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Management techniques for elasmobranch fisheries

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Management techniques for elasmobranch fisheries

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8. Mortality estimation

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8.1 INTRODUCTION

Mortality is an essential 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. First, 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 second fishing morality (referred to by the letter F) which, as the name suggests, is the loss to the population from fishing. Fishing and natural mortality combine to give total mortality (referred to by the letter Z), such that

$$Z = M + F \qquad (8.1)$$

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

$$f = e^F \qquad (8.2)$$

where f = finite fractionof a population number removed by fishing.

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 relating 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 fishes and as sharks reach their maximum age, they are more likely to die of old age than from predation. 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 Section.

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 difficult and 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 use relationships between life history parameters and typically, natural mortality from species where research has been undertaken. The relationships used for sharks are based on teleost fishes, although some use data from broader taxonomic groups.

This Section describes methods for estimating mortality rates in shark populations, starting with the simple indirect methods and then discusses 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

8.2.1 Introduction

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. Hoenig (1983) and Brander (1981) 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 assume that mortality is independent of age, but two methods that give age-dependent values are also described.

8.2.2 Age-independent methods

8.2.2.1 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

$$\log M = -0.2107 - 0.0824 \log L_\infty + 0.6757 \log K + 0.4627 \log T \ 135,11 \quad (8.4)$$

Estimation of natural mortality using these equations is straightforward as long as von Bertalanffy parameter values are available. Jensen (1996) reanalysed the data of Pauly and used this to produce a simpler relationship (Section 8.2.2.4).

8.2.2.2 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 ten North Sea teleost species and uses maximum female GSI. The calculation of GSI is covered in Section 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) 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.

8.2.2.3 Hoenig (1983)

The most widely used indirect method of estimating mortality in shark species is that of Hoenig (1983) (see Section 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

$$\ln Z = 1.44 - 0.982 \ln t_{max} \tag{8.9}$$

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 $F \approx 0$. 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.

8.2.2.4 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

$$M = 1.65 / x_m \tag{8.10}$$

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

$$M = 1.5K \tag{8.11}$$

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

$$M = 1.60K \tag{8.12}$$

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

8.2.2.5 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 a year is known. Brander (1981) proposed a 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 biological information and some assumptions as detailed below. It 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) and in Section 9. Brander's method borrows the conventions of demographic analysis and considers only the female part of the population for simplicity.

The method calls for 3 types of information:

(i) 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).

(ii) The rate of reproduction (how many offspring are produced a year; in the case of elasmobranchs this would be the number of eggs laid a year for species such as

the skates (Rajidae) and sharks of the Heterodontidae and Scyliorhinidae families, or the number of pups a year for live-bearing sharks and rays).

(iii) An estimate of the instantaneous total mortality rate of the immature part of the stock.

This method relies on two assumptions:

(i) 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, this is not always 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.

