Mortality estimates and demographic analysis for the Australian sharpnose shark, *Rhizoprionodon taylori*, from northern Australia

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Abstract.–Natural mortality was estimated for *Rhizoprionodon taylori* by using seven indirect methods based on relationships between mortality and life history parameters and one direct method, catch curve analysis. Estimated values from indirect methods were 0.60 to 1.65, whereas catch curves produced values of 0.56 for females and 0.70 for males. Demographic analysis was undertaken by using standard life history table techniques. Life history tables where each of the seven indirect estimates of natural mortality for *R. taylori* produced intrinsic rates of natural increase from –1.297 to 0.212 for an unfished population, and only two of the seven produced positive population growth. The implications of these results are discussed in relation to the accuracy of indirect methods for estimating natural mortality for *R. taylori* and other species of shark. The catch curve method was considered the best estimate of natural mortality and gave an intrinsic rate of increase of 0.27 and a doubling time of 2.55 years. The results of life history table analysis with the estimate of natural mortality from the catch curve analysis indicated that a *R. taylori* population could sustain fishing mortality up to 0.18 if applied evenly over all age classes, or 0.67 if age at first capture was two years. The implications of this study are discussed in relation to sustainability of elasmobranch stocks, particularly short-lived, fast growing, early maturing species.

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In a paper entitled “Problems in the rational exploitation of elasmobranch populations and some suggested solutions,” Holden (1974, p. 137) concluded that “elasmobranch stocks offer very limited opportunities for long-term exploitation.” Holden’s conclusion was based on the fact that elasmobranch life history traits, such as slow growth, long lifespan, late age at maturity, and low fecundity, make populations very susceptible to recruitment overfishing. Holden’s hypothesis has been supported by evidence from a number of shark stocks that have been rapidly overfished. These stocks include the spiny dogfish off Scotland and Norway (*Squalus acanthias*; Holden, 1968, 1977), the soupfin shark off California (*Galeorhinus galeus*; Ripley, 1946), the basking shark of the Irish Sea (*Cetorhinus maximus*; Parker and Stott, 1965), the porbeagle of the western Atlantic (*Lamna nasus*; Casey et al., 1978), and the sandbar and dusky sharks of the western North Atlantic (Musick et al., 1993). The majority of these examples are long-lived, slow growing, late maturing, temperate-water species. This group of commonly cited examples does not, however, represent the full range of elasmobranch life history traits and as such represents a biased set of data on which to base conclusions about sustainability of elasmobranch stocks. In particular, the examples lack representatives from tropical areas, especially short-lived, rapidly growing, early maturing species. With adequate information on species with a wide range of life histories, a more accurate assessment of the ability of elasmobranch stocks to sustain fishing pressure should be possible.

In recent years the use of demographic analysis (i.e. life history tables) has become popular in the assessment of elasmobranch populations and their ability to be sustainably fished (e.g. Hoenig and Gruber, 1990; Cailliet, 1992; Cailliet et al., 1992; Cortes, 1995; Cortes and Parsons, 1996; Sminkey and Musick, 1996; Au and Smith, 1997; Cortes, 1998). This style of analysis requires only knowledge of the life history traits of a species. Because demographic models are static representations of populations with a stable age structure, they have limitations in respect to density-dependent responses (e.g. density-dependent natural mortality) and dynamic processes (e.g. fishing and variable recruitment) that can be included in dynamic models. The latter types of

Table 1

Methods used to estimate mortality for *Rhizoprionodon taylori* from life history parameter relationships. GSI = gonadosomatic index; K = von Bertalanffy growth parameter; L_∞ = von Bertalanffy growth parameter; M = natural mortality; T = average water temperature; t_{max} = maximum age; x_m = age at maturity; Z = total mortality.

