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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, Wydoski and Prince, 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, Wydoski and Prince, 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 programmes 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 programme with 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 programme. 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 to increase our biological understanding of elasmobranch populations and ultimately the information on 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 focuses on issues related to tag-recovery programmes and the analysis of tag recovery data, primarily because the cost effectiveness of these types of studies has rendered them a common approach for inferring life history characteristics of aquatic populations. A stand-alone section on the design of tag-recovery studies is not included in the chapter, largely because it is difficult to accommodate all types of data collection and subsequent analyses using a single study design. However, it is important to base the development of a tag-recovery programme on a clearly and rigorously defined study design. I 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 readers may consult the comprehensive monographs of Burnham *et al.* (1987) and Pollock *et al.* (1990).

4.2 TAG TYPE AND PLACEMENT

4.2.1 Tag selection

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 programme. 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, Wydoski and Prince, 1990; Kohler and Turner, 2001):

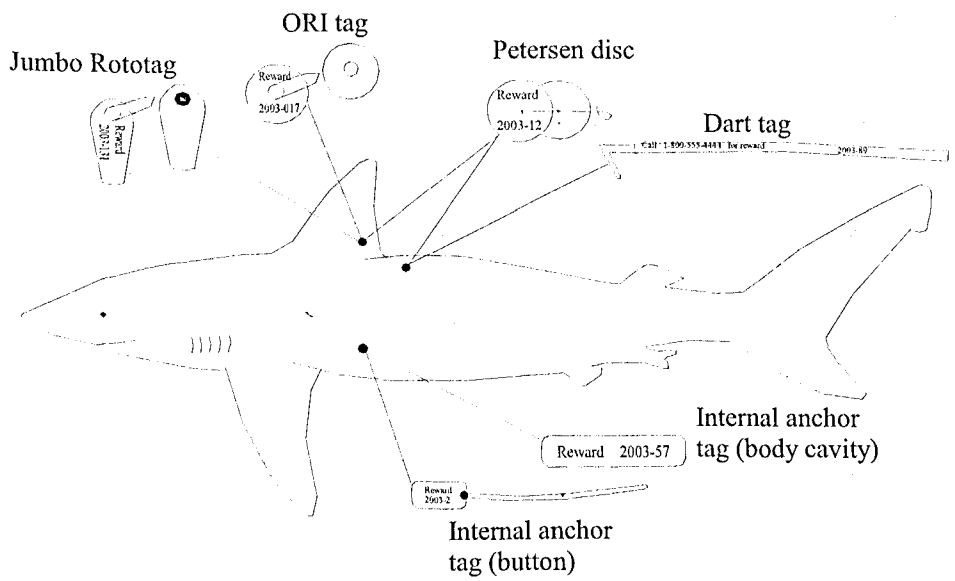
- objectives of the tagging study or programme;
- effect of the tag on the life history characteristics of the species under study, i.e. reproduction, survival, and growth;
- durability, longevity and stability of the tag;
- stress associated with the capture, handling and tagging process;
- size and number of individuals to be tagged;
- ease of tag application;
- cost of purchasing the tags and conducting the tagging experiment, and
- 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, Wydoski and Prince, 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) (Figure 4.1).

4.2.2 Petersen disc tag

The Petersen disc tag (Petersen, 1896), is one of the first tags used to study fish populations. Although the Petersen disc tag has undergone modifications over the years, in essence, the tag consists of two plastic discs that are placed on each side of the individual and are connected by a wire or a pin running through either the dorsal

FIGURE 4.1
Types of internal and external tags typically used to tag sharks. The appropriate anatomical location for attachment is indicated for each tag-type.



fin or the musculature at the base of the dorsal fin (Figure 4.1). 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 main drawbacks associated with the use of Petersen disc tags, they are 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. The 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).

4.2.3 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 4.1). All pertinent information 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 4.2). The disc serves as the anchor and is also 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 4.1).

