Reviews in Fisheries Science, 8(4): 299–344 (2000)

Life History Patterns and Correlations in Sharks

Enric Cortés
Southeast Fisheries Science Center, National Marine Fisheries Service, 3500 Delwood Beach Road, Panama City, FL 32408

ABSTRACT: This study examines life history patterns and correlations between traits related to body size, reproduction, age, and growth in sharks, using data from 230 populations representing 164 species, 19 families, and 7 orders. The analysis focused on interspecific life history variability, but intraspecific and intrapopulation variation were also considered. Interspecifically, body size correlated positively with litter size and offspring size, and a trade-off between litter size and offspring size was found after factoring out the effects of body size. Offspring size correlated negatively with growth completion rate (K), but the correlation became positive after correcting for the effects of body size. Parental size for males and females was negatively correlated with K. Parental size and size at maturity exhibited a strong positive correlation, with sexual maturity occurring at about 75% of maximum size in both sexes. Males were 10% smaller than females and reached their maximum length 34% faster than females on average. Females tend to mature later and live longer than males, but age at maturity is reached at about 50% of maximum age in both sexes. Maximum size and empirical longevity were not significantly correlated in females, but were positively correlated in males. Size and age at maturity also exhibited a moderate positive correlation in males, especially after excluding data for *Squalus acanthias*. Principal component and cluster analyses were used to reflect similarities among life history traits of 40 populations from 34 species, and at least three separate life history strategies were identified.

KEY WORDS: life history correlations, sharks, life history strategies, growth, longevity.

I. INTRODUCTION

Throughout their evolutionary history during at least 400 million years, the cartilaginous fishes (Chondrichthyes) in general, and sharks (Selachii) in particular, have remained major components of marine communities, having the ability to adapt to varying selective pressures. Indeed, selachians are a successful and speciose group comprising about 394 extant species in eight orders (Compagno, 1999) that have adopted alternative life history styles and exploited diverse niches in the aquatic environment (Compagno, 1990).

It is commonly accepted that shark life history patterns are characterized by slow growth, long life, large adult size, late sexual maturity and reproduction, long gestation period, reduced fecundity, iteroparity, and precocial offspring. All sharks employ internal fertilization and viviparity is the predominant reproductive strategy

1064-1262/00/$.50
©2000 by CRC Press LLC

in extant species. In addition, reproductive constraints seem to dictate a direct relationship between population size and recruitment (Holden, 1972, 1977). Despite these apparently restrictive life history traits, sharks have remained successful predators in the marine ecosystem, as evidenced by their ecological diversity and abundance (Compagno, 1990).

Although the diversity of life history strategies in sharks has been qualitatively well documented (Compagno, 1990) and some general trends identified (Branstetter, 1990; Hoenig and Gruber, 1990; Pratt and Casey, 1990), very little quantitative information on life history patterns and correlations between traits is available, especially at the intraspecific and intrapopulation level. Furthermore, knowledge and understanding of life history trade-offs in selachians is still very limited, owing to the paucity of basic biological information for numerous species. This is unfortunate because a better understanding of life history patterns and trade-offs in this group would be advantageous for comparative studies of vertebrate life history evolution and would help shed light on connections between life histories and natural selection in this group.

Moreover, increased human exploitation over the last 2 decades and increasing habitat deterioration and loss pose immediate threats to shark populations worldwide. A better understanding of their life histories and the way in which life history traits covary would be very beneficial for developing demographic and other population dynamics models that require knowledge of key life history features and thus would aid in the conservation and management of this group.

The goal of this study is to quantify life history patterns in sharks and examine potential correlations between traits related to body size, reproduction, age, and growth. The analysis focuses on interspecific variability but also examines limited data on intraspecific and intrapopulation variation in some life history traits of sharks.

II. MATERIALS AND METHODS

A. DATA COLLECTION AND REPORTING

I reviewed the literature and opted to include only studies that clearly identified how estimates of life history parameters had been derived. Although some valuable biological information may have been overlooked, questionable data subject to multiple sources of variability that could thus potentially confound the analysis of quantitative relationships were eliminated.

For each species or population, up to seven life history parameter estimates were extracted when available and included in the analyses (Appendix). Different studies sometimes used alternative criteria to define life history traits and so a compromise had to be reached at times. Parental size is expressed as the maximum total length (TL) in centimeters reported for females, males, or sexes combined. When possible, litter size is reported as an average measure of the population- or species-specific number of pups—generally the mean—and as a range. I used the total length (in centimeters) of offspring at birth as a measure of offspring size because offspring weight is seldom reported in the literature. Size at maturity is

generally the size at which maturity is first reached, in some cases the size at which 50% of individuals are mature, or an average measure or range reported in the original study.

I used K (yr^{-1}), the growth completion rate or growth constant from the von Bertalanffy equation (von Bertalanffy, 1938), traditionally utilized to describe age and growth in sharks and other animal and plant species (Roff, 1992), as a calculated life history trait related to growth. Age at maturity is the value reported in each study, which is seldom measured directly, but rather obtained after transforming size into age through the von Bertalanffy growth equation. Empirical longevity is the value of the oldest shark aged in each study using vertebrae or dorsal spines, or a value obtained through mark-recapture techniques or observations of animals held in captivity. Theoretical longevity was calculated as the age at which 95% of parameter L_∞ (asymptotic length) from the von Bertalanffy equation is reached (Fabens, 1965; Cailliet *et al.*, 1992).

B. DATA ANALYSIS

For the analysis of life history patterns, medians are reported to account for non normality of the data and asymmetrical confidence intervals were calculated as the 2.5th and 97.5th percentiles to encompass the central 95% of each parameter distribution. At the species level, the effect of body size on correlations involving offspring size was factored out by expressing offspring size as a percentage of parental size. The Pearson correlation coefficient (r) was used to analyze correlations between pairs of life history traits, and in some cases the Y-axis was log-transformed to linearize the relationship.

To analyze similarities among species, I applied a principal component analysis (PCA) of five life history traits (adult female body size, offspring size, maximum litter size, K, and empirical longevity) only to species for which all five traits were available to eliminate cases with missing values. The scores of the first three components of the PCA were then used in a cluster analysis to examine further similarities among species. The distance metric used was 1-r (Systat for Windows, ver. 5 ed., Evanston, IL: Systat, Inc., 1992, unpublished). Using the scores from the PCA eliminated covariation between variables before clustering (Van Buskirk and Crowder, 1994), and using Pearson coefficients standardized the data to a common scale, thus giving all variables comparable influence in the analysis.

III. RESULTS

A. GENERAL LIFE HISTORY PATTERNS AND CORRELATIONS

Values of life history traits were obtained for 230 populations representing 164 species, 19 families, and 7 orders (Appendix). Life history traits exhibit remarkable diversity, and, as in other taxa, this variation is more pronounced at the interspecific level but can also be observed intraspecifically. Adult size, litter size, offspring size, age and size at maturity, growth completion rate, and longevity vary widely among species, yet some trends are apparent.

At the species level, correlations indicate that several reproductive life history traits vary with body size. I found a moderate but highly significant positive correlation between maximum maternal size and maximum litter size (r = 0.50, P < 0.0001, n = 170; Figure 1A), and between maximum maternal size and offspring size (r = 0.80, P < 0.0001, n = 155; Figure 1B). I found no significant correlation between offspring length and log-transformed maximum or mean litter size (r = 0.13, P = 0.101, n = 151 and r = 0.16, P = 0.86, n = 117, respectively; Figure 2A), but after factoring out the effects of body size there was a highly significant negative correlation between log-transformed maximum or mean litter size and offspring size (r = –0.62, P < 0.0001, n = 142 and r = -0.51, P < 0.0001, n = 109, respectively; Figure 2B). Offspring are born on average at approximately 1/4 of the maximum adult size. Offspring size expressed as a percentage of maternal size ranges from 3% in the whale shark, *Rhincodon typus*, to 49% in the carcharhinid *Loxodon macrorhinus*, and averages 27% (13 to 43% CL, n = 164) in the species analyzed.

Traits related to growth also appear to vary with body size. There was a moderate, almost significant, decreasing relationship between offspring size and K for sexes combined (r = –0.36, P = 0.061, n = 28; Figure 3A), but this relationship became positive (r = 0.28, P = 0.161, n = 27; Figure 3B), but still non-significant, when offspring size was expressed as a percentage of maximum adult size. K and log-transformed maximum parental size were significantly, negatively correlated in females (r = –0.32, P = 0.045, n = 39; Figure 4) and males (r = –0.33, P = 0.045, n = 37; Figure 4).

There are differences between males and females in traits related to body size and growth. Males reach their maximum length faster than females as indicated by generally higher K values in males: 34% (median expressed as a percentage of female K-values) faster (–15 to 239% CL, n = 45). In only nine of 45 cases (20%) was the K value for males lower than that for females. Females are generally larger than males. Maximum size in males was 10% (median expressed as a percentage of female maximum size) smaller (-27 to 12% CL, n = 178) than in females, and in only 21 of 178 cases (12%) did males reach a larger size than females. Maximum parental size was strongly, positively correlated with size at maturity in both females (r = 0.97, P < 0.0001, n = 169) and males (r = 0.98, P < 0.0001, n = 152). The ratio of length at maturity to maximum length (expressed as a percentage) was remarkably similar in males (median = 76.2%, 53 to 89% CL, n = 148) and females (median = 75.5%, 50 to 91% CL, n = 178). In absolute terms, males generally mature at a smaller size than females (median = –8%, –28 to 7% CL, n = 162), and in only 23 of 162 cases (14%) did males mature at a larger size than females.

Traits related to age also differ between male and female sharks. Females tend to live longer than males. Empirical longevities for females ranged from 4.5+ years in *Carcharhinus acronotus* to 81 years in *Squalus acanthias* and averaged (median) 16 years (5 to 60 CL, n = 57). Expected theoretical longevities in females averaged 28 yr (9.5 to 95 CL, n = 48). In males, empirical longevities averaged 12 years (5 to 40 CL, n = 52), and theoretical longevities averaged 22 years (3 to 86 CL, n = 48). Empirical longevities were shorter than theoretical longevities in almost all cases. Maximum size was not correlated with log-transformed empirical longevity in females (r = 0.17, P = 0.264, n = 44; Figure 5), but after eliminating data for *S. acanthias*, a long-lived species that only grows to slightly over 1 m TL, the correlation became almost significant (r = 0.28, P = 0.067, n = 42; Figure 5).