Method	Relationships
Hoenig (1983)	$\ln(Z) = 1.46 - 1.01 \ln (t_{max})$
Pauly (1980)	$\ln(M) = -0.0066 - 0.279 \log (L_x) + 0.6543 \log (K) + 0.4634 \log (T)$
Gunderson (1980)	$M = 4.64\ GSI - 0.370$
Gunderson and Dygert (1988)	$M = 0.03 + 1.68\ GSI$
Jensen (1996) (age)	$M = \frac{1.65}{x_m}$
Jensen (1996) (growth)	$M = 1.5K$ (theoretical)
Jensen (1996) (Pauly)	$M = 1.6K$

models require abundance data (e.g. CPUE time-series data or fishery-independent surveys) that are not available for many elasmobranch populations. In cases where abundance data are not available, demographic models may represent the best available technique for the analysis of stock dynamics.

The Australian sharpnose shark, *Rhizoprionodon taylori*, is an ideal example of a small, short-lived, fast growing, early maturing tropical species (Simpfendorfer, 1992, 1993). It is endemic in the inner continental shelf waters of northern Australia between the Northwest Shelf and southern Queensland (Last and Stevens, 1994). It is captured throughout much of its range as bycatch in commercial fishing operations, including gillnet fisheries for barramundi, mackerel, and shark, and prawn trawl fisheries (Simpfendorfer and Milward, 1993; Last and Stevens, 1994). This paper reports the results of mortality estimation and demographic analysis for *R. taylori*. Mortality was estimated in two ways. First, a number of relations between mortality and life history parameters from the literature were used to evaluate the appropriateness of these methods for estimating natural mortality in sharks. Second, catch curve analysis was conducted to produce a direct estimate of mortality. The results of the demographic analyses are used to comment on the probable sustainability of short-lived, fast growing, early maturing, tropical elasmobranch populations.

Materials and methods

Estimation of mortality

Two approaches were taken to estimate mortality in *R. taylori*. The first was to employ relationships between life history parameters and natural mortality (M) or total mortality (Z) from the literature. Seven relationships were chosen (Table 1) to investigate variability in their results. All seven were based heavily on data from teleost fish, although most included some data from elasmobranchs. The most widely used relationship in elasmobranch studies is that of Hoenig (1983), which uses a linear function to estimate total mortality from maximum age. Although this method estimates total mortality, it was assumed to represent natural mortality for *R. taylori* because there was little or no fishing for this species in the study area (Simpfendorfer, unpubl. data). The method of Pauly (1980) uses two parameters of the von Bertalanffy growth curve (L_∞ and K) and average temperature to estimate natural mortality. Jensen (1996) reanalyzed Pauly's (1980) data and found that natural mortality could be estimated with the same level of accuracy based only on the value of K. In the same paper Jensen (1996) also gave two other relationships for estimating natural mortality based on life history theory, one based on K and the other on age at maturity. The final two relationships selected used maximum female gonadosomatic index (GSI) as an indicator of reproductive effort to estimate natural mortality. The method of Gunderson (1980) was based on only 10 species; Gunderson and Dygert (1988) expanded this to 20 species. Data for calculation of M were taken from Simpfendorfer (1992; GSI) and Simpfendorfer (1993; von Bertalanffy parameters, maximum age, and age at maturity).

The second approach to the estimation of mortality was catch curve analysis (e.g. Ricker, 1975; Vetter, 1987). Age data for the catch curves were taken from Simpfendorfer (1993). Ages were converted to whole years and the natural log of the number of individuals (ln N) was plotted against age for males and females separately. Mortality for each sex was calculated as the negative value of the slope of the regression line for points to the right of, and including, the peak ln *N* value. Ricker (1975) used only points to the right of the peak ln *N* value to calculate mortality; however, the small number of age classes in *R. taylori* meant that including the peak value would increase the reliability of the estimate. To confirm that the peak ln *N* value should be included in the regression calculations, linear and quadratic functions were fitted to the data. If the quadratic function provided a significantly improved fit as judged by an *F* test, then it was assumed that the inclusion of the peak ln *N* value introduced significant curvature into the data set and so violated the assumption of catch curve calculations that mortality is constant across all age classes. In this situation the peak ln *N* value was not used in the calculation. As with the Hoenig (1983) method, the estimate of mortality from the catch curves was taken to be natural mortality because there was little or no fishing pressure on the stock from which the age data were collected.