Each type of internal anchor tag has been used for a variety of shark tagging studies (Olsen, 1953; Grant, Sandland and Olsen, 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. However, body cavity tags are only detectable once an individual is gutted. This 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.

4.2.4 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 4.3) 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 4.1). 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,

FIGURE 4.2
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.

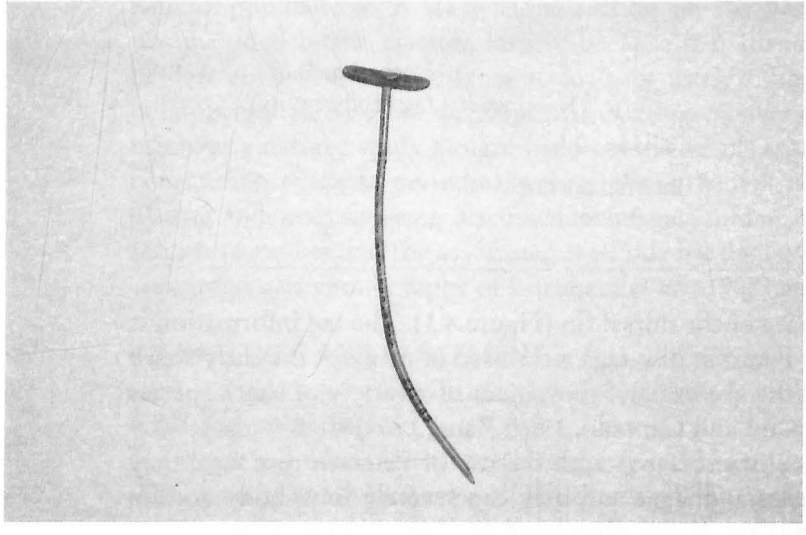
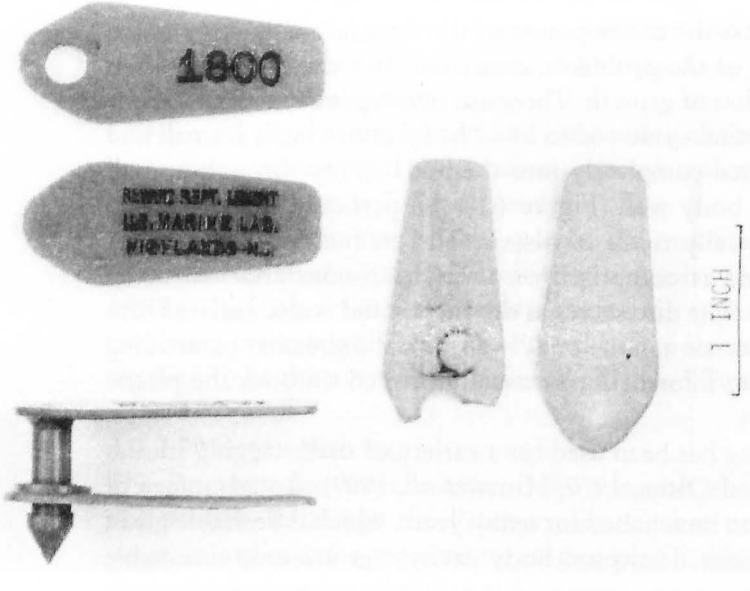


FIGURE 4.3
Jumbo rototag showing tag number and mailing address [from the NMFS Cooperative Shark Tagging Programme website (*http://na.nefsc.noaa.gov/sharks/intro.html*)].



Casey and Turner, 1998). Until 1988, they were the primary tag used in the common skate (*Dipturus batis*) tagging programme 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 programme.