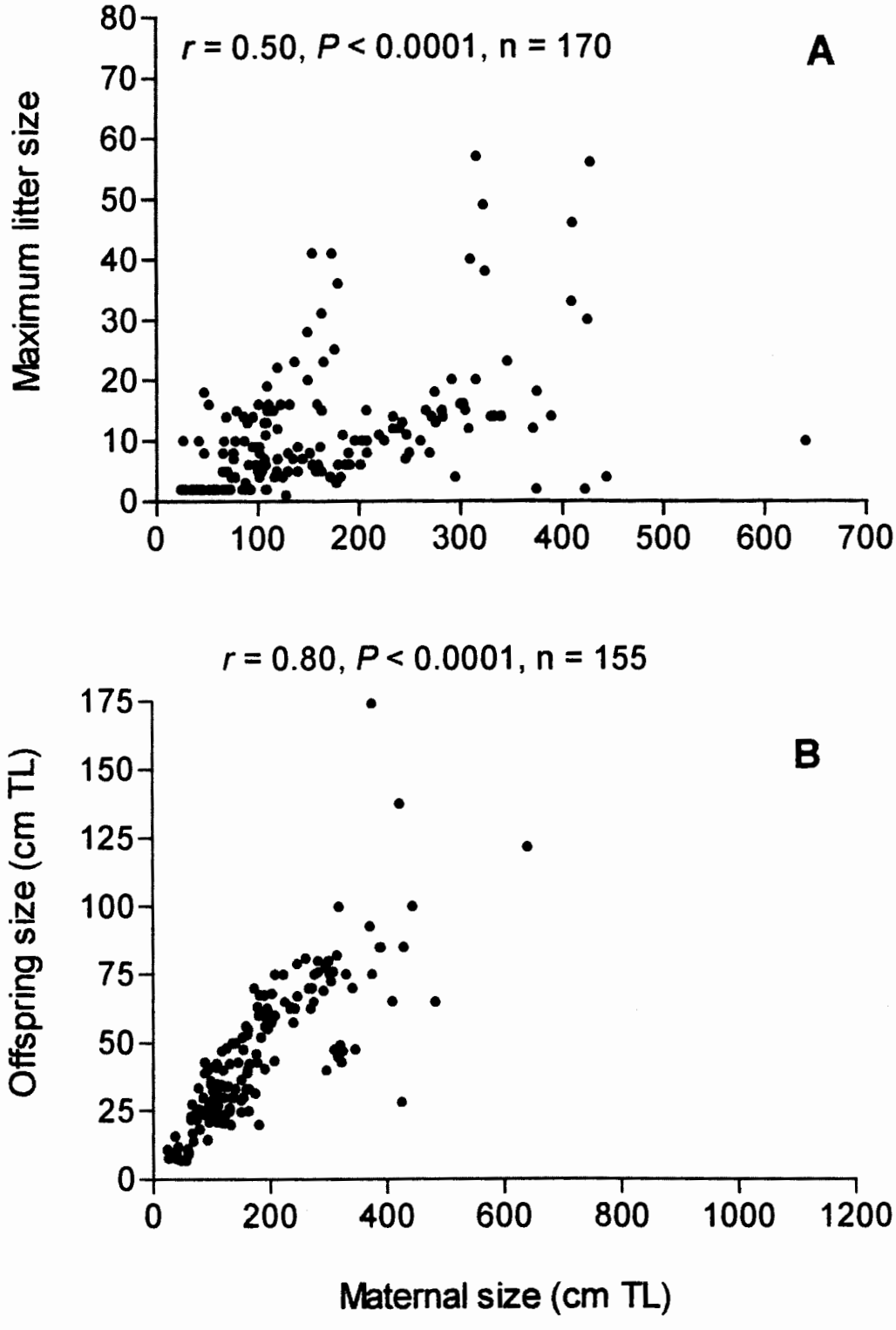

FIGURE 1. Maximum litter size (A) and offspring size (B) in relation to maternal size in sharks.

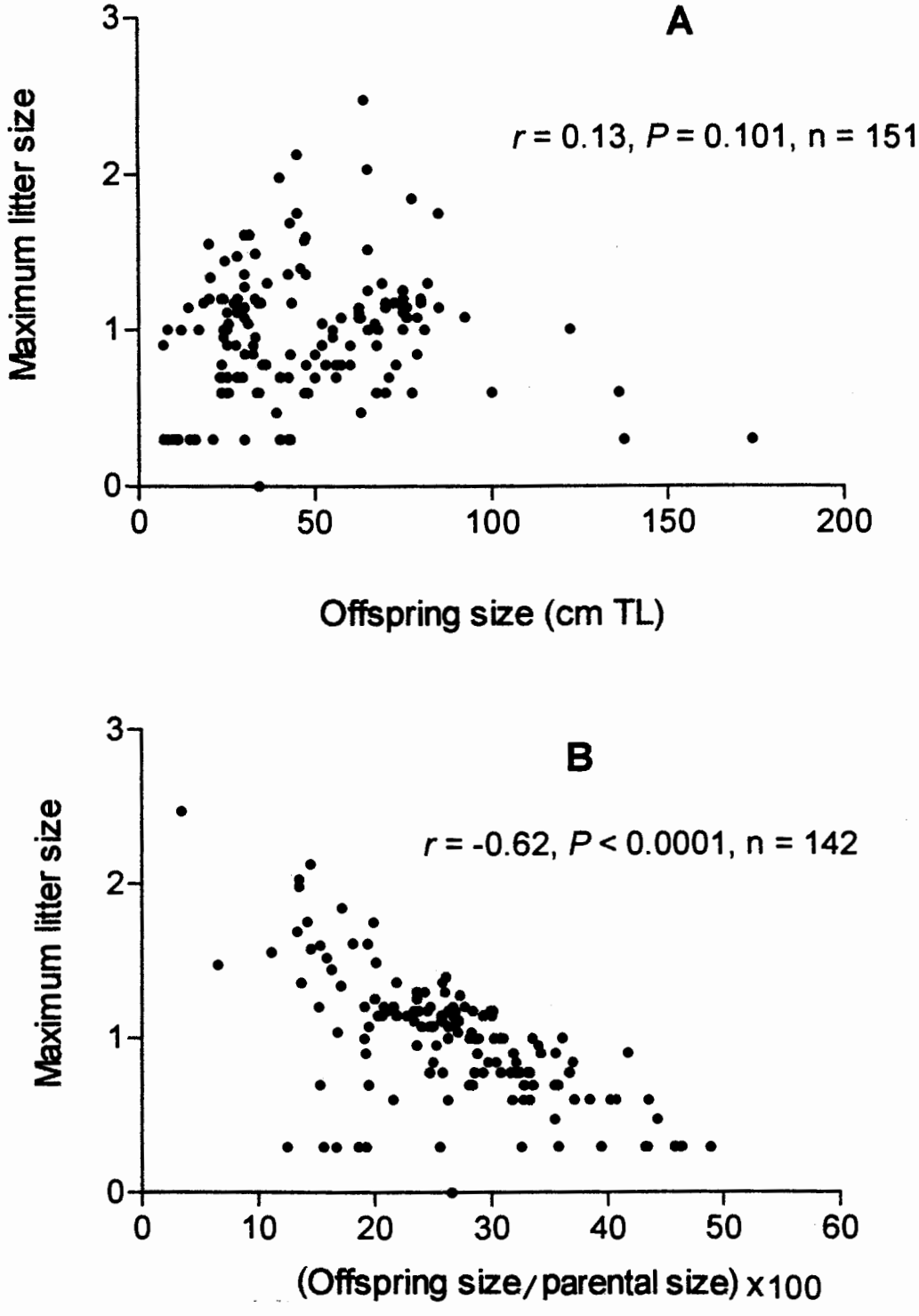

FIGURE 2. Semi-log plot of maximum litter size in relation to offspring size (A) and to offspring size expressed as a percentage of parental size (B).