Demographic analysis

Demographic analysis of *Rhizoprionodon taylori* was undertaken with standard life history table methods (e.g. Krebs, 1985). The parameters estimated from the life history table were net reproductive rate (R_0), generation time (G), intrinsic rate of population increase (r), and population doubling time (t_{X2}). Positive values of r indicate that a population is able to replace itself and thus will not decline, whereas negative values of r indicate that the population is unable to replace itself and will decline. Values of r were calculated by solving the Euler equation (Krebs 1985):

$$\sum_{x=0}^{x_{\max}} l_x m_x \cdot e^{-rx} = 1$$

where x = age;
x_{max} = maximum age;
l_x = the proportion of animals surviving to the beginning of a given age class; and
m_x = age-specific natality.

Age and growth data for the demographic analysis were taken from Simpfendorfer (1993). Maximum age was taken as 6 years for males and 7 years for females, and age at maturity for males and females was taken to be one year. Because Simpfendorfer (1993) was not able to validate age estimates (but did have supporting marginal increment and length-frequency data), sensitivity tests were run to investigate the influence of the uncertainty of age estimates (maximum age 10 years, age at maturity 2 years).

Reproductive data were taken from Simpfendorfer (1992). Litter size varied significantly with maternal length (Fig. 1; r^2=0.33, P<0.05). Because observations of litter size were made throughout the year, the litter size for each age class was calculated from the size of females at the midpoint of the age class. Mature females produce a litter each year. The sex ratio of the embryos was not significantly different from 1:1; therefore the litter size for each age class was halved to give the number of female pups per female. Although *R. taylori* matures at the age of one, the first litter is not produced until the end of the second year. Thus only females that survive to the end of that age class produce young. To accommodate this in the life history table, age-specific natality was calculated from the number of animals surviving to the end of a given age class (i.e. the number at the start of the next age class). Similarly, the age-specific natality of the final age class was set to zero because it was assumed that no animals survived to the end of the last age class. To assess the difference in results between calculating age-specific natality from the number present at the beginning and end of an age class, separate life history tables were constructed and the results compared.

A life history table was constructed for each of the values for natural mortality, calculated as described above, to investigate the sensitivity of demographic parameters to different values. To simulate increased mortality of the youngest age class, a number of other authors have doubled the normal value of *M* for the first age class (e.g. Hoenig and Gruber, 1990; Smith and Abramson, 1990; Cailliet, 1992; Sminkey and Musick, 1996). A life history table was constructed with double the normal value of *M* for the first *R. taylori* age class to test the sensitivity of outcomes to this approach.

Fishing mortality (F) was incorporated into the survivorship function of the life history table such that total mortality was the sum of M and F. The critical value of F, at which r equaled zero (i.e. the level of fishing beyond which the population could not replace itself, F_c), was calculated for each life table. For the calculation of F_c, fishing mortality was assumed to be equal for each age class. Negative values of F_c occurred when the population was declining without fishing and indicated that the population could sustain no fishing. The main source of fishing mortality on *R. taylori* in northern Australia is gill nets, which do not normally catch animals until they are at least one year of age. To investigate the effect of the age at which *F* begins (age at first cap-

Table 2

Life history table for *Rhizoprionodon taylori* based on various estimates of female natural mortality (M). R_0 = net reproducdtive rate; G = generation time; r = intrinsic rate of population increase; t_{x2} = population doubling time; F_c = level of fishing beyond which the population can not replace itself.

