demands of consumers and the capabilities and willingness of the producers to meet those demands (Wessells et al*.,* 2001).

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CHAPTER 14. SHARK UTILIZATION

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14.1 INTRODUCTION

Sharks and their relatives may provide a multitude of usable products including but not restricted to: meat, fins, liver, skin, cartilage, and jaws and teeth. Unfortunately, tens of millions of sharks taken in fisheries each year have their fins removed and their carcasses discarded overboard (Fowler and Musick, 2002). This practice, called finning, represents a considerable waste as the fins on average make up only about 5% of the total weight of a shark (Vannuccini, 1999). Such waste is contrary to the United Nations Food and Agricultural Organization (FAO) Code of Conduct for Responsible Fisheries (Article 7.2.2 (g)) which stresses the importance of avoiding waste and discards in fisheries. In addition, the FAO International Plan of Action for the Conservation and Management of Sharks (IPOA- Sharks) encourages full use of dead sharks and retention of sharks from which fins have been removed (paragraph 22). Therefore, this chapter will briefly review the wide spectrum of uses that may be afforded by elasmobranchs in order to encourage their more complete and effective use. For a more comprehensive review see Vannuccini (1999) wherein an entire volume (470 pages) is devoted to the subject. A strong word of caution is necessary here: full utilization of shark carcasses should not be used as a pretext to fish unsustainably (Camhi, 2002). The goal of this manual is to provide information necessary to lead to sustainable elasmobranch fisheries.

14.2 CONSUMPTIVE UTILIZATION OF ELASMOBRANCHS

14.2.1 Meat

Shark meat has been used as food in coastal regions for over 5,000 years (Vannuccini, 1999). Most historical use of shark meat was local because the meat does not travel well without refrigeration. Sharks retain urea in their blood and tissues as part of their osmoregulatory physiology (Musick and McMillan, 2002). After a shark dies the urea breaks down into ammonia which imparts a strong smell and odor to the meat and which may be toxic in high concentrations. This problem may be avoided easily by rapid bleeding of the freshly caught animal, and thorough washing of the carcass with seawater. Usually the head, fins, gills and viscera are removed from larger sharks at sea, or in some artisanal fisheries immediately upon landing. Subsequent soaking of the meat in a weak acid solution (citrus juice or vinegar) may remove up to 90% of the urea (Gordievskaya, 1973). Various species have different concentrations of urea, spiny dogfish (*Squalus acanthias*) having the lowest and hammerheads (Sphyrnidae) having the highest concentrations of several species measured (Gordievskaya, 1973). In addition, elasmobranchs captured in brackish estuaries should have lower urea concentrations than those taken in full seawater (Evans et al., 2004).

After bleeding and soaking, carcasses should be iced or frozen to prevent enzymatic and bacterial breakdown. Small species with naturally low urea content like spiny dogfish (which also occurs in cold water (<12°C)) may be landed whole to be processed onshore (Kreuzer and Ahmed,

1978). Small sharks are preferred for meat in many markets because they usually have lower concentrations of urea and mercury, which is naturally absorbed from sea water and through dietary uptake may reach high concentrations in larger, older sharks (Forrester et al., 1972, Walker, 1980). However, in some markets such as Hong Kong larger sharks are preferred (Parry-Jones, 1996).

Shark fillets also may be salted and diced or smoked. In Germany, the belly flaps of spiny dogfish are smoked as *Schillerlocken*, an expensive gourmet item. Meat from blue sharks (*Prionace glauca)* which is not used directly for food in most places may be processed into *surimi* and subsequently used in a variety of seafood recipes (Nakano, 1999), shark paste or *happen,* (Kiyono, 1996).