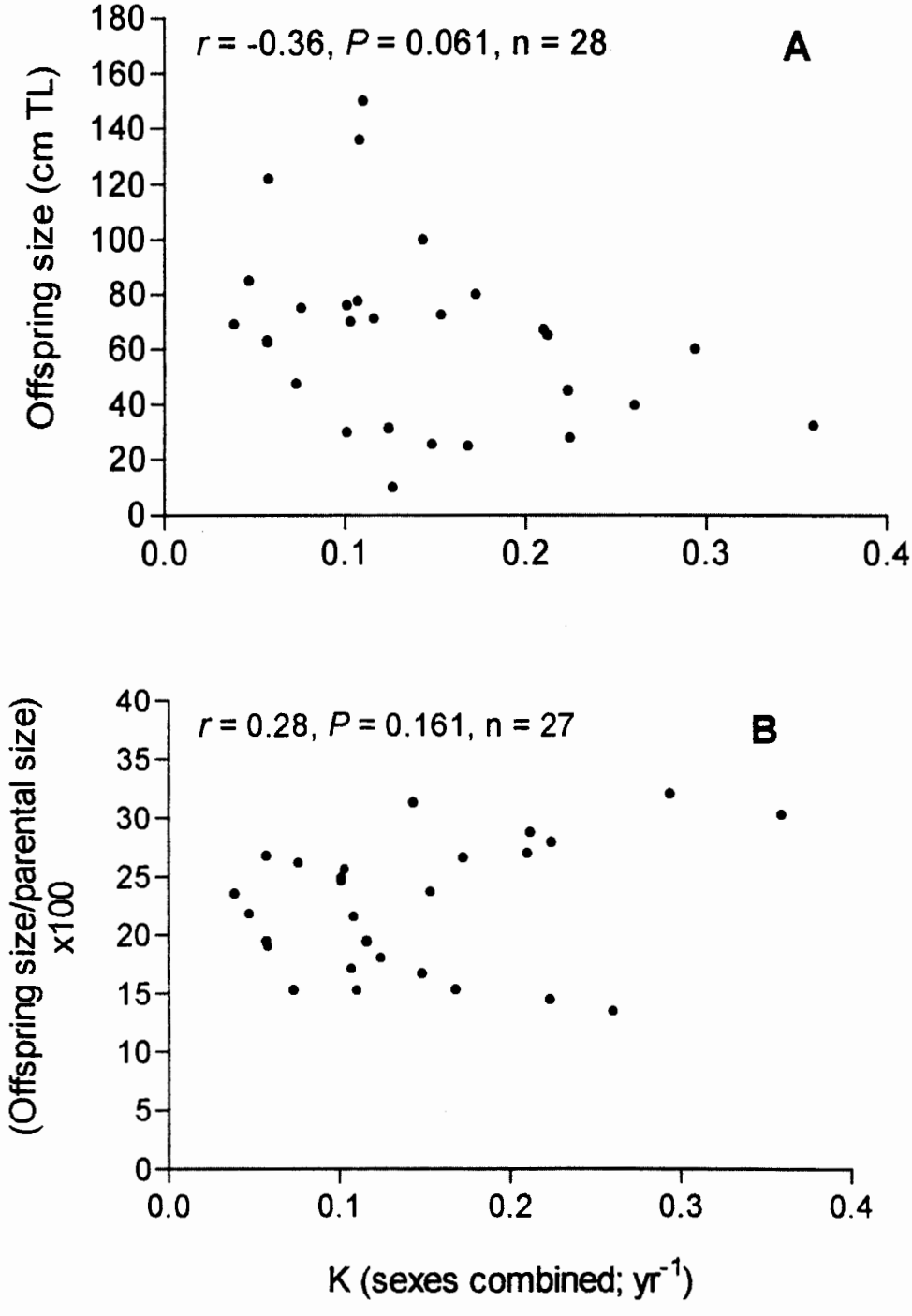

FIGURE 3. Relationship between growth completion rate (K) from the von Bertalanffy growth function and offspring size (A) and offspring size expressed as a percentage of parental size (B).

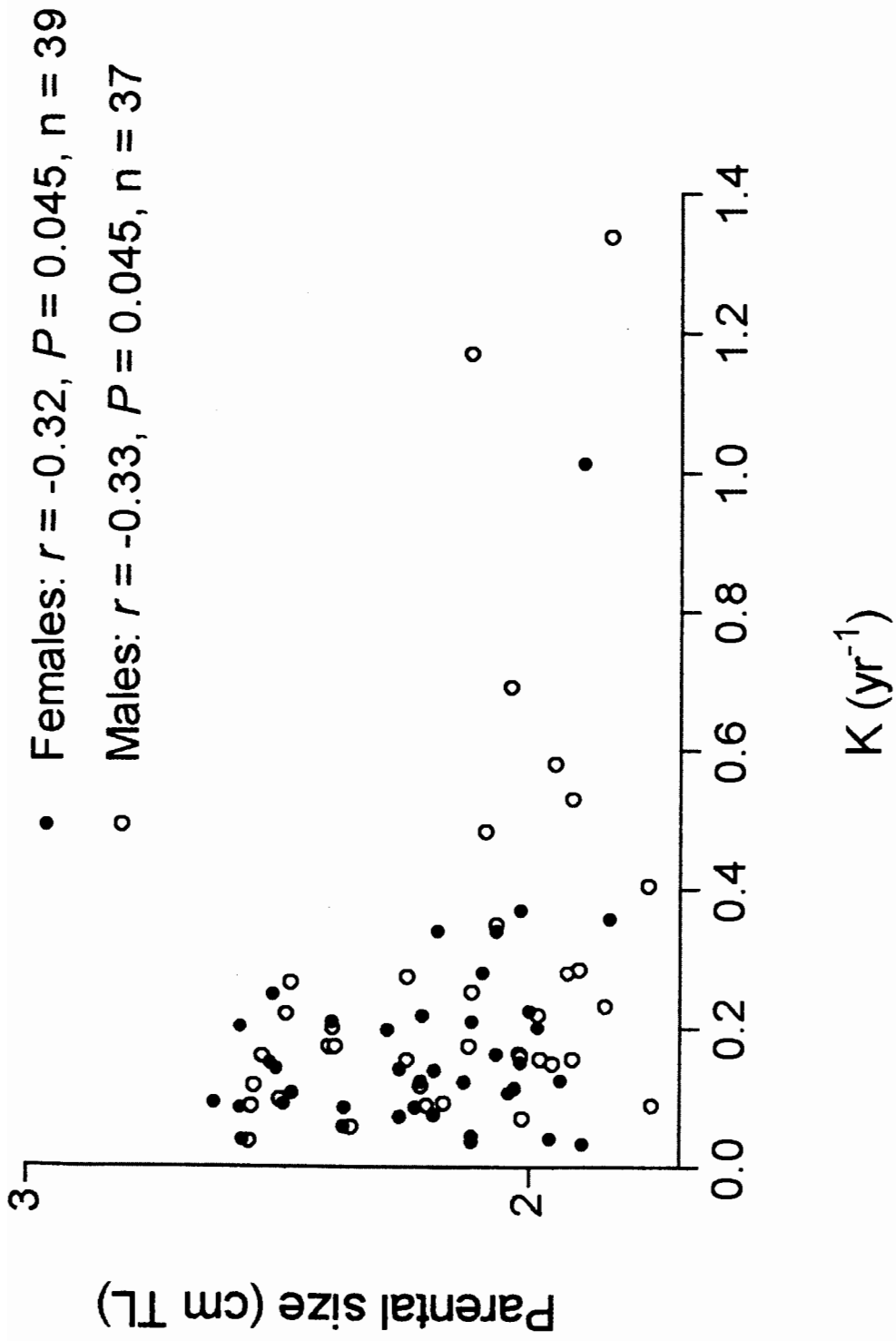

FIGURE 4. Semi-log plot of K and parental size for males and females.

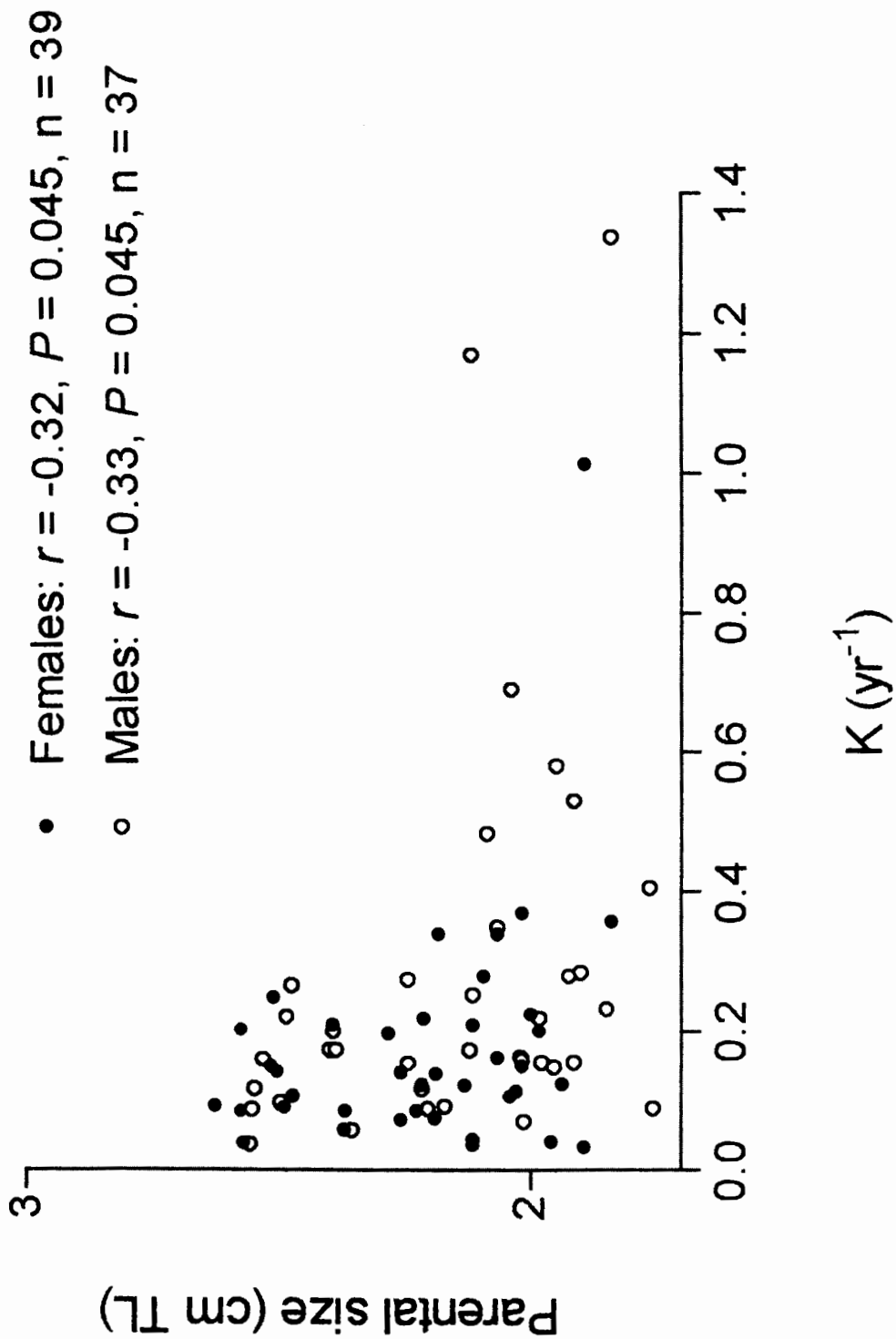

FIGURE 4. Semi-log plot of K and parental size for males and females.

Maximum size was significantly correlated with log-transformed empirical longevity in males (r = 0.40, P = 0.012, n = 38; Figure 5), especially after eliminating data for *S. acanthias* (r = 0.47, P = 0.0036, n = 37; Figure 5). Maximum size and log-transformed theoretical longevity were not correlated in females (r = 0.22, P = 0.177, n = 39) but were correlated in males (r = 0.48, P = 0.003, n = 37).

Males also tend to mature earlier than females. On average (median value), males mature at 6 years (1.4 to 19 CL, n = 59) and females at 8 years (2 to 25 CL, n = 68) of age. Size at maturity was not correlated with log-transformed age at maturity in females (r = 0.21, P = 0.105, n = 60; Figure 6), but after excluding data for *S. acanthias* the correlation became significant (r = 0.34, P = 0.011, n = 55). Size at maturity and log-transformed age at maturity were correlated (r = 0.45, P = 0.001, n = 51; Figure 6) in males, especially after excluding data for *S. acanthias* (r = 0.54, P = 0.0001, n = 47).