Scenario	Source of M	M	R_0	G	r	t_{x2}	F_c
A	Hoenig (1983)	0.60	1.547	2.233	0.212	3.273	0.140
B	Pauly (1980)	1.34	0.200	1.442	–0.869	–0.798	–0.600
C	Jensen (1996) (age)	1.65	0.096	1.301	–1.297	–0.534	–0.910
D	Jensen (1996) (growth)	1.52	0.130	1.353	–1.119	–0.619	–0.780
E	Jensen (1996) (Pauly)	1.62	0.103	1.312	–1.256	–0.552	–0.880
F	Gunderson (1980)	1.49	0.140	1.366	–1.078	–0.643	–0.750
G	Gunderson and Dygert (1988)	0.70	1.123	2.063	0.057	12.102	0.038
H	Catch curve (female)	0.56	1.758	2.304	0.271	2.554	0.179

ture, AAFC) the values of r at different levels of F and AAFC were calculated. F after AAFC was assumed to be constant across all ages.

Results

Mortality

The calculation of M from the various life history relations produced estimates ranging from 0.6 to 1.65 (Table 2). All the methods based on von Bertalanffy growth parameters gave results greater than one. Only the Hoenig (1983) and Gunderson and Dygert (1988) methods yielded estimates less than 1.

The length and age frequency data for *R. taylori* on which the age analysis of Simpfendorfer (1993) was based are shown in Figure 2. Estimates of M from the catch curves were 0.698 for males and 0.561 for females (Fig. 3). The first age class (0) for both males and females was excluded from the regression analysis to estimate M because it was lower than, and to the left of, the peak ln N value. Fitting of quadratic functions to the data did not significantly improve the fit to the data points selected (male: F=3.86, P=0.188; female: F=1.35, P=0.329), confirming that their inclusion did not violate the assumption relating to constant mortality.

Demographic analysis

Life history tables were constructed to obtain demographic results for the eight different estimates of M for an unfished *Rhizoprionodon taylori* population (Table 2). Three of the eight (A, G, and H) gave positive values of r: the methods of Hoenig (1983), Gunderson and Dygert (1988) and the catch curve method. The catch curve and Hoenig (1983) methods produced similar demographic results, with r values between 0.2 and 0.3, and with doubling times of 2.5 to 3.5 years (Table 2). These were considerably higher than for the Gunderson and Dygert (1988) method, which gave an r value of 0.057 and a doubling time of 12.1 years. The values of r for the remaining scenarios (B–F) were all much less than zero (–0.869 to –1.297; Table 2), indicating population decrease even with no fishing.

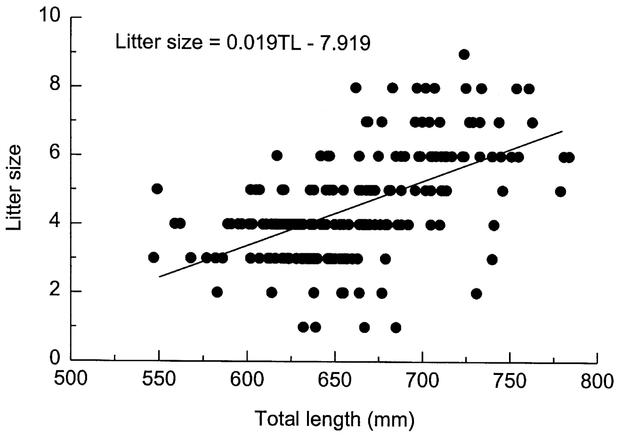

Figure 1

Litter size of *Rhizoprionodon taylori* as a function of maternal length. Data from Simpfendorfer (1993).

The value of M from the catch curve method was used to test the sensitivity of the life history table values to changes in model structure and age parameters. There was a large difference in age-specific reproductive rate calculated with a proportion of the