(ii) 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 and not decrease or increase in size (i.e. be in *equilibrium*), the total rate of mortality of adults or mature fish (Z_m) must 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 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 a year), Z_i is the total mortality of the immature part of the stock (as mentioned above, Z_i is assumed to be constant throughout immature ages) and t_m is the number of years from birth to sexual maturity. To simplify, only females are considered by Brander, usually it is assumed that half of the total eggs laid or embryos *in-utero* will develop into females but it is advisable to check if this applies to the species being analysed. Thus, for the population to remain in equilibrium
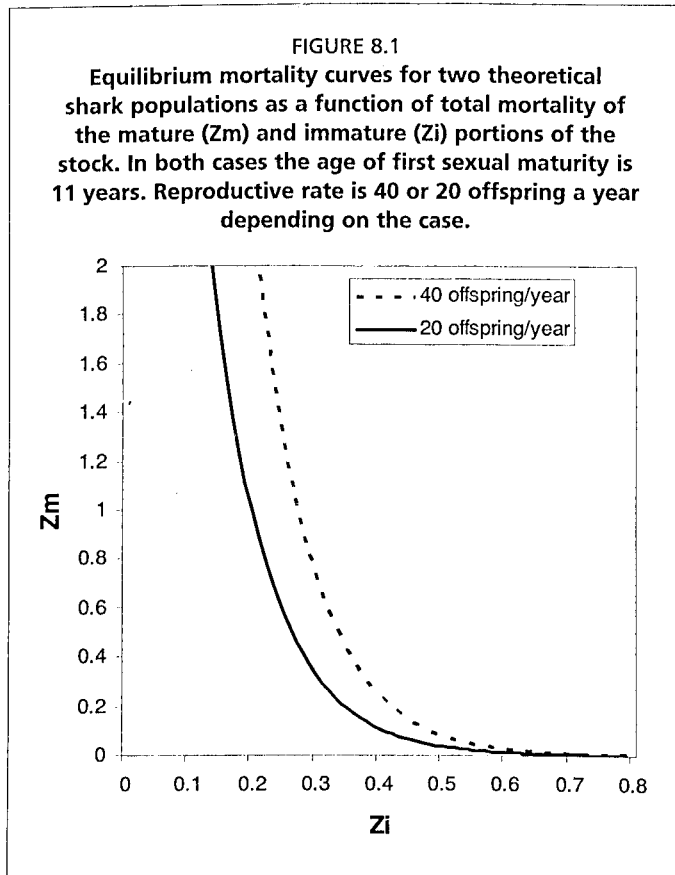
$$Z_m = (E/2)e^{-Z_i t_m} \tag{8.15}$$

This is Brander's equation and substituting the values of the age at maturity, the rate of reproduction and the total mortality of immature fish for the species being analysed gives 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 8.1. 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 a year). Mortality values to the right and above 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 (Section 8.3.2) 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 discussed in Section 10.

While the two curves in Figure 8.1 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 8.1

Equilibrium mortality curves for two theoretical shark populations as a function of total mortality of the mature (Zm) and immature (Zi) portions of the stock. In both cases the age of first sexual maturity is 11 years. Reproductive rate is 40 or 20 offspring a 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 useful for deriving reference points and making comparative analyses; however, it has never been adopted for the management of an actual 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 and (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.

8.2.3 Age-dependent methods

8.2.3.1 Peterson and Wroblewski (1984)

Peterson and Wroblewski (1984) estimate natural mortality that varies with age using 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

$$M_w = 1.92w^{-0.25} \tag{8.16}$$

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 Cortes (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.

8.2.3.2 *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.

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

where

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

and

$$t_M = -\frac{1}{k}\ln\left(1 - e^{kt_0}\right) + t_0$$ (8.19)

Cortes (1999) used this method to estimate the survival of sandbar sharks (*Carcharhinus plumbeus*) by age-class. He demonstrated no increasing mortality in older age classes due to senescence. The survival values that Cortes (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 Bertalannfy parameters, but the mathematics are more involved. This technique can be simply implemented in a spreadsheet using the formulae provided (8.17 – 8.19).