Age at maturity is reached at about 50% of maximum age in both males and females. The ratio of age at maturity to empirical maximum age (expressed as a percentage) was very similar in males (median = 47.6%, 17 to 81% CL, n = 42) and females (median = 53.8%, 20 to 80% CL, n = 49).

Longer-lived species tend to complete their growth at a slower rate than their shorter-lived counterparts. There was a highly significant negative correlation between K and log-transformed empirical longevity in both females (r = –0.53, P = 0.0005, n = 40; Figure 7) and males (r = –0.57, P = 0.0002, n = 39; Figure 7).

Additional nonsignificant correlations between life history traits are presented in Table 1. There was no significant correlation between litter size and log-transformed longevity, litter size and log-transformed K for females, or between offspring size and log-transformed longevity.

B. SIMILARITIES AMONG LIFE HISTORY TRAITS

A PCA of five life history traits for 40 populations from 34 species revealed that three factors explained about 88% of the variance (Table 2). The first factor explained 41% of the variance in the five variables and correlated positively with adult body size and offspring size, and negatively with K. The second and third factors explained 27 and 20% of the variance, respectively. The second factor mainly correlated negatively with empirical longevity and positively with K, whereas the third factor correlated mainly positively with litter size. The first and second factors help to clearly separate *Rhizoprionodon taylori* from other species because of its small size and offspring, rapid growth (high K), and low longevity (Figure 8A). Large species with large offspring but moderate longevity, such as the lamniforms *Alopias vulpinus, A. superciliosus, A. pelagicus,* and *Carcharodon carcharias* fall toward the upper-right portion of the graph, whereas small but slow-growing and long-lived species, such as *S. acanthias* and *Galeorhinus galeus* are set apart on the bottom-left portion of the graph. Figure 8A also shows some grouping of species that share similar life history traits or close taxonomic position. For example, *Rhizoprionodon terraenovae, Sphyrna tiburo,* and *Carcharhinus sorrah* are all small carcharhiniform sharks characterized by small offspring, rapid growth, and low longevity, and *Carcharhinus limbatus, Carcharhinus brevipinna, C. acronotus,* and *Carcharhinus tilstoni* all share moderate size, growth, and

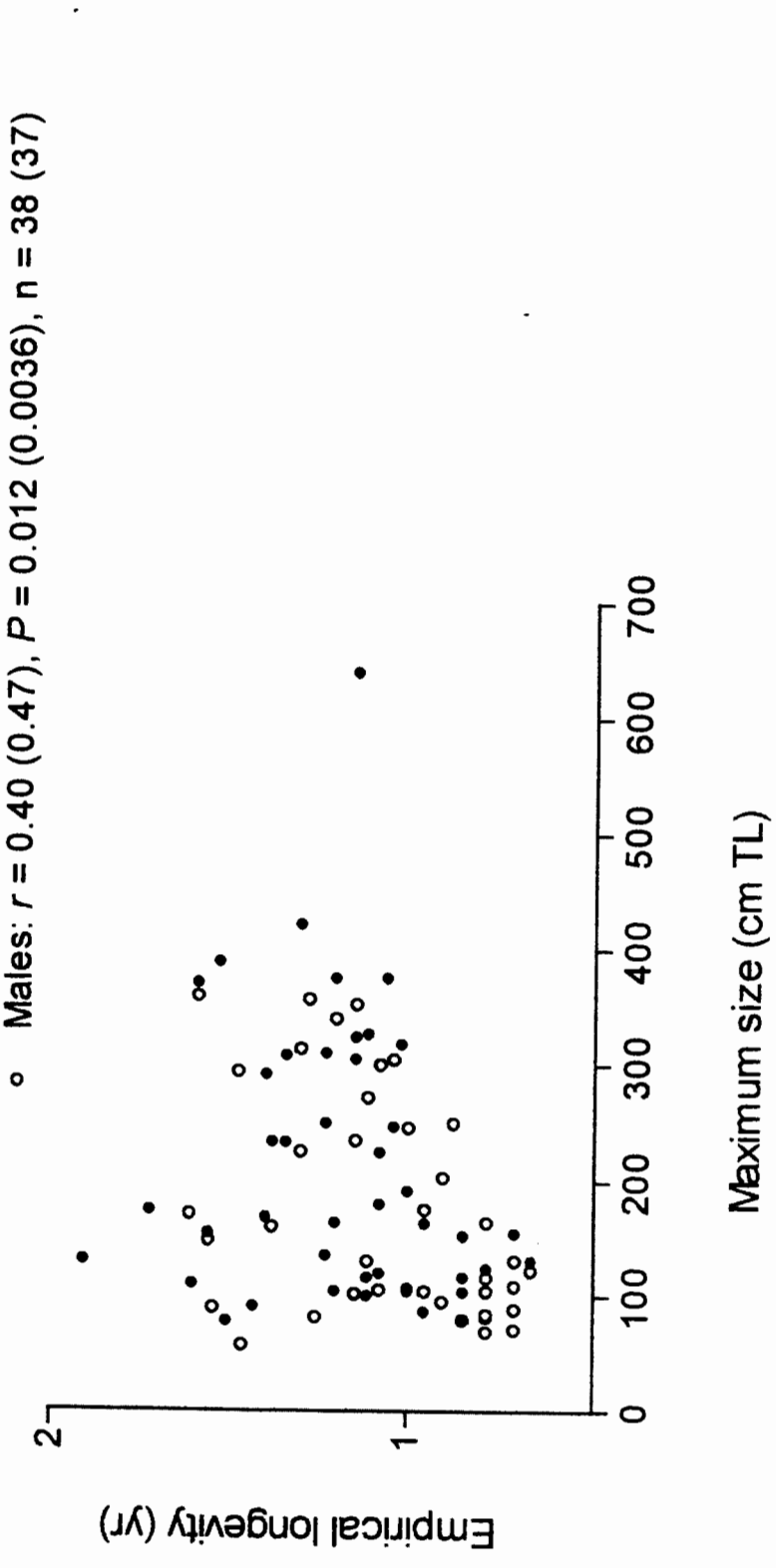

FIGURE 5. Semi-log plot of maximum size in relation to lifespan. Numbers in parentheses refer to the correlation after eliminating data for *Squalus acanthias*.

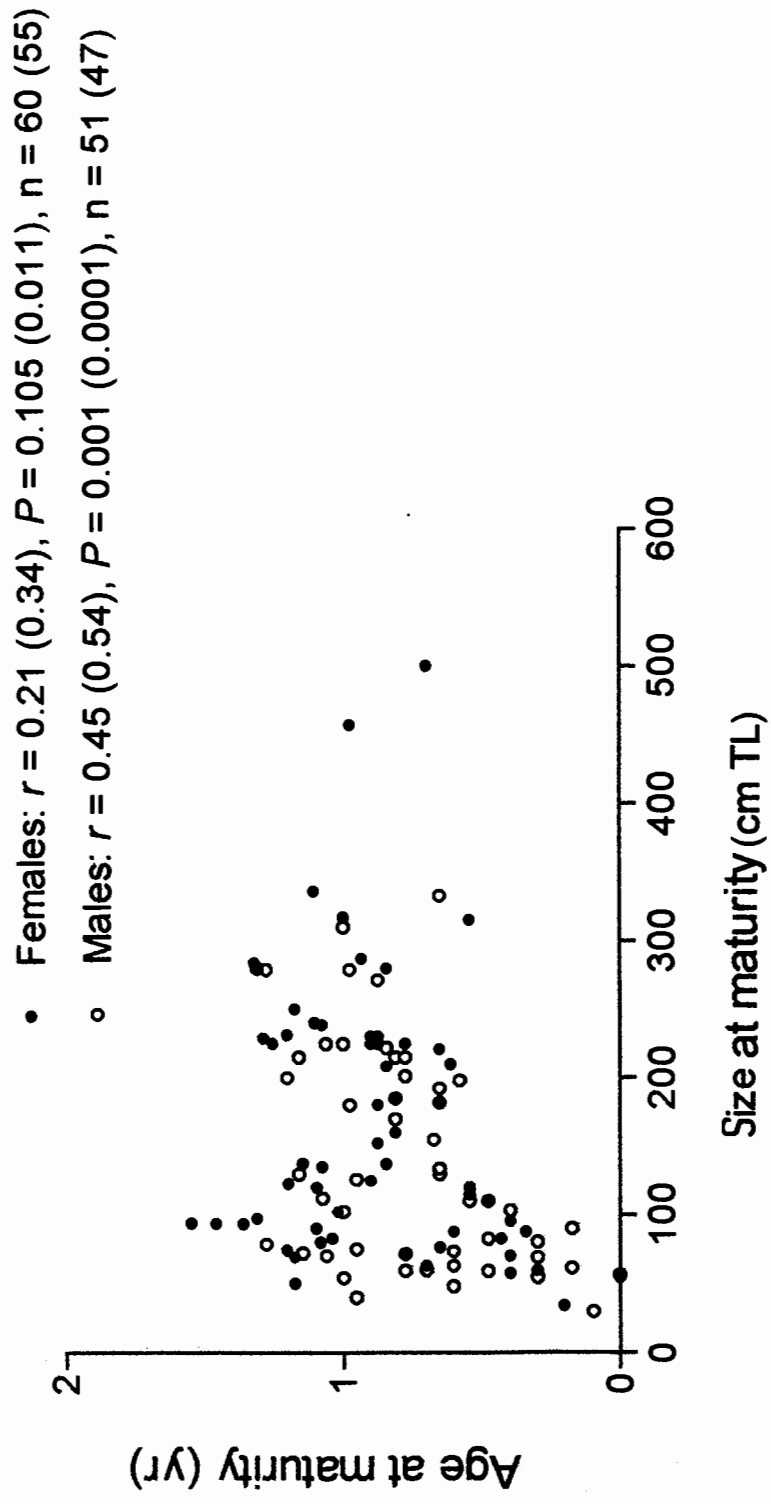

FIGURE 6. Semi-log plot size at maturity against age at maturity. Numbers in parentheses refer to the correlation after eliminating data for *Squalus acanthias*.