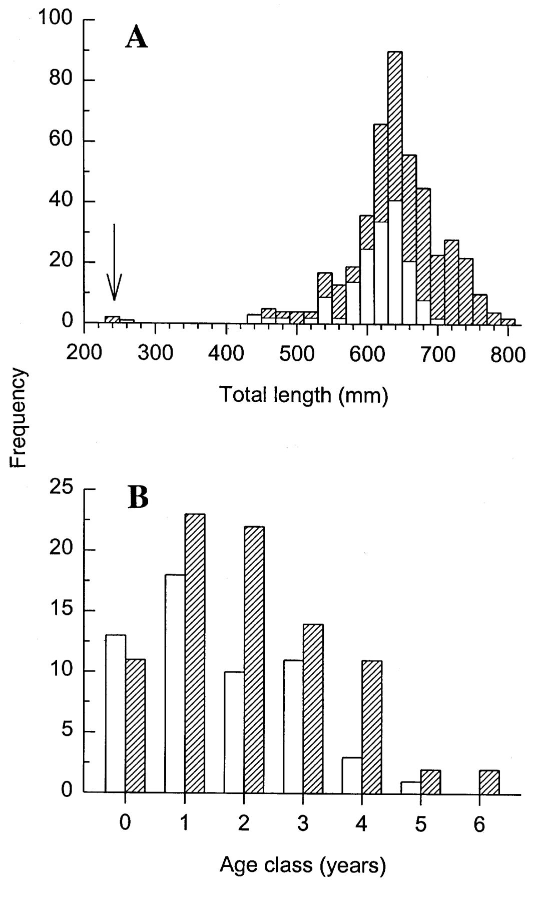

Figure 2

(A) Length and **(B)** age-frequency distributions of male (open bars) and female (hatched bars) *Rhizoprionodon taylori* from the waters of Townsville, Queensland. The arrow indicates size at birth.

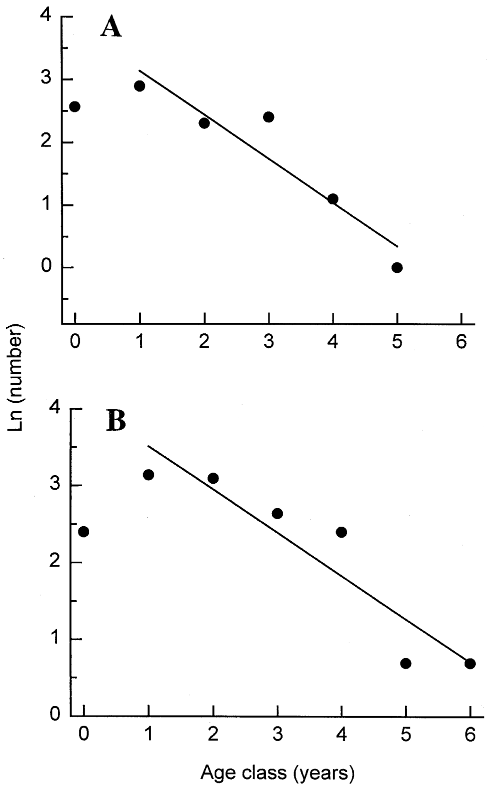

Figure 3

Catch curves for **(A)** male and **(B)** female *Rhizoprionodon taylori* derived from data from Simpfendorfer (1993). Data points for the first age class were not used to calculate regression lines.

population surviving to the beginning of an age class (J) rather than to the end (I). The value of *r* increased from 0.271 to 0.600, doubling time decreased from 2.544 years to 1.155 years, and the maximum value of *F* sustainable by the population (F_c) increased from 0.179 to 0.600 (Table 3) when the beginning of an age class was used. Doubling the value of *M* in the first year of life (I vs. K) caused a reduction in the value of *r* from 0.271 to 0.001, and population doubling time increased from 2.544 to 529.2 years (Table 3). The maximum level of fishing mortality that the population could sustain under such a scenario decreased from 0.179 to 0.001. Doubling first-year *M* and also calculating age-specific natality from the number surviving at the beginning of age classes (L) produced results identical to the base case (Table 3).

Increasing the maximum age to 10 years resulted in a small increase in *r*, from 0.271 to 0.276, and decreased population doubling time from 2.544 to 2.516 years (Table 3). Setting age at maturity at two years instead of one resulted in an *r* of 0.035, and a population doubling time of 19.82 years (Table 3).

Values of *r* varied considerably with changes in *F* and AAFC (Fig. 4). With an AAFC of 0, F_c = 0.18; with an AAFC of one, F_c = 0.27; and with an AAFC of two, F_c = 0.67. When AAFC was three or more the population was sustainable at *F* values up to at least 1.0.