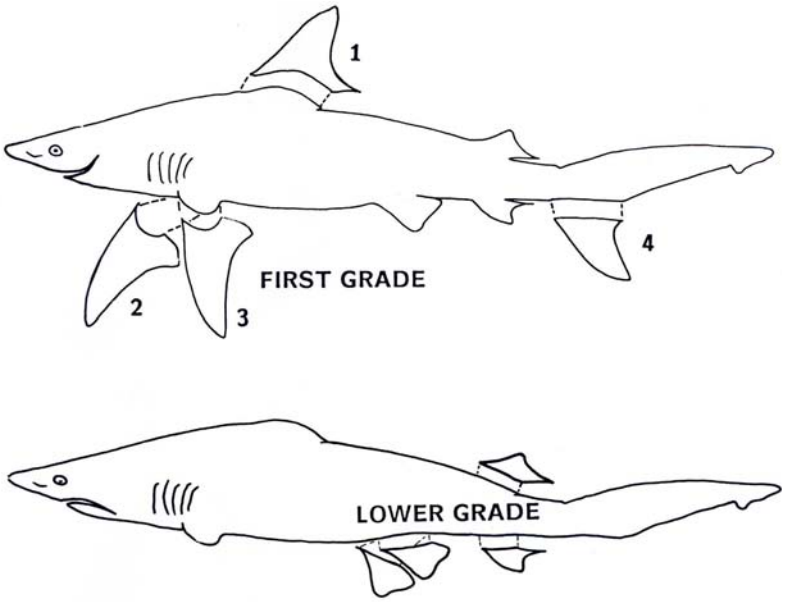
Batoid meat is also used widely throughout the world. In many areas batoid landings may approach those of sharks (Shotton, 1999) and in some places there are directed batoid fisheries (Agnew et al., 1999; Kulka and Mowbray, 1999; Pawson and Vince, 1999).

Some batoids such as the guitarfishes (Rhinobatidae) and sawfishes (Pristidae) are very shark-like in their morphology and their meat is processed similarly to that of sharks. However, in more typical batoids such as the skates (Rajidae), stingrays (Dasyatidae) and eagle rays (Myliobatidae) the body is dominated by the wing-like pectoral fins which, unlike those of sharks, are thick and muscular. These "wings" are cut from the body, then the dorsal and ventral meat is filleted away from the cartilage framework and usually skinned. Depending on the taxonomic group, the meat may vary from very delicate and white (Rajidae) to thick and dark (Myliobatidae). Batoids should be bled upon capture and the meat soaked as in sharks. Batoid wings do not contain the "needles" so valuable in shark fins (see below), but sawfish, guitarfish, and wedgefish dorsal fins contain needles and are some of the preferred fins in the market.

14.2.2 Fins

Shark fins are used to make a traditional shark fin soup in the Chinese culture, and are among the most valuable fish products in the world (Camhi et al., 1998). Only the fine collagenous fibers called "needles" which support the fin margin are used in the soup. In most sharks the first dorsal, pectorals and lower lobe of the caudal fin are the most valuable and these are usually sold as a set from each shark. The lower lobe of the caudal is used because it contains the collagenous needles whereas the upper lobe is supported by the vertebral column and has no needles. The smaller second dorsal and pelvic fins ("chips"), also are taken but are of much lower value and lots are mixed from several sharks. Because the base of the fin contains large cartilaginous supporting elements called radials and muscle not used in soup, the fin is removed with a semi-circular cut (Fig 14.1) to eliminate some of these materials at the base of the fin (Trachet et al., 1990). Any meat left adhering to the base of the fin will spoil during drying thus lowering the quality or even destroying the value of the fin. The greater care taken in removing fins the greater their value (Vannuccini, 1999).

Figure 14.1 Method for cutting shark fins (after Trachet et al., 1990).



Fins are traded virtually during all stages of processing. These include:

1) Wet fins; fresh, iced or frozen
2) Dried “raw” fins; with skin (including denticles) and some radial elements intact. Fins salted before drying are usually of lower value because they retain more moisture. Fins are sun-dried, and turned frequently to facilitate drying to prevent curling. Fins should be kept out of the rain and dew and away from insects. Drying may take 7-14 days to produce an acceptable product (18% moisture content (Vannucinni, 1999)). Dried fin sets are usually packed in 25 kg sacks and dried “chips” in 50 kg sacks.
3) Semi-processed or “cooked” fins; with the denticles and radials removed, but needle fan intact. In this presentation fins are soaked in water for 8-10 hours (wet fins) or 16-24 hours (dry fins), then further soaked in water pre-heated to 80-90°C until the scales and skin be come loose. Then softened fins are placed into chilled water and scales and skin removed with a wire brush. After washing again, any remaining meat and the cartilaginous radials are removed. The pre-processed fins are then dried on bamboo mats for 4-6 days.
4) Fully processed; with the needle fans separated into individual strands. Semi-processed fins may be further processed to separate the needle bundles by soaking in water for up to 12 hours then boiling for 5-10 minutes. The needles may then be easily separated from the surrounding membrane in cold water. Fin needles may be traded as wet fin needles or pro cessed into fin nets.
5) Fin nets; usually from smaller fins, the fin needles have been boiled, separated, re-dried and packaged in loose clumps.

6) Ready to eat products; canned or instant shark fin soup.

Most fins are traded as dried fins and imported for further processing in Hong Kong, Singapore or Taiwan for domestic use or subsequent re-export.