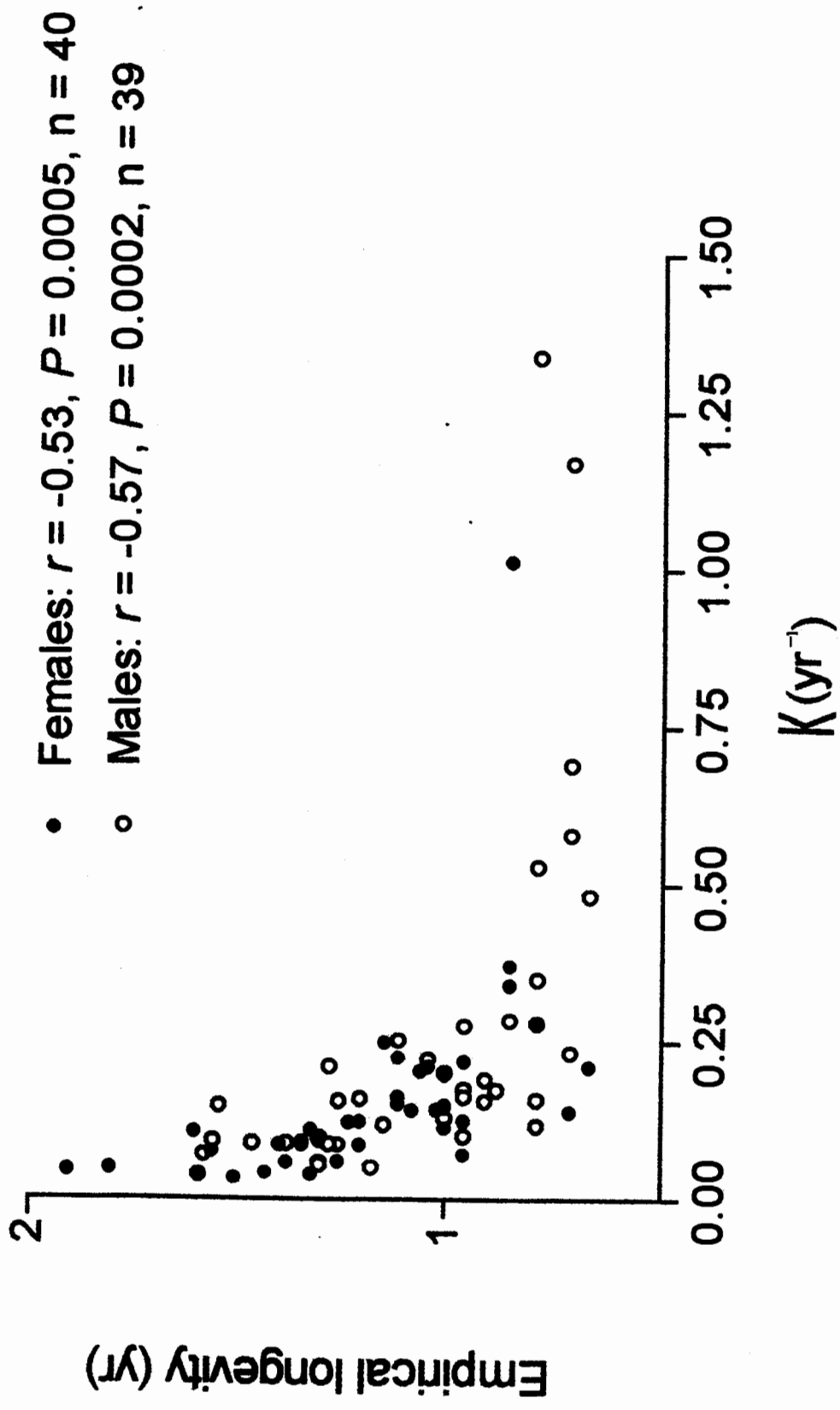

FIGURE 7. Semi-log plot of K and lifespan for males and females.

TABLE 1

Correlations between Life History Traits of Sharks at the Species Level[a]

	Body size	Litter size	Offspring size	K			Longevity	
				Males	Females	Combined	Males	Females
Body size	X	0.50 < 0.0001 170	0.80 < 0.0001 155	–0.33[b] 0.045 37	–0.32[b] 0.045 39	–0.59[b] 0.002 25	0.40[c] 0.012 38	0.17[c] 0.264 44
Litter size	—	X	0.13[b] 0.101 151	—	0.07[c] 0.674 34	—	—	0.26[c] 0.107 41
Offspring size	—	–0.62[c] < 0.0001 142	X	—	—	–0.36 0.061 28	—	0.13[c] 0.427 39
K	—	—	0.28[d] 0.161 27	—	X	—	–0.57[c] 0.0002 39	–0.53[c] 0.0005 40
Longevity (females)	—	—	–0.26[b] 0.116 37	—	—	—	—	X

[a] *The upper-right side of the table shows correlations between traits uncorrected for body size and the lower-left side shows correlations between those same traits after correcting for the effect of body size. From top to bottom, each line gives the Pearson correlation coefficient, P-value, and sample size. Litter size and longevity are maximum litter size and empirical longevity, respectively.*

[b] *Life-history trait in row is log-transformed.*

[c] *Life-history trait in column is log-transformed.*

[d] *K is for sexes combined.*

TABLE 2

Results of a Principal Component Analsis of Five Life History Traits of 40 Populations from 34 Species of Sharks[a]

Life history trait	Factor (1)	Factor (2)	Factor (3)
Adult body size	0.90	0.19	0.28
Offspring size	0.89	0.35	–0.04
K	–0.64	0.56	0.11
Longevity	0.19	–0.84	–0.31
Litter size	–0.10	–0.40	0.91
Percent of total variance	41.3%	26.6%	20.2%

[a] *Shown are the component loadings of the first three factors and the percent of the total variance explained by each factor.*

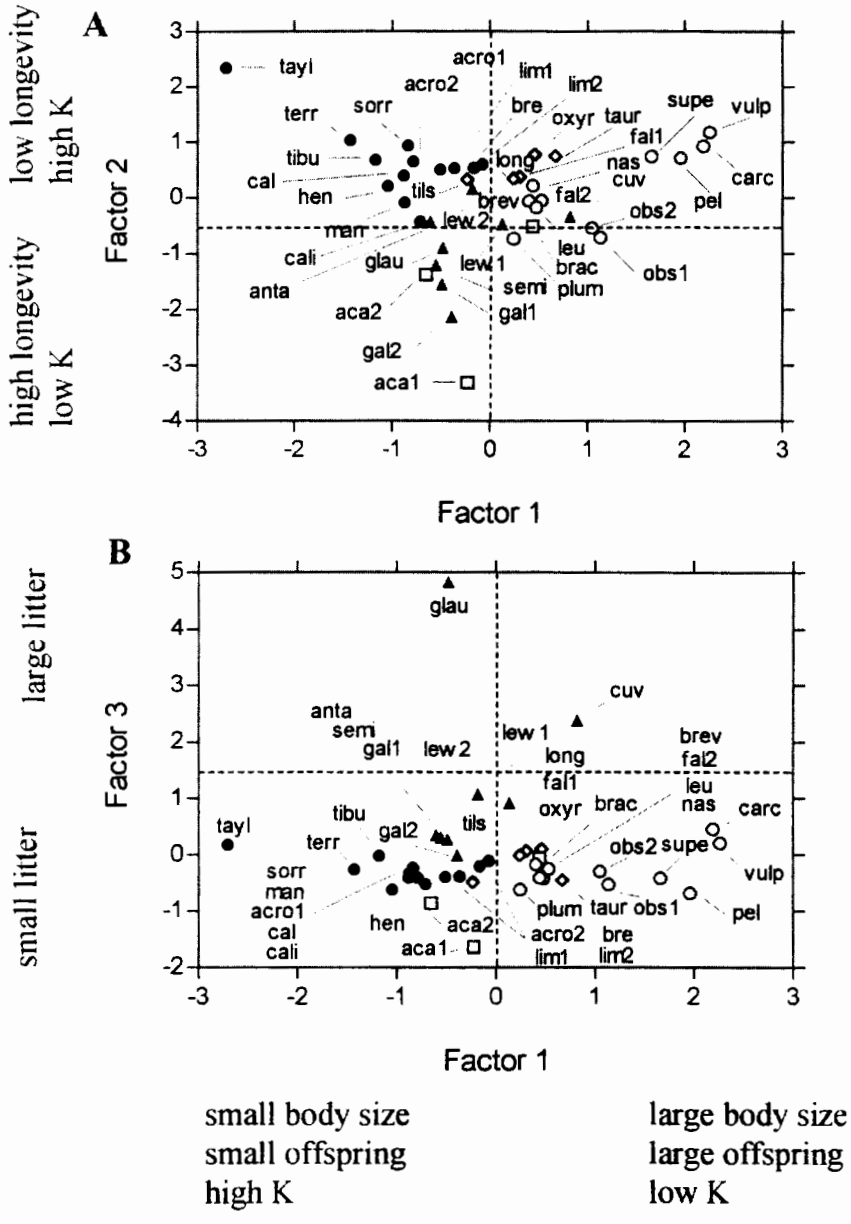

FIGURE 8. Plots of the component scores from a principal component analysis of five life history traits of 40 populations from 34 species of sharks. (A) shows the position of the 40 populations in relation to the first two factors and (B) in relation to the first and third factors. Species and populations codes are as follows (see text for meaning of symbols and appendix for an explanation of the geographic codes): aca1 = *Squalus acanthias* (NEP), aca2 = S. *acanthias* (NWA), acro1 = *Carcharhinus acronotus* (NWA), acro2 = *C. acronotus* (EGM), anta = *Mustelus antarcticus* (SEI/SWP), brac = *Carcharhinus brachyurus* (SWI), bre = *Carcharhinus brevipinna* (NWGM), brev = *Negaprion brevirostris* (GM/NWA), cal = *Mustelus californicus* (NEP), cali = *Squatina californica* (NEP), carc = *Carcharodon carcharias* (NWA), cuv = *Galeocerdo cuvier* (NWA), fall = *Carcharhinus falciformis* (NWGM), fal2 = *C. falciformis* (SGM), gal1 = *Galeorhinus galeus* (SWA), gal2 = *G. galeus* (SWP), glau = *Prionace glauca* (NEP), hen1 = *Mustelus henlei* (NEP), leu = *Carcharhinus leucas* (NGM), lew1 = *Sphyrna lewini* (NWGM), lew2 = *S. lewini* (WP), lim1 = *Carcharhinus limbatus* (EGM), lim2 = *C. limbatus* (SWI), long = *Carcharhinus longimanus* (CP/WP), man = *Mustelus manazo* (NWP), nas = *Lamma nasus* (NWA), obs1 = *Carcharhinus obscurus* (NWA), obs2 = *C. obscurus* (SWI), oxyr = *Isurus oxyrinchus* (NWA), pel = *Alopias pelagicus* (NWP), plum = *Carcharhinus plumbeus* (NWA), semi = *Triakis semifasciata* (NEP), sorr = *Carcharias taurus* (NWA), tayl = *Rhizoprionodon taylori* (SWP), terr = *R. terraenovae* (GM), tibu = *Sphyrna tiburo* (GM), tils = *Carcharhinus tilstoni* (SWP), vulp = *Alopias vulpinus* (NEP).

longevity, and a close taxonomic position. The third factor mainly helps clearly separate species with large litters, such as *Prionace glauca, Galeocerdo cuvier,* and *Sphyrna lewini* (Figure 8B).