Discussion

Mortality estimates

In most studies where natural mortality has been estimated for shark populations, particularly for use in demographic analysis, indirect estimation methods have been used (e.g. Hoenig and Gruber, 1990; Cortes, 1995; Sminkey and Musick, 1996; Au and Smith, 1997). The results of the current study indicate that these indirect methods may provide a wide

Table 3

Sensitivity of life history tables to changes in model structure and age parameters. $l_{x+1}m_x$ indicates that age-specific natality was calculated from the number sharks surviving to the end of age classes; l_xm_x indicates that age-specific natality was calculated from the numbers surviving at the beginning of classes; $2M_1$ indicates that natural mortality was doubled for the first age class; $1M_1$ indicates that natural mortality was constant for all age classes. Definitions of parameters are given in Table 2.

Scenario	Sensitivity test	R_0	G	r	t_{x2} (years)	F_c
I	Base case ($l_{x+1}\ m_x$, $1M_1$)	1.758	2.304	0.271	2.554	0.179
J	$l_x\ m_x$, $1M_1$	3.080	2.304	0.600	1.155	0.600
K	$l_{x+1}\ m_x$, $2M_1$	1.003	2.304	0.001	529.2	0.001
L	$l_x\ m_x$, $2M_1$	1.758	2.304	0.271	2.554	0.271
M	Maximum age = 10	1.820	2.488	0.276	2.516	0.183
N	Age at maturity = 2	0.035	3.061	0.035	19.82	0.026

range of estimates of natural mortality for a single population. Testing these values of natural mortality for *R. taylori* in life history tables showed that most of the methods produce values of r that would result in a population decreasing even when it was unfished. Such a result is biologically unreasonable. In contrast, Simpfendorfer (1999) made similar comparisons of indirect estimation methods for the dusky shark (*Carcharhinus obscurus*) and found that results did not differ greatly between methods. The difficulties in applying many of the indirect methods to *R. taylori* may relate to its short lifespan and fast growth because all but two of the methods used age or growth parameters to estimate natural mortality.

Among the indirect methods for estimating natural mortality, only those of Hoenig (1983) and Gunderson and Dygert (1988) yielded estimates that would allow an unfished population to increase. Although the values of natural mortality from the two methods were relatively similar (0.60 and 0.70, respectively), they produced different results when used in the life history tables to calculate r, with the Hoenig (1983) estimate producing a much higher value. This difference indicates that the results of demographic analysis are highly sensitive to changes in natural mortality. It is unlikely that the Gunderson and Dygert (1988) method produced a realistic value of natural mortality because it is based on the assumption that GSI is an index of total reproductive effort. Although this is true for most fish species, it is not the case for placental forms (such as *R. taylori*) in which much of the energy invested in reproduction is supplied during development rather than stored in the ovary prior to fertilization. Of the indirect methods used, the Hoenig (1983) method is therefore likely to be the most realistic estimate of natural mortality for *R. taylori*.

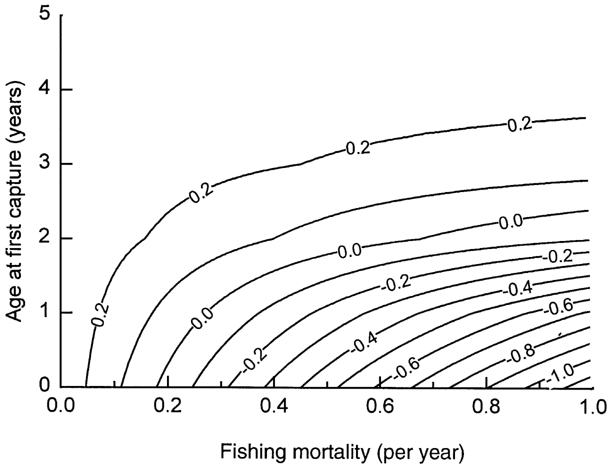

Figure 4

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 (scenario H in Table 2). Fishing is sustainable at values of $r > 0$.