14.2.3 Skin

14.2.3.1 Skin as Food

Shark skin may be consumed as food in several countries including the Maldives, Japan, Taiwan, and the Solomon Islands (Vannuccini, 1999). Preparation involves drying, removing the denticles, bleaching, then drying again (Chen et al., 1996). Skin from dusky, thresher and whale sharks as well as skin from the giant guitarfish (*Rhynchobatus djiddensis*) is eaten in Taiwan. Shark skin is processed into the gelatinous food *nikigori* in Japan (Kiyono, 1996). In Singapore and Malaysia, after processing, cooked shark skin is marketed as "shark lips" or "fish lips." In the Solomon Islands shark skin is salted and then sun dried or smoked after which it is boiled and the denticles are removed. The resulting product is then made into soup with coconut milk (Matthew, 1996).

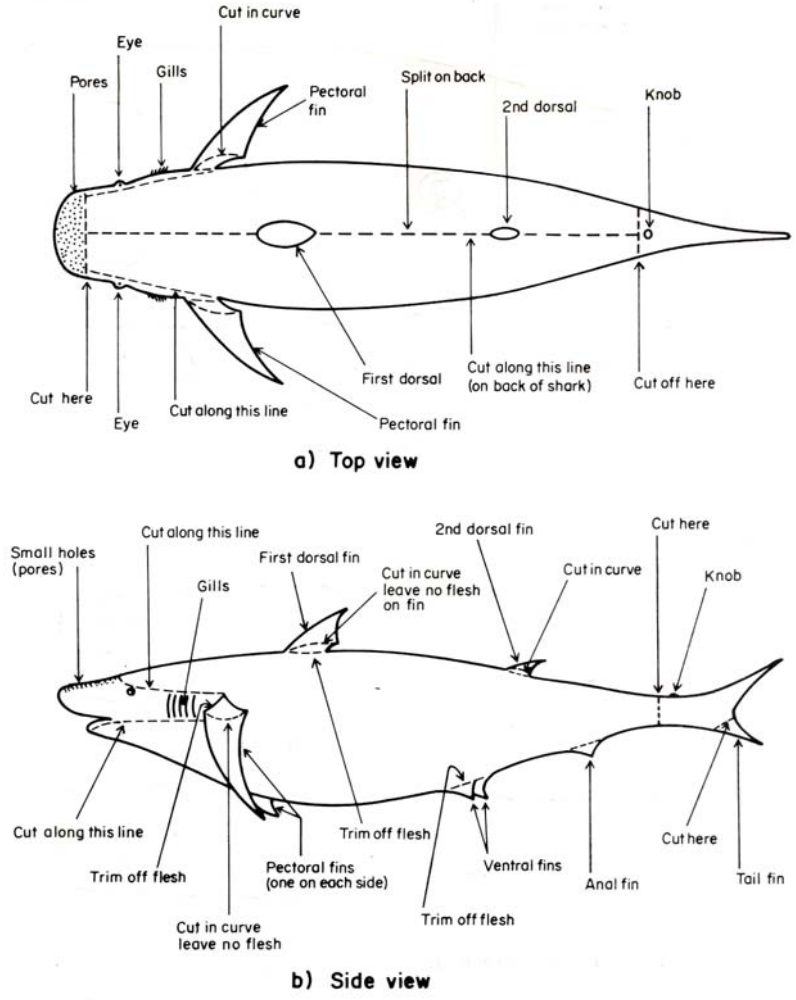
14.2.3.2 Shark skin leather

Untanned shark skin, with the rough denticles attached is called shagreen and has been used as sandpaper in woodworking and other industries for centuries. It has also been used to cover sword hilts (providing a slip-free grip) and as a striking surface for matches (Kuang, 1999). The greatest use for shark skin has been for leather. Shark skin is tanned much in the same way as are the skins of other animals (Tanikawa, 1985). Shark leather may be used to make a variety of products including furniture, bookbinding, shoes and handbags. Historically, the major markets for shark leather products have been in the USA, Germany, France and Japan with tanneries located in several countries. Today, because of environmental restrictions on the tanning industry and problems with a steady supply of raw skin, most tanned leather is produced in Mexico (Kuang, 1999). Top quality skins usually come from larger sharks which must be carefully skinned soon after capture. Skin from shark carcasses used for meat and frozen or stored on ice are usually damaged to the point that they are useless for making leather.