A cluster analysis of the scores of the first three factors of the PCA further helps elucidate similarities among life history traits of the 40 populations analyzed (Figure 9). Three species, *Triakis semifasciata, G. cuvier*, and *S. lewini* from the northwestern Gulf of Mexico, form a cluster characterized by large litter sizes and in some cases similar adult size, offspring size, or growth completion rate (K), features that they share with the two populations of *G. galeus*. Interestingly, *Mustelus antarcticus* is set apart from the other *Mustelus* species and is in this same cluster with *S. lewini* from the western Pacific (Hawaiian Islands) and *P. glauca*, probably because of similar empirical longevities and high litter sizes.

The two populations of *Carcharhinus obscurus* and *Carcharhinus plumbeus* stand apart based mostly on their slow growth, high longevity, and similar litter sizes. These species form another cluster with a number of large species also characterized by large offspring, slow growth, high longevity, and similar litter sizes. Interestingly, *C. carcharias* is not as close to other lamniforms in the dendrogram as would be expected from taxonomy. *Carcharodon carcharias* is grouped with *Negaprion brevirostris*, *Carcharhinus falciformis* from the southern Gulf of Mexico, and *Carcharhinus leucas* according to the present analysis. In contrast, the three alopiids, *A. vulpinus*, *A. pelagicus*, and *A. superciliosus*, are grouped together based mostly on large offspring and adult sizes, very small litter sizes, and very similar growth rates. *Lamna nasus* also shares similar longevity, low litter size, and moderate growth rate with the three *Alopias* species.

Another main cluster is formed by species of small and moderate size. The two populations of *C. limbatus* and *C. brevipinna* are characterized by moderate body and offspring size, and moderate growth rate and longevity. The northwestern Atlantic population of *C. acronotus* is closer to the three populations above than the Gulf of Mexico population, probably because of slightly larger body and offspring size in the former. The Gulf of Mexico population of *C. acronotus* is closer to the smaller triakids *Mustelus henlei* and *Mustelus californicus*, and the carcharhinid *C. sorrah*, probably owing to similar litter sizes and slightly higher growth rates. These species in turn form another cluster with the small, fast-growing, and short-lived carcharhiniforms *R. terraenovae*, *R. taylori*, *S. tiburo*, and *Mustelus manazo*. Included in that cluster is the squatinid *Squatina californica*, probably because of similar litter and offspring sizes.

A group of five large-size carcharhiniform and lamniform species is closer to the cluster of small- and moderate-sized species than to the group of large-sized carcharhiniforms and lamniforms identified previously. *Carcharias taurus*, *C. falciformis* from the northwestern Gulf of Mexico, *Carcharhinus longimanus*, *Isurus oxyrinchus*, and *C. tilstoni* form a cluster of their own, based mostly on similar longevity, and growth rate and offspring size to a lesser extent. Finally, the two populations of *S. acanthias* and *Carcharhinus brachyurus* are grouped together owing to their high longevity, slow growth rate, and similar litter sizes.

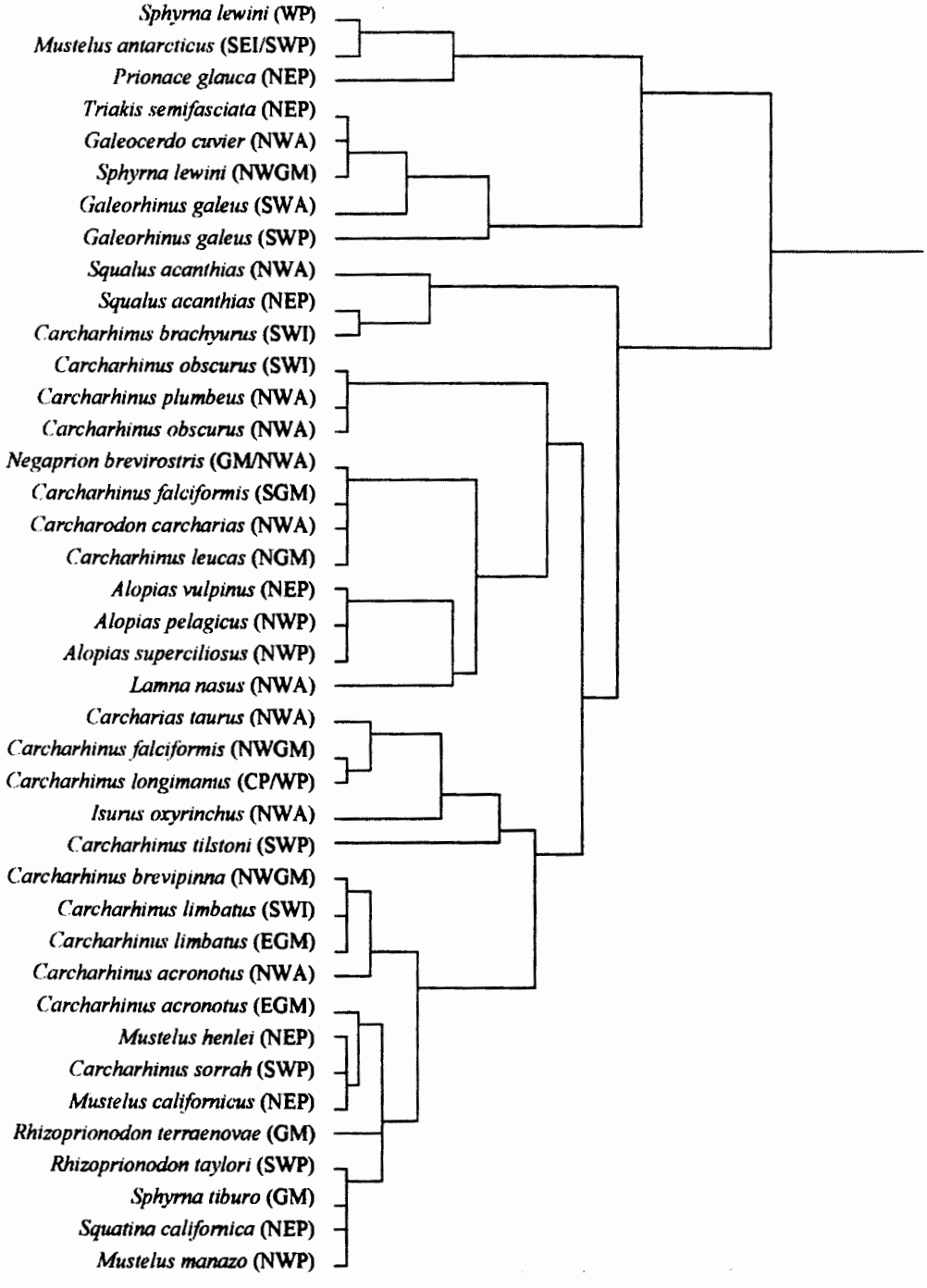

FIGURE 9. Dendrogram from a cluster analysis of five life history traits of 40 populations from 34 species of sharks. The groupings show similarities in life history traits among species and populations. (See appendix for an explanation of geographic codes.)

IV. DISCUSSION

A. LIFE HISTORY PATTERNS AND CORRELATIONS

The two reproductive traits analyzed, litter size and offspring size, varied with size. Larger species tend to have more and larger pups. This confirms on a more general basis the positive correlation between maximum length and maximum litter size that had been reported previously in three families of carcharhiniform sharks (Compagno, 1988; Simpfendorfer, 1992).

The observed patterns of increasing litter and offspring size with increasing body size are influenced by the various reproductive modes present in sharks. For example, inclusion of scyliorhinids and proscylliids—small-sized, mostly oviparous sharks that generally lay only two eggs (Compagno, 1988)—likely contributed to the variability in the relationship between maternal size and litter size. Also, the patterns of increasing litter and offspring size with maternal size in aplacental viviparous species may differ from those in placental viviparous species. Future studies of reproductive life history traits in sharks should investigate differences among reproductive modes.

There also are discernible trends between reproductive traits and body size at the intrapopulation level. In some species of sharks, larger females in a population tend to produce more offspring (e.g., *Carcharhinus amblyrhynchos, C. brachyurus, Carcharhinus cautus, Carcharhinus fitzroyensis, C. limbatus, C. plumbeus, C. sorrah, C. tilstoni, Galeocerdo cuvier, P. glauca, Rhizoprionodon acutus, R. taylori, R. terraenovae, Eusphyra blochii, S. lewini, Sphyrna mokarran, Furgaleus macki, G. galeus, M. antarcticus, M. manazo, Mustelus mustelus, Mustelus palumbes, Mustelus schmitti, Triakis megalopterus, T. semifasciata, Hemigaleus microstoma, Hemipristis elongatus, Parmaturus xaniurus* [Carcharhiniformes], *I. oxyrinchus* [Lamniformes], *S. acanthias, Squalus japonicus, Squalus mitsukurii* [Squaliformes], the same number of—possibly larger—offspring (e.g., *Carcharhinus albimarginatus, C. amblyrhynchos, Carcharhinus isodon, C. limbatus, C. longimanus, C. melanopterus, Isogomphodon oxyrhinchus, P. glauca, S. tiburo* [Carcharhiniformes], *S. californica* [Squatiniformes]), or even both more and larger offspring (e.g., *C. limbatus, Apristurus brunneus*). However, in at least some viviparous species of sharks, given the limited space available for a female to carry young, there is a trade-off between litter size and offspring size (Parsons, 1983; Branstetter, 1990; Simpfendorfer, 1992; Callard *et al.*, 1995). Thus, there is evidence of an inverse intrapopulation relationship between litter size and offspring size in some carcharhiniform species (e.g., *R. terraenovae, M. schmitti*).