8.2.4 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 that researchers may wish to investigate. These 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).
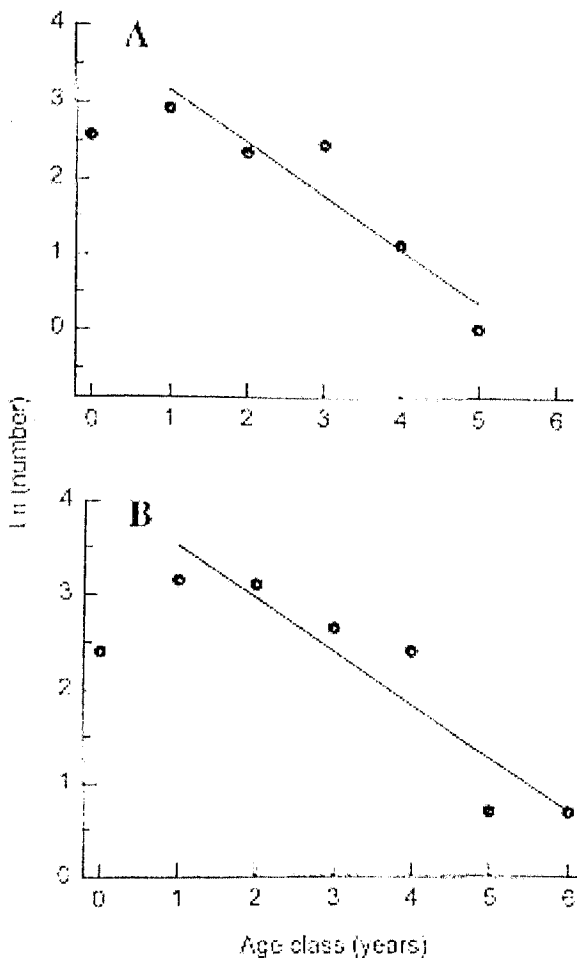
8.3 DIRECT METHODS

8.3.1 Requirements

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.

8.3.2 Catch curves

One powerful method of estimating total mortality (i.e. 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 only of mortality:

$$N_{t+1} = N_t e^{-Z} \tag{8.20}$$

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

(i) The number of animals in each class is determined.

(ii) The numbers are log (base e) transformed.

(iii) The log-transformed numbers are plotted against age.

(iv) A linear regression is fitted to the descending limb (right hand side) of the catch curve.

(v) The value of total mortality is calculated as the negative slope of the regression.

(vi) 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 (*Rhiozprionodon taylori*) from Simpfendorfer (1999a) is given in Figure 8.2.

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 8.3a.). However, in reality most catch curves have an ascending limb for the youngest age classes, due to incomplete recruitment of some age classes to the fishing gear or to the

FIGURE 8.2
Catch curves for (A) male and (B) female Australian sharpnose sharks derived from data from Simpfendorfer (1993). Data points for the first age class were not used to calculate the regression line. From Simpfendorfer (1999a).

available population and an asymptote for the older age classes (Figure 8.3b). 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 Cortes 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 the 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). When 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. First, the aged animals are representative of the age-structure in the population. Second, the ages are accurately determined. Third, the total mortality rate is constant across the age classes to which the linear function is fitted. Fourth, the mortality rate is constant between years (if more than one year's data are used). Fifth, recruitment is constant between years. Last, vulnerability to fishing gear is equal for all ages and constant over year classes.

FIGURE 8.3
Hypothetical catch curves from (a) the "perfect" case based on $N_{t+1} = N_t e^{-z}$ 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.

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). Cortes and Parsons (1996) used an age-based catch curve and an age-length key derived catch curve for the bonnethead shark. Both methods produced similar results.