There are relatively few studies of shark populations in which natural mortality has been estimated directly with either tagging studies (e.g. Grant et al., 1979; Manire and Gruber, 1993) or catch curves (e.g. Cortes and Parsons, 1996). Although direct approaches to determining mortality would be expected to produce more realistic estimates, they must also meet a number of criteria in order to produce accurate results. The assumptions for the catch curve technique used in the present paper included constant mortality, recruitment, and selectivity over all age classes used in the calculations as well as random collection of samples from the population. The data on which the calculations for *R. taylori* were based are likely to have met at least two of these assumptions. Because the area from which samples were collected was subject to little or no fishing, the population size should have remained relatively constant and thus fluctuations in recruitment would be minimized. The necessity of excluding the first age class from the catch curve analysis resulted from the selectivity of the gill nets used to collect specimens. For the age classes included in the analysis, the size of individuals was similar because growth rapidly reaches an asymptote, and therefore selectivity was probably reasonably constant. The assumption that mortality was constant was more difficult to test. However, the small size of *R. taylori* and the small change in its size after the first year or two of growth (Simpfendorfer, 1993) suggest that all age classes are likely to be subject to similar levels of predation.

The estimates of natural mortality for female *R. taylori* from the catch curve and from the indirect method of Hoenig (1983) were similar: 0.56 and 0.60, respectively. Such a finding is contrary to that reported by Cortes and Parsons (1996), who suggested that the Hoenig (1983) method would produce lower natural mortality estimates than those from catch curves. The present study suggests that for some species the Hoenig method will produce acceptable results. However, Cortes and Parsons' (1996) caution that demographic studies based solely on a natural mortality estimate from the Hoenig (1983) method should still be heeded because it is clear that the accuracy of this method may vary between species.

The most biologically plausible estimates of natural mortality for *R. taylori* (0.698 for males and 0.561 for females) are significantly higher than those reported so far for many other species of shark. Species with mortality levels of a similar magnitude are the bonnethead shark (*Sphyrna tiburo*) (0.625; Cortes and Parsons, 1996) and the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) (0.42; Cortes, 1995). Each of these three species (*R. taylori*, *R. terraenovae*, and *S. tiburo*) are short-lived (6–12 yr). In longer-lived shark species, estimates of natural mortality are much lower. For example, Sminkey and Musick (1996) estimated an *M* of 0.105 for *Carcharhinus plumbeus*, which lives at least 30 years, and Smith and Abramson (1990), Cailliet (1992), and Au and Smith (1997) estimated that *Triakis semifasciata*, which lives to 30 years, has an *M* between 0.139 and 0.15.

The small size of *R. taylori* probably results in it being subject to high levels of predation throughout life. The small size at birth (220–260 mm) means that the first age class is particularly vulnerable to predation. The results of the sensitivity test, in which natural mortality was doubled for the youngest age class, indicate that this technique, which has previously been used to account for increased predation of young sharks, was not realistic for *R. taylori*. This is a result of the high value of natural mortality assumed for older age classes. It was not possible to estimate what, if any, increase in predation occurs for the youngest age class of *R . taylori*. However, any increase in predation would result in reduced estimates of *r*.

Demographic analysis

The most likely demographic results for *R. taylori*, those based on natural mortality estimated from the catch curve, indicate that the maximum value of *r* is about 0.27. This value is one of the highest for a species of shark. Cortes and Parsons (1996) estimated a similar rate (0.272–0.283) for *Sphyrna tiburo* from Florida with Hoenig's method to estimate natural mortality. *Rhizoprionodon taylori* and *S. tiburo* have similar life histories, with short lifespans, rapid growth, early maturity, and high natural mortality. All other published studies of shark demography have estimated intrinsic rate of increase at less than 0.1 (e.g. Hoenig and Gruber, 1990; Cailliet, 1992; Cailliet et al., 1992; Cortes, 1995; Sminkey and Musick, 1996; Au and Smith, 1997; Cortes, 1998). In most cases these species have been longer lived and slower to mature and have exhibited lower natural mortality than *R. taylori* or *S. tiburo*. The exception to this is *R. terraenovae*, which grows larger than *R. taylori* and is relatively short-lived (10 yr), but has a lower reproductive rate (Cortes, 1995).