There are no reported cases of reproductive senescence in female sharks, thus the largest—and probably oldest—females appear to be the most fecund (Pratt and Casey, 1990). However, as fecundity in sharks is generally measured in terms of litter size, one may be able to detect reproductive senescence when examining the relationship between embryo size and maternal size. For example, Parsons (1983) observed an optimal embryo size that occurred well before the maximum maternal size in *R. terraenovae*. Ideally, the total reproductive output, that is, the product of the number and weight of embryos should be used as a measure of fecundity, but this is very seldom reported in reproductive studies of sharks.

At the interspecific level, Holden (1972) reported a significant negative relationship between litter size and offspring size expressed in weight (n = 15). I observed no correlation between litter size and offspring length (n = 151). However, a trade-off between these two traits was confirmed for sharks after factoring out the effects of body size (n = 142), in agreement with Garrick (1982), who also found a negative relationship between median litter size and median length at birth when expressed as a percentage of maximum length for sharks of the genus *Carcharhinus* (n = 21). Life history theory predicts this trade-off between litter sizes and the energy spent on individual offspring, which has been observed in other animal taxa at the interspecific, intraspecific, and intrapopulation levels (Roff, 1992). In fishes, there is mounting evidence of a trade-off between litter size and offspring size (Fleming and Gross, 1990; Roff, 1992 and references therein).

Body size also masked the true nature of the relationship between growth completion rate (K) and offspring size. There appeared to be a negative correlation between these two traits before correcting for the effects of body size, when in fact there is a weak, positive, but nonsignificant, trend. This, in conjunction with the negative correlation between K and body size, suggests that those species with the highest values of K, and so generally smaller sharks, are born at a higher proportion of their maximum size than slower growing and larger species. These results are in agreement with patterns outlined by Pratt and Casey (1990), although these authors did not statistically test the correlations.

Males and females seem to have adopted somewhat different life history strategies. I found that maximum size of males was about 10% smaller than in females (n = 178), in agreement with Garrick (1982), who reported that males reach a maximum size about 7% smaller than females (range 2 to 14%) in sharks of the genus *Carcharhinus* (n = 24). Additionally, I found that the ratio of length at maturity to maximum length was almost identical in both males and females (about 75%). This agrees with Holden (1972), who found that the ratio of length at 50% maturity to maximum observed length for females of 16 species of sharks ranged from 0.64 to 0.92 and with Garrick (1982), who reported that first maturity in sharks of the genus *Carcharhinus* (n = 24) is reached at about 70% of maximum size for sexes combined, and that it ranges from 50 to 85% of maximum size in males, and from 60 to 90% of maximum size in females. In general, it appears that females attain maturity at a larger size and older age than males and reach a larger maximum size and older age while growing slower than males. This pattern may be in part explained by the need for females to attain a larger size to support pups and to a smaller investment in growth in favor of reproduction, which would translate in a delayed onset of sexual maturity in females. Interestingly, however, both males and females seem to reach maturity roughly at 3/4 of their maximum size and 1/2 of their maximum (empirical) age.

A positive correlation between body size and lifespan has been found in mammals and birds (Schmidt-Nielsen, 1984), but this relationship has not been fully investigated in fishes. In sharks, especially in males, longevity seems to covary with body size across species, but the relationship is not very strong. At the individual level, sharks, as other fishes, appear to grow continually throughout life, although the rate of growth progressively decreases with age, as predicted by the von Bertalanffy growth function.

B. SIMILARITIES AMONG LIFE HISTORY TRAITS

Branstetter (1990) classified a number of carcharhinoid and lamnoid sharks according to their size at birth as a proportion of maximum size, litter size, absolute size at birth, K-value, and first year's growth as a proportion of length at birth. His categories are generally in good agreement with the results of the PCA and cluster analyses conducted in the present study, despite the studies not using exactly the same life history traits. For example, Branstetter (1990) categorized *C. leucas, C. plumbeus*, and *N. brevirostris* as species with small offspring, size at birth > 20% of maximum adult size, K < 0.10, and first-year growth < 30% of birth length, and *C. taurus, C. obscurus*, and *C. carcharias* as having the same characteristics as those above, differing only in that they have larger offspring. All these species fell under the same general area in the PCA (upper- and lower-right quadrants in Figure 8A and lower-right quadrant in Figure 8B) and cluster (Figure 9) analyses I conducted. Likewise, Branstetter (1990) grouped species with small offspring, size at birth > 20% of maximum adult size, but fast growth (K > 0.10 and first-year growth > 40% of birth length). These included the coastal species *R. terraenovae, S. tiburo, C. acronotus, C. limbatus,* and *C. brevipinna,* and the pelagic species *C. falciformis, L. nasus, I. oxyrinchus, A. superciliosus*, and *A. vulpinus,* which were grouped in the upper-left and upper-right (Figure 8A) and lower-left and lower-right (Figure 8B) quadrants in my PCA analysis. In contrast, the cluster analysis did not group as closely together the pelagic species examined by Branstetter (1990). Finally, Branstetter distinguished *S. lewini* as having a size at birth < 20% of maximum adult size, K < 0.10, first-year growth < 30% of birth length, and small young, and *G. cuvier* and *P. glauca* as having the same features, except for faster growth (K > 0.10 and first-year growth > 40% of birth length). These three species also fell in the same general area (Figure 8A and 8B) and cluster (Figure 9) in the present study.

Sharks have developed alternative life history strategies that have enabled them to occupy diverse niches (Compagno, 1990), but all within the context of relatively low fecundity and precocial offspring when compared with other fishes. The results of the principal component and cluster analyses of the life history traits of the 40 populations analyzed enable us to distinguish three main groups, which are suggestive of separate strategies. It has to be remembered that these are artificial groupings proposed for the sake of simplicity and that in the real world life history traits of these and other species probably vary along a continuum rather than fall within discrete categories.

The first group is mainly characterized by species with large litter sizes (median = 41, range 31 to 135), variable but generally high longevity (17, 9 to 53 years), intermediate to large body size (244, 155 to 450 cm TL), small offspring size (39, 20 to 78 cm TL), and fairly slow growth (K; 0.117, 0.07 to 0.25), and includes all populations denoted by a solid triangle in Figures 8A and 8B and all those between *S. lewini* and *G. galeus* in Figure 9. The second group encompasses large species (371, 234 to 640 cm TL) with large offspring (85, 62.5 to 174 cm TL), reduced litter size (10, 2 to 14), slow growth (K; 0.08, 0.04 to 0.12), and generally high longevity (22, 14 to 39 years), and includes all populations denoted by an open circle in Figures 8A and 8B, and all those between *C. obscurus* and *L. nasus* in Figure 9. The third group's most salient features are reduced litter size (8, 5 to 15), small to

moderate body size (152, 78 to 247 cm TL), low to moderate longevity (9, 4.5 to 22 years), small offspring size (35, 24 to 67 cm TL), and generally fast growth (K; 0.21, 0.11 to 1.01), and includes all populations denoted by a solid circle in Figures 8A and 8B and all those between *C. brevipinna* and *M. manazo* in Figure 9.

There are also two subgroups linked to the second and third life history strategies identified. The group composed of *C. taurus*, *C. falciformis* from the northwestern Gulf of Mexico, *C. longimanus*, *I. oxyrinchus*, and *C. tilstoni* (Figure 9 and populations denoted by an open diamond in Figures 8A and 8B) is characterized by features close to those for the second, but especially the third, life history strategies. Thus, it encompasses species with moderate to large body size (305, 180–375 cm TL), medium to large offspring (73, 60–100 cm TL), reduced litter size (10, 2 to 15), and moderate growth (0.15, 0.10 to 0.20) and longevity (12, 11 to 16 years). Finally, the two populations of *S. acanthias* and *C. brachyurus* (Figure 9 and populations denoted by an open square in Figures 8A and 8B) form a subgroup characterized mainly by slow growth (0.04, 0.039 to 0.11), high to extreme longevity (40, 25 to 81 years), and fairly high litter sizes (17, 15 to 20).

The three main alternative life history strategies identified give some insight into how different species may cope with neonate and juvenile mortality. Species in the first group can be exemplified by *P. glauca*, a pelagic shark that invests in a large number of small young, born at a low percentage of their maximum size, and which are probably highly vulnerable to predators in the early life stages. The second group can be typified by a large, slow-growing species such as *C. obscurus*, that produces a limited number of large young, which are much less vulnerable to predation than their counterparts in the other two groups. Species in the third group allocate their reproductive effort differently, with the production of a limited number of small offspring, but born at a higher percentage of their maximum size and that grow more quickly than their counterparts in the first and second groups to overcome mortality in the early life stages. *Rhizoprionodon taylori* and *C. brevipinna* define the limits of the range of strategies within this group.

The life history strategies identified here are based mostly on carcharhiniform and lamniform sharks, and thus probably do not cover the full spectrum of strategies followed by all shark species. As more data on age, growth, and reproduction of different species become available, additional strategies are likely to be identified. For example, very little is known of the life history — especially the growth dynamics — of deepwater squaliform sharks. *Squalus acanthias* may typify the strategy followed by sharks in this speciose order.

In conclusion, the present study has provided a synthesis of life history patterns in sharks and a summary of updated values of key life history parameters, which are ultimately needed for population assessment and management. Patterns of covariation between traits were also examined quantitatively in an effort to provide comparisons with other taxa and to set the ground for analyses of their evolution. With the incorporation of breeding frequency to the life history traits reported herein and estimation of size- or age-based natural mortality estimates, demographic models can be developed for a variety of species of sharks. Furthermore, following the rationale applied by Van Buskirk and Crowder (1994) to marine turtles, demographic models of species with well-defined life history traits, such as the three general life history strategies identified in the present study, can be extended to

species with incomplete life history information but which seem to follow the life history strategy of the better-known species.

ACKNOWLEDGMENTS

I thank B. Wetherbee, G. Parsons, and J. Carlson for reviewing an earlier version of this manuscript and providing helpful ideas and suggestions. Thanks also go to J. Morrissey and H. G. Binis for helpful insight and comments.

REFERENCES

Branstetter, S. Early life history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. pp. 17–28. **In:** *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries.* (H. L. Pratt, S. H. Gruber, and T. Taniuchi, Eds.). NOAA Tech. Rep. NMFS 90, U.S. Dept. of Comm., Washington, D.C. (1990).