Most shark leather products have had the denticles removed. However, some products such as the expensive Boroso leather made from small Moroccan shark hides retain their denticles which are polished to a high gloss (Kuang, 1999). Recently stingray skin has been used in luxury leather products in the USA (Boncompagni, 2003).

Shark skin is thick and tough and may be difficult for a novice to remove properly. However, with practice, experienced shark skinners can efficiently remove a shark's hide in a matter of minutes. A diagram of the skinning process is provided in Fig. 14.2 (after Kreuzer and Ahmed, 1978).

Figure 14.2 Method for skinning sharks for leather (after Kreuzer and Ahmed, 1978).



14.2.4 Cartilage

14.2.4.1 Shark cartilage as food

Shark cartilage is used as food in China and Japan where it is boiled, cleaned of meat, and sun dried for later cooking. Cartilage utilized includes fin radials (left over from fin processing), pieces of jaw and chondrocranium, and most importantly the vertebral column. The latter is usually marketed dry as a cyclindrical rod about one meter long with the vertebral processes removed (Vannuccini, 1999).

14.2.4.2 Dried cartilage pills

Shark cartilage has been dried and pulverized into a powder that can be delivered in pills or capsules. The market for shark cartilage pills expanded dramatically after the publication of a book (Lane and Comac, 1992) that purported to show that sharks do not get cancer (an assertion shown to be incorrect, Musick and McMillan, 2002), and that claimed that shark cartilage pills could cure human cancers. The use of shark cartilage pills ingested orally subsequently has been found to be worthless

in the treatment of cancer in humans (Horsman et al., 1998; Leitner et al., 1998; Miller et al., 1998). These results were not surprising as the digestive system would breakdown any biologically active proteins in cartilage into constituent amino acids before absorption through the gut lining (Kava, 1995). However, cartilage in general is a good source of chonrdroitin and glucosomine sulfate, and shark cartilage is no exception. These compounds have been found to be useful in treating various forms of arthritis, and to that end, shark cartilage capsules are marketed today.

14.2.4.3 Shark cartilage extracts

It has been known for many years that tumors require the development of blood vessels (angiogenesis) in order to grow, and that some substances in cartilage could inhibit angiogenesis and retard tumor growth. Recently, Aeterna Laboratories, a pharmaceutical company based in Toronto, Canada, http://www.aeterna.com/, has developed a unique proprietary process to extract biologically active molecules contained in cartilage. Aeterna uses shark cartilage as raw material because cartilage makes up to 6% of a shark's body weight and shark cartilage has been a readily available by-product of shark fisheries for which fins and/or meat are the principal targets. The resulting product from Aeterna's process, called Neovastat, has been shown to have multiple mechanisms of antiangiogenesis action, and to be effective in treating cancers of many types as well as other diseases where angiogenesis is a mitigating factor. Neovastat is in the final stages of clinical trials at this writing, but should be available for use shortly.

14.2.5 Liver

14.2.5.1 Liver as food

Shark liver has been eaten as food in China and the Solomon Islands and elsewhere (Vannuccinni, 1999). The liver may be cooked fresh or salted for later preparation.

14.2.5.2 Liver extracts

Shark liver is rich in various hydrocarbons, and oils extracted from livers have been used in the farming and textile industries, as lubricants, in cosmetics, as lamp fuel, as a wood preservative on boat hulls, and in the pharmaceutical industry (Kuang, 1999). The pharmaceutical use of shark oil products holds most present interest and future promise.

14.2.5.2.1 Vitamin A

Shark liver is high in vitamin A and target fisheries for shark livers developed in the 1940s. These fisheries were short-lived because of the development of synthetic vitamin A (Kreuzer and Ahmed, 1978). Even so, the short but intense fishery for the soupfin shark (*Galeorhinus galeus*) off the west coast of the United States led to rapid stock collapse (Ripley, 1946) that has lasted for several decades (Camhi et al., 1998).

14.2.5.2.2 Squalene

Squalene is a highly unsaturated aliphatic hydrocarbon found primarily in the livers of deep-sea dogfishes (Squaliformes). This low density (0.86 s.d.) compound provides buoyancy to the sharks (Thorson, 1990). Squalene has been used as a fine lubricant because it is stable over a wide temperature range (-75ºC to 330ºC) (Kuang, 1999). Its most widespread use appears to be in skin creams to soften skin, and as a moisturizer, to speed up wound healing, and as a bactericide. It is often hydrogenated to the more stable form Squalane before use (Anonymous, 1996; Kuang, 1999). The problem in developing further markets for squalene is that the squaloid sharks from which it comes are among the slowest growing, latest maturing sharks known. Thus, these species may be very quickly overfished if harvesting is not controlled at some low level (Musick et al., 2000).