Demographic analysis of *R. taylori* is sensitive to the way age-specific reproductive rate is calculated because of this species's short lifespan. Whether age-specific natality is calculated on the basis of the proportion of a population surviving at the beginning or the end of an age class leads to a very large difference in *r*. This effect is magnified by the high natural mortality of *R. taylori*. It is therefore important to take account of gestation period in the calculation of reproductive rate. This is less important in longer lived species in which natural mortality is lower and in which there is a relatively small difference between the proportions of a population surviving until the beginning and the end of an age class.

This study indicates that accurate age data are required for demographic analysis. The results for *R. taylori* showed a high level of sensitivity to changes in age at maturity, but only limited sensitivity to changes in maximum age. Given that the age data on which this research were based have not been validated, there remains some uncertainty about the results. Further work to validate these data (especially age at maturity) would decrease uncertainty. However, the length-frequency data supplied by Simpfendorfer (1993) support the hypothesis that *R. taylori* mature at age one and produce their first litter at age two.

Increasing age at first capture for *R. taylori* increased the level of fishing mortality that the population could sustain. Allowing individuals to remain unfished until they had produced one litter (AAFC=2) made fishing mortality levels up to 0.67 sustainable, whereas any level of fishing mortality was sustainable if individuals were allowed to produce two litters (AAFC=3). In a practical sense, AAFC restrictions are implemented as size restrictions. On the basis of the growth curves given by Simpfendorfer (1993), size of female *R. taylori* at the end of each of the first three years is 55, 67, and 71 cm total length (TL), respectively. The fact that size changes only slightly after the first two years makes the use of age restrictions unworkable for older individuals.

The gillnet fishery in which *R. taylori* is most often captured in northern Australian waters uses mesh sizes no smaller than 10 cm (stretched mesh). Gill nets of this size rarely catch animals less than 60 cm TL. The age at first capture in this fishery is therefore approximately one year. Although *R. taylori* less than one year of age are caught by trawlers, this fact was noted by the author only once in observations of research trawls between 1986 and 1992 in the Townsville region. On the basis that age at first capture of *R. taylori* in northern Australia is probably one year, demographic analysis indicates that the level of fishing mortality (F_c) that the population can sustain is approximately 0.27. However, Ricker (1975) showed that the level of fishing mortality needed to achieve maximum sustainable yield (MSY) is $r/2$. Thus for *R. taylori* $F_{\text{MSY}} = 0.135$.

Sustainability of fisheries

The comparison of demographic assessments of short-lived, fast growing, early maturing elasmobranch species such as *R. taylori* and *S. tiburo,* to those of longer-lived, slow growing, late maturing species indicates that they are likely to be able to sustain higher levels of fishing pressure than the latter species. For example, Sminkey and Musick (1996) reported that *Carcharhinus plumbeus* was most likely to be sustainable when $F_c \leq 0.1$, or $F_c = 0.25$ if a minimum size of 178 cm was used. Similarly, Cailliet (1992) reported that for *Triakis semifasciata*, $F_c = 0.084$ did not reduce the population, but that fishing mortality at double this level was sustainable only if animals 12 years and older were caught. This contrasts markedly with the results for *R. taylori* that the population may be sustainable at F_c=0.18, or F_c = 0.27 if age at first capture was one year. It is therefore possible that at least some species of elasmobranchs, in particular the shorter-lived, fast growing, early maturing species, are able to sustain limited commercial levels of fishing pressure. The apprehensive conclusion of Holden (1974) regarding sustainable fishing of elasmobranch stocks may need to be revised for selected species. However, the real challenge is to manage the development and regulation of such elasmobranch fisheries effectively.

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