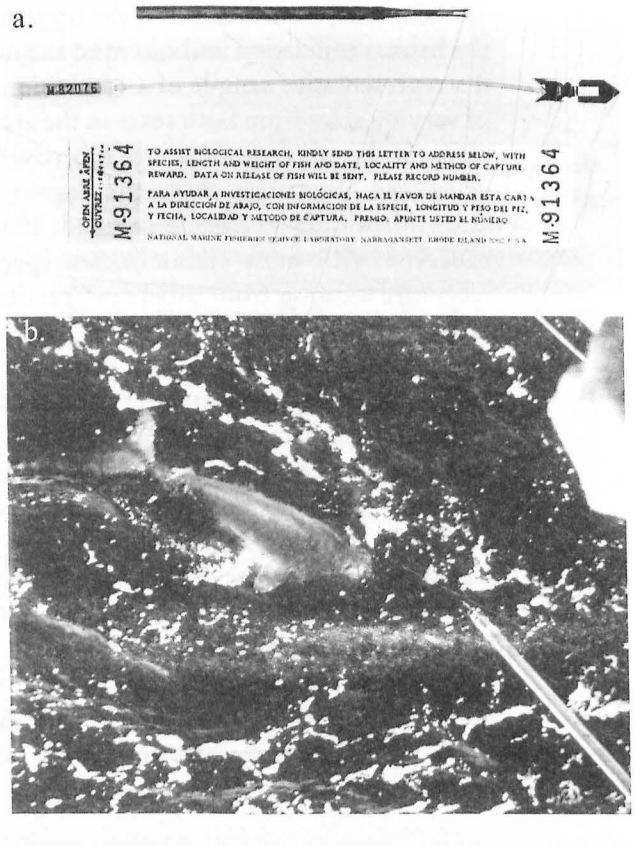
4.2.5 Dart tag

The origin of the dart tag can be traced back to early tagging studies of marine pelagic fish, particularly tunas (McFarlane, Wydoski and Prince, 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 programmes 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 4.1, Figure 4.4a). 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 fish (Figure 4.4b). Efforts are generally made to apply the tag at an angle so that streamer lies alongside the individual when 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, 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 use the dart tag include the NMFS Cooperative Shark Tagging Program (Kohler, Casey and Turner, 1998; Kohler and Turner, 2001) and the Australian Cooperative Game-Fish Tagging Program (Pepperell, 1990).

FIGURE 4.4

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



4.3 DATA COLLECTION AND ANALYSIS

4.3.1 Uses of data

Tag-recovery studies facilitate the collection of information on the species under study. These data can be used to delineate nursery areas, define habitat utilization, identify stock and determine growth rates, gear selectivity, patterns

of movement, survival and mortality, spatial and temporal distribution, relative abundance, species and size composition and sex ratio (Kohler and Turner, 2001). The following subsections contain detailed presentations of these data types and their associated methods of analysis. A more complete treatment of deriving survival and mortality information is provided in Section 8.3.2.

While many of the aforementioned analyses are fairly simple and straightforward, it is still important that data 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 and 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. 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 systematic sampling design must be adopted. Also, efforts should be made to sample with a gear-type that is relatively non-selective; i.e. one that will capture a wide variety of species and that will capture males and females of all sizes with approximately equal probability.

4.3.2 Delineation of nursery areas, habitat utilization, stock identification

It is possible, but often 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 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 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 so 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). For this, high-power, ultrasonic transmitters must be surgically or externally implanted in a representative sample of the target species. Receivers then monitor transmitter output intermittently to track 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 use non-arbitrary sampling and successfully characterize patterns of movement and degree of site fixity in any elasmobranch species.

4.3.3 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, e.g. 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 linear regression coefficients to be estimated. Prior to fitting 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.

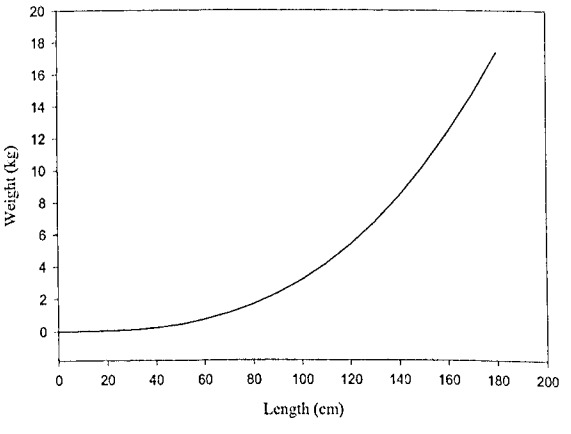
In addition to predictive relationships among various types of length measurements, it is also possible to use the size data collected at the time of first capture to establish a length/weight predictive relationship. This type of relationship is typically derived using the following power function (Figure 4.5).