14.2.5.2.3 Squalamine

Squalamine is one of several aminosterols (steroids) found in shark liver (oore et al., 1993; Rao et al., 2000). This steroid has been found to be a broad spectrum antibiotic which exhibits potent bactericidal activity against both gram-negative and gram-positive bacteria. Also, squalamine induces osmotic lysis of protozoa and is fungicidal (Moore et al., 1993). In addition, squalamine has recently been shown to be an effective inhibitor of angiogenesis and directly blocks blood vessel cell activation, migration and proliferation by many growth factors (Sills et al., 1998). Genaera corporation (http://www.genaera.com/antiangiogenesis.htm) has recently synthesized squalamine and although its pharmaceutical potential is vast, the future demand for the compound directly from shark livers is probably minimal at best (as with vitamin A).

14.2.5.2.4 Other liver extracts

Shark liver contains many biologically active compounds some of which may remain to be discovered. Among known compounds alkoglycerols have been shown to have some benefit in the regression of tumor growth (Hallgren and Larsson, 1962; Brohult et al., 1986).

14.2.6 Miscellaneous Products

Rose (1996) has reviewed the use of peripheral shark products from various regions around the world. These include

1) Jaws and teeth as curios
2) Sawfish rostra as curios
3) Whole preserved small sharks as curios
4) Bait in pot or long-line fisheries
5) Fishmeal and fertilizer
6) Dogfish as dissection specimens in schools
7) Exhibition in public aquaria
8) Small specimens in private aquaria

14.3 NON-CONSUMPTIVE UTILIZATION OF ELASMOBRANCHS

14.3.1 Recreational diving

Recreational diving has been one of the fastest growing recreational activities worldwide for several years (Anderson, 2002). Estimates of the number of active recreational divers run to several million. Sharks and rays are always the major diving attraction wherever they occur (Anderson, 1999). Diving magazines regularly carry articles and advertisements concerning dive destinations where "shark watching" is offered (Murphy, 1993; Saunders, 1995). Shark diving destinations are widespread throughout the developing and developed world and include (among others) South Africa, Egypt and Sudan, the Maldives, Myanmar, throughout Southeast Asia, Australia, Palau, French Polynesia, California, and the Bahamas (Anderson, 2002). The shark diving industry generates hundreds of millions of dollars for local economies worldwide. Divers may pay from $75 to $200 for a single dive with sharks and rays, and recreational diving expeditions to cage dive with sharks may cost several thousand dollars (Anderson, 2002). Because many species of sharks may be residential at particular dive sites, and because individual sharks may live for at least a decade, an individual shark may be observed by a multitude of divers over time. Therefore, considering the cumulative input to the economy by shark divers, Anderson and Ahmed (1993) estimated that in 1992 a single gray reef shark (*Carcharhinus amblyrhynchus*) was worth US $33,500 per year at the most popular shark watching site in the Maldives. In contrast, a dead gray reef shark was calculated to have a one time value of US $32 to local fishermen (Anderson and Ahmed, 1993). Likewise, in the Bahamas where shark watching contributed about six million dollars a year in the early 1990s (Hall, 1994), a single Caribbean reef shark (*Carcharhinus perezi)* was calculated to be worth between $13,300-$40,000 annually (Amsler, 1997; Anderson, 2002), yet a dead Caribbean reef shark was estimated to have a one time value of US $50-60. Therefore in those areas where recreational diving may be a viable industry non-consumptive use of sharks may contribute several orders of magnitude more to the local economy than consumptive uses.

14.3.2 Recreational catch and release fishing

Recreational shark fishing has been popular in many areas at least since the mid-1970s when the motion picture film "Jaws" was released (King and Cailliet, 1992; Pepperell, 1992). In recent years an increasing number of recreational shark fishers have been choosing to release their catches often after tagging (Casey and Kohler, 1992; Hueter, 1996). The value of recreational fishing to local communities may be huge considering the costs to fishers of food, accommodation, bait, tackle, boat charter, etc.

Therefore, the value of an individual shark in a recreational fishery even where harvest is practiced is several fold greater than its value in a commercial fishery. Catch and release provides even greater value because individuals may be caught multiple times by several anglers, and even with

some post-release mortality (Heuter, 1996; Skomal and Chase, 1996) catch and release fishing clearly contributes to the sustainability of the shark stocks. Post-release survivorship may be increased through the use of circle hooks, and care in handling the animals when landing and releasing.

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