8.3.3 Tagging
Tagging experiments can be separated into two general categories: (a) studies where the tagged individuals of population are killed upon recapture, as in a commercial fishery and (b) 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
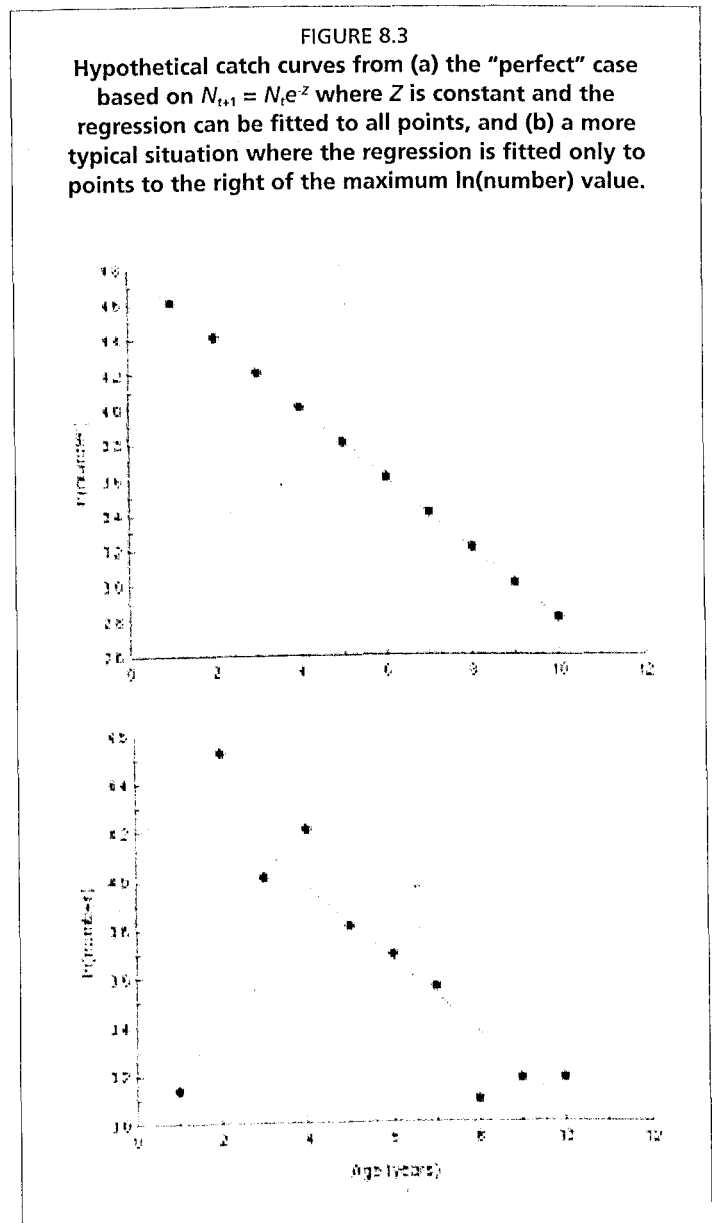
occasions. Moreover, tag-recovery studies are typically viewed as fishery-dependent since the data obtained is strictly a function of fishing activities, while for capture-recapture studies it is best to use a fishery-independent sampling design to generate capture histories for tagged individuals. Here we focus on the use of multiyear tag-recovery studies as a method to derive estimates of mortality and note that there is a wealth of literature on the analysis of capture-recapture data (e.g. Burnham *et al.*, 1987, Pollock *et al.*, 1990)

The general structure of a multi-year tag-recovery study is to tag N_i individuals at the start of each year i, for $i = 1,...,$ I years. 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 $j = i, i+1, ..., J$ 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 multi-year 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 multi-year 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 survives to the end of year i, 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 analyse 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 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 the following assumptions: (a) the tagged sample is representative of the target population; (b) 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; (c) 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); (d) all tagged individuals within a cohort experience the same annual survival and tag-recovery rates; (e) the decision made by a fisher on whether or not to return a tag does not depend on when the individual was tagged; (f) survival rates are not affected by tagging process or, if they are, the effect is restricted to a constant fraction dying immediately after tagging, (g) and 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:
(i) 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 - 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 (a) 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.
(ii) 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 (d).
(iii) 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 (a) and (d) 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 using Ricker's (1975) equation:

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

and if information about M is available (e.g. from one of the methods previously described), then estimates of F_i are possible. Given estimates of the instantaneous rates, it is then possible to estimate u_i if the timing of fishing (i.e. single pulse (Type I) fishery or continuous (Type II) fishery is known (Ricker, 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) by

$$u_i = \frac{f_i}{\phi \lambda}$$ (8.26)

where *f* is the short-term probability an individual survives the handling and tagging process with the tag intact and *l* is the tag-reporting rate (i.e. probability the tag will be reported given that that individual is harvested). The parameter *f* 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. to estimate 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). A variety of techniques specific to shark tagging studies 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*); Xiao *et al.* (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 enabled increasingly powerful techniques. These techniques, however, have been rarely used for shark populations. Grant, Sandland and Olsen (1979) estimated the fishing and natural mortality rates of school sharks 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, Stevens and West (1999) estimated fishing and natural mortality rates of the school shark using a probabilistic model.