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

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.

FIGURE 4.5

General shape of the power function typically used to relate length and weight under the assumption that α = 0.000005 and β = 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.



Despite the fact that equation 4.2 is frequently used to relate length and weight data, 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, that fits two or more models 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 (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.

4.3.4 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 4.6):

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

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 both sexes combined (see Section 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). The method here described was developed by Gulland and Holt (1959) and is fairly straightforward. However, efforts should be made to use several methodologies when analyzing growth data and statistically compare the results.

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

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

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

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

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

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

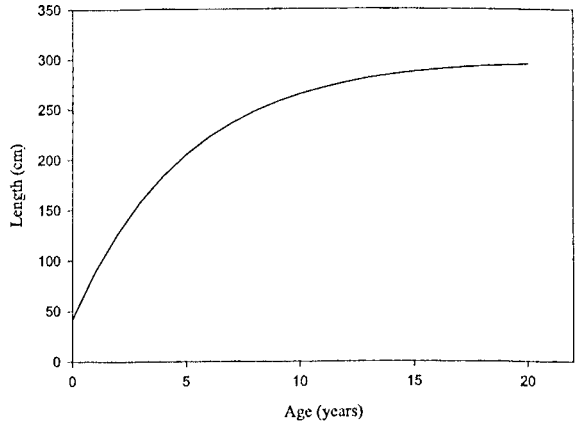
If x represents the midpoint of the length interval (l_t, l_{t+a}), then $x = \frac{1}{2}(l_t + l_{t+a})$, and after some algebraic manipulations, the following equation holds:

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

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

FIGURE 4.6

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.



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

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:

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

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):

(i) within-species comparisons of growth parameters when two sets of estimates are obtained from different time periods, areas or sexes and

(ii) 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

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

the T^2-statistic is calculated as

$$T^2 = [G_1 - G_2]' V^{-1} [G_1 - G_2] \tag{4.11}$$

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 is $\chi^2(\alpha)$, where α is the desired level of significance.

4.3.5 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 difficult to estimate because it is not easy to quantify how swimming speed influences the probability of capture. However, 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, Geaghan and Condrey, 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:

$$E[r_{i,g,l}] = N_{i,l}R_{i,g}U_{i,g}S_{g\,b} \tag{4.12}$$

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 $p_{i,g,l} = R_{i,g}U_{i,g}S_{g\,l}$, the generalized linear model takes the form:

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

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 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.

4.3.6 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, Nelson and Morrisey (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. More examples of studies that derived information on the movement of sharks from tag-recovery data described in the literature (Kohler and Turner (2001)).

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 the tagged population is representative of the total population). However, the decision to exclude these "immediate" recaptures often depends 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:

(i) 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.).

(ii) 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:

$$t = \frac{d_1 - d_2}{S_p\sqrt{\frac{1}{n_1} + \frac{1}{n_2}}} \tag{4.14}$$

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:

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

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).

The t-test is appropriate 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 ANOVA procedure must be used. For more information on ANOVA consult a statistical methods textbook (e.g. Zar, 1999). Francis (1988) provides an example of ANOVA used to compare the mean distances traveled by several groups of a shark species.

4.3.7 Survival/mortality

Brownie *et al.* (1985) developed a series of models for multi-year 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, Hoenig and Jones (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.

4.3.8 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.

4.3.9 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 is the first step to 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 determine growth rates, gear selectivity, patterns of movement, and survival/mortality, it is generally necessary to make the following assumptions.

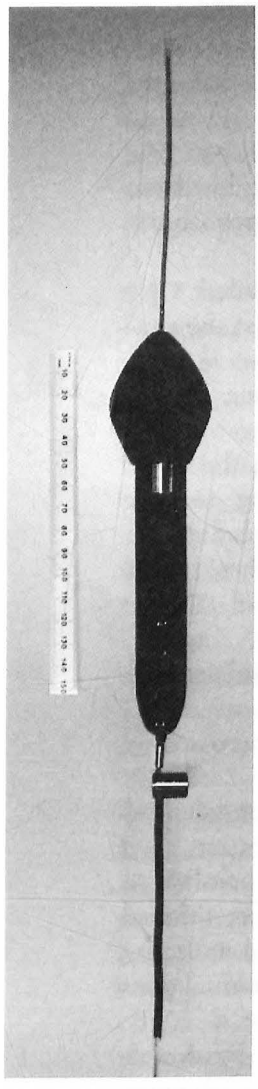
(i) The tagged sample is representative of the target population.
(ii) There is no tag loss or, if tag loss occurs, a constant fraction of tags is lost from each cohort and all tag loss occurs immediately after tagging. Also, the probability of immediate tag loss is not sex or size-dependent.
(iii) The time and location of tagging and tag recovery are correctly recorded.
(iv) The lengths and weights of individuals are measured without bias at the time of tagging.
(v) The lengths of individuals are measured without bias at the time of tag-recovery.
(vi) 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 the probability of immediate tag-induced mortality is not sex- or size-dependent.
(vii) The fate of each tagged individual is independent of the other tagged individuals.
(viii) Tagging does not affect growth.
(ix) There are no significant size-selection processes for individuals within similar age ranges.
(x) All tagged individuals within a cohort experience the same annual survival and tag-recovery rates.
(xi) 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 many factors, it is possible to conduct auxiliary studies to assess the possibility of violating a few of the aforementioned assumptions. 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, de Marignac and Hoenig, 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 here, knowledge of these tag-reporting rates can be extremely useful, particularly when trying to derive survival/mortality information. Rates of tag-reporting are best increased by offering large rewards (Henny and Burnham, 1976; Pollock *et al.*, 2001). Additional remedies to problems of tag-recovery studies as they pertain to survival/mortality estimation are discussed in Section 8.3.2.

4.5 ARCHIVAL TAGS

Archival, or data storage tags are designed to intermittently record data on the depth of an individual, ambient temperature and light intensity. The data from these tags are 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, United Kingdom, has used archival tags to study the movements of thornback rays (*Raja clavata*) in the Irish Sea and the Thames Estuary (Arnold and Dewar, 2001). Similarly, Australia's Commonwealth Scientific and Industrial Research Organisation

FIGURE 4.7
Wildlife Computers Pop-up Archival Transmitting (PAT) tag.



(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 has the potential to solve some important ecological questions (Arnold and Dewar, 2001).

Pop-up archival satellite tags were developed in part to alleviate some of the problems associated with low tag-recovery rates. These tags combine data storage tags with satellite transmitters and detach themselves from fish at a predetermined time (Figure 4.7). 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 assist in studying long-term movements of Atlantic bluefin tuna (Block *et al.*, 1998). Some of these tags were programmed to record hourly temperature information while others took measurements on a daily basis. 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 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 unknown. Pop-up satellite tags are typically attached to pelagic teleosts via a dart inserted into the dorsal musculature. 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, varying in shape and construction material. At present 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 the attachment method.

4.6 SUMMARY

It is possible to initiate either an angler-based cooperative programme or an agency-based programme, and in most cases, the objective(s) of the study and available funding dictate the appropriate choice. The advantages and disadvantages associated with each type of programme should be considered during the design phase. Several data analysis methods can be used to infer various aspects of the biology and life history of elasmobranch species. A wide variety of methods are described 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 data analysis and to the success of a tag-recovery programme is an assessment of the validitity of assumptions should be done to determine if the sampling, handling and tagging protocols minimize the potential for violation assumptions.

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