8.3.4 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 most systems impractical for monitoring 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, Jackson and Pollock (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 8.4), 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 a season within the relatively small and well-confined study site. Heupel and Simpfendorfer (2002) and Hightower, Jackson and Pollock (2001) provide more details of this approach.

8.3.5 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 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-

FIGURE 8.4
Kaplan-Meier estimates of finite rate of survival from (a) natural mortality and (b) fishing mortality for juvenile blacktip sharks (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).

age and fishing effort information, are greater than are normally available. However, for populations where good data are available 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 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. 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 all 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
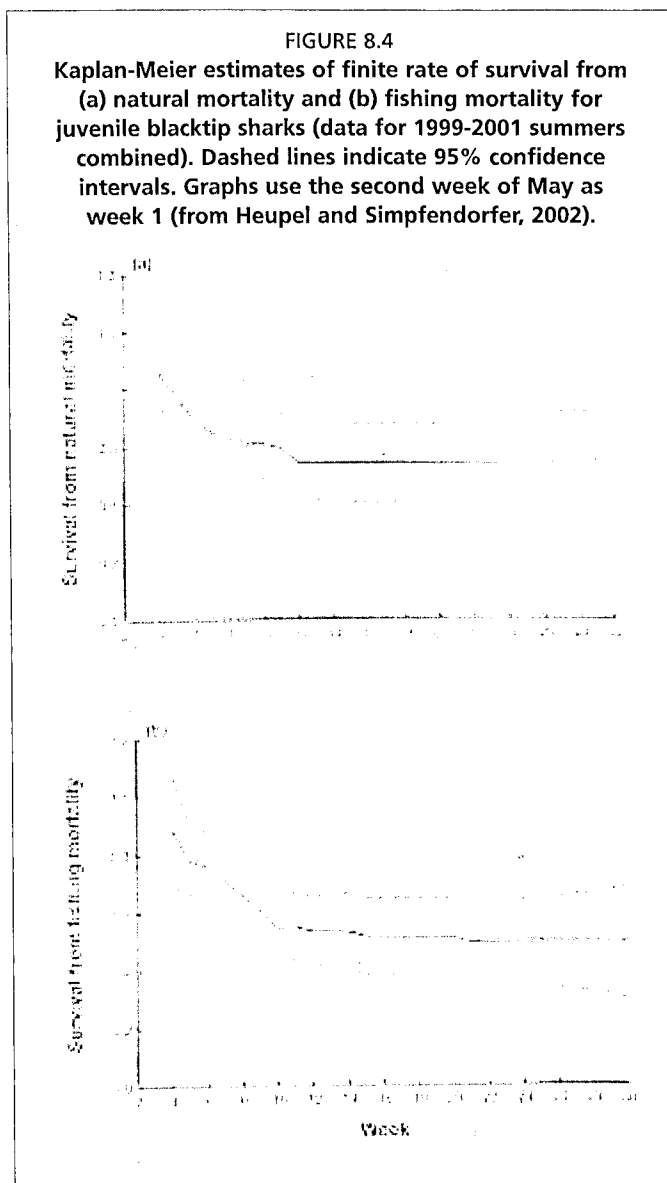
of the results fell within the range of 0.081 to 0.086. Alternatively, the estimates of different methods can be very variable. Simpfendorfer (1999a) used seven methods for the Australian sharpnose shark and found a range of values from 0.56 to 1.65.

One first obvious result in population assessments is that the results are always 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 direct 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 accurate results, but the data must meet several assumptions (Section 8.3.2) to do so. Finally, telemetry methods are best used in situations where the mortality within a given system is required and the system can be adequately sampled acoustically, normally with data-logging monitors. While a telemetry approach may seem like a dream for some populations, 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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