Cailliet, G. M., H. F. Mollet, G. G. Pittinger, D. Bedford, and L. J. Natanson. Growth and demography of the Pacific angel shark (*Squatina californica*), based upon tag returns off California. *Aust. J. Mar. Freshwater Res.*, **43**: 1313–1330 (1992).

Callard, I. P., O. Putz, M. Paolucci, and T. J. Koob. Elasmobranch reproductive life-histories: endocrine correlates and evolution. pp. 204–208. **In:** *Proceedings of the Fifth International Symposium on the Reproductive Physiology of Fish.* (F. W. Goetz and P. Thomas, Eds.). Fish Symposium 95, Austin, Texas (1995).

Compagno, L. J. V. *Sharks of the Order Carcharhiniformes.* Princeton, New Jersey: Princeton Univ. Press (1988).

Compagno, L. J. V. Alternative life history styles of cartilaginous fishes in time and space. *Environ. Biol. Fish.*, **28:** 33–75 (1990).

Compagno, L. J. V. Checklist of Living Elasmobranchs (Appendix) pp. 471-498. **In:** *Sharks, Skates, and Rays: The Biology of Elasmobranch Fishes.* (W.C. Hamlett, Ed.). Baltimore, Maryland: Johns Hopkins Univ. Press (1999).

Fabens, A. J. Properties and fitting of the von Bertalanffy growth curve. *Growth*, **29:** 265–289 (1965).

Fleming, I. A. and M. R. Gross. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. *Ecology,* **71:** 1-11 (1990).

Garrick, J. A. F. Sharks of the Genus *Carcharhinus.* NOAA Tech. Rep. NMFS Circ. 445, U.S. Dept. of Comm., Washington, D.C. (1982).

Hoenig, J. M. and S. H. Gruber. Life history patterns in the elasmobranchs: implications for fisheries management. pp. 1-16. **In:** *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries.* (H. L. Pratt, S. H. Gruber, and T. Taniuchi, Eds.). NOAA Tech. Rep. NMFS 90, U.S. Dept. of Comm., Washington, D.C. (1990).

Holden, M. J. Are long-term sustainable fisheries for elasmobranchs possible? *J. Cons. Int. Explor. Mer.*, **164:** 360–367 (1972).

Holden, M. J. Elasmobranchs. pp. 187–214. **In:** *Fish Population Dynamics.* (J. A. Gulland, Ed.). New York: John Wiley and Sons (1977).

Parsons, G. R. The reproductive biology of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae* (Richardson). *Fish. Bull.*, **81**: 61–73 (1983).

Pratt, H. L. and J. G. Casey. 1990. Shark reproductive strategies as a limiting factor in directed fisheries, with a review of Holden's method of estimating growth-parameters. pp. 97–109.

In: *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries.* (H. L. Pratt, S. H. Gruber, and T. Taniuchi, Eds.). NOAA Tech. Rep. NMFS 90, U.S. Dept. of Comm., Washington, D.C. (1990).

Roff, D. A. *The Evolution of Life Histories.* New York: Chapman and Hall (1992).

Schmidt-Nielsen, K. *Scaling: Why is Animal Size so Important?* New York: Cambridge Univ. Press (1984).

Simpfendorfer, C. A. Reproductive strategy of the Australian sharpnose shark, *Rhizoprionodon taylori* (Elasmobranchii: Carcharhinidae), from Cleveland Bay, northern Queensland. *Aust. J. Mar. Freshwater Res.*, **43:** 67–75 (1992).

Van Buskirk, J. and L. B. Crowder. Life history variation in marine turtles. *Copeia*, **1994:** 66–81 (1994).

von Bertalanffy, L. A quantitative theory of organic growth (inquiries on growth laws, II). *Human Biol.*, **10:** 181–213 (1938).

REFERENCES USED TO ELABORATE APPENDIX TABLE

Aasen, O. Length and growth of the porbeagle (*Lamna nasus*, Bonnaterre) in the Northwest Atlantic. *Fisk. Dir. Skr.*, **13:** 20–37 (1963).

Aasen, O. Some observations on the biology of the porbeagle (*Lamna nasus*, Bonnaterre). ICES, C. M. Copenhagen 1961, near Northern Sea Committee 109. pp. 1–7 (1961).

Backus, R. H., S. Springer, and E. L. Arnold. A contribution to the natural history of the white-tip shark, *Pterolamiops longimanus* (Poey). *Deep Sea Res.*, **3:** 178–188 (1956).

Bane, G. W., Jr. Observations on the silky shark, *Carcharhinus falciformis*, in the Gulf of Guinea. *Copeia*, **1966:** 354–356 (1966).

Bass, A. J., J. D. D'Aubrey, and N. Kistnasamy. Sharks of the east coast of southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). Invest. Rep. Oceanogr. Res. Inst., Durban 33. 168 pp. (1973).

Bass, A. J., J. D. D'Aubrey, and N. Kistnasamy. Sharks of the east coast of southern Africa. II. The families Scyliorhinidae and Pseudotriakidae. Invest. Rep. Oceanogr. Res. Inst., Durban 37. 64 pp. (1975a).

Bass, A. J., J. D. D'Aubrey, and N. Kistnasamy. Sharks of the east coast of southern Africa. III. The families Carcharhinidae (excluding *Mustelus* and *Carcharhinus*) and Sphyrnidae. Invest. Rep. Oceanogr. Res. Inst., Durban 38. 100 pp. (1975b).

Bass, A. J., J. D. D'Aubrey, and N. Kistnasamy. Sharks of the east coast of southern Africa. IV. The families Odontaspididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. Invest. Rep. Oceanogr. Res. Inst., Durban 39. 102 pp. (1975c).

Bass, A. J., J. D. D'Aubrey, and N. Kistnasamy. Sharks of the east coast of southern Africa. V. The families Hexanchidae, Clamydoselachidae, Heterodontidae, Pristiophoridae and Squatinidae. Invest. Rep. Oceanogr. Res. Inst., Durban 40. 50 pp. (1975d).

Bass, A. J., J. D. D'Aubrey, and N. Kistnasamy. Sharks of the east coast of southern Africa. VI. The families Oxynotidae, Squalidae, Dalatiidae, and Echinorhinidae. Invest. Rep. Oceanogr. Res. Inst., Durban 45. 103 pp. (1976).

Batista, V. S. and T. C. Silva. Age and growth of juveniles of junteiro shark *Carcharhinus porosus* in the coast of Maranhão, Brazil. *Rev. Brasil. Biol.*, **55(Suppl. 1):** 25–32 (1995).

Bedford D. W. and G. M. Cailliet. The biology of three pelagic sharks from California waters, and their emerging fisheries: a review. Calif. Coop. Oceanic Fish. Invest. Rep. 24 (1983).

Beebe, W. and J. Tee-Van. The fishes of Port-au-Prince Bay, Haiti. *Zoologica*, **10:** 279 pp. (1928).

Beebe, W. and J. Tee-Van. Fishes from the tropical eastern Pacific, part 2. Sharks. *Zoologica, N. Y.*, **26:** 93–122 (1941).

Bigelow, H. B. and W. C. Schroeder. Sharks. pp. 59–546. **In:** *Fishes of the Western North Atlantic, Part 1.* (J. Tee-Van, C. M. Breder, S. F. Hildebrand, A. E. Parr, and W. C. Schroeder, Eds.). Mem. Sears Found. Mar. Res., Yale University, New Haven, CT (1948).

Bonfil, R., R. Mena, and D. de Anda. Biological parameters of commercially exploited silky sharks, *Carcharhinus falciformis*, from the Campeche Bank, Mexico. pp. 73–86. **In:** *Conservation Biology of Elasmobranchs.* (S. Branstetter, Ed.). NOAA Tech. Rep. NMFS 115, U.S. Dept. of Comm., Washington, D.C. (1993).

Bonham, K., F. Sanford, W. Clegg, and G. C. Buchner. Biological and vitamin A studies of dogfish landed in the state of Washington. *Wash. Dept. Fish.*, **1949:** 85–114 (1949).

Branstetter, S. Biological notes on the sharks of the north central Gulf of Mexico. *Contrib. Mar. Sci.*, **24:** 13–34 (1981).

Branstetter, S. Biological parameters of the sharks of the northwestern Gulf of Mexico in relation to their potential as a commercial fishery resource. Doctoral Dissertation, Texas A&M University, College Station, TX. 138 pp. (1986).

Branstetter, S. Age, growth and reproductive biology of the silky shark, *Carcharhinus falciformis*, and the scalloped hammerhead, *Sphyrna lewini* from the northwestern Gulf of Mexico. *Environ. Biol. Fish.*, **19:** 61–173 (1987a).

Branstetter, S. Age and growth estimates for blacktip, *Carcharhinus limbatus*, and spinner, *Carcharhinus brevipinna*, sharks from the northwestern Gulf of Mexico. *Copeia*, **1987:** 964–974 (1987b).

Branstetter, S. Early life history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. pp. 17–28. **In:** *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries.* (H. L. Pratt, S. H. Gruber, and T. Taniuchi, Eds.). NOAA Tech. Rep. NMFS 90, U.S. Dept. of Comm., Washington, D.C. (1990).

Branstetter, S. and J. A. Musick. Age and growth estimates for the sand tiger shark in the northwestern Atlantic Ocean. *Trans. Am. Fish. Soc.*, **123:** 242–254 (1994).

Branstetter, S., J. A. Musick, and J. A. Colvocoresses. A comparison of the age and growth of the tiger shark, *Galeocerdo cuvieri*, from off Virginia and from the northwestern Gulf of Mexico. *Fish. Bull.*, **85:** 269–279 (1987).

Branstetter, S. and R. Stiles. Age and growth of the bull shark, *Carcharhinus leucas*, from the northern Gulf of Mexico. *Environ. Biol. Fish.*, **20:** 169–181 (1987).

Bridge, N. F., D. Mackay, and G. Newton. Biology of the ornate angel shark (*Squatina tergocellata*) from the Great Australian Bight. *Mar. Freshwater Res.*, **49:** 679–686 (1998).

Brown, C. A. and S. H. Gruber. Age assessment of the lemon shark, *Negaprion brevirostris*, using tetracycline validated vertebral centra. *Copeia*, **1988:** 747–753 (1988).

Bruce, B. D. Preliminary observations on the biology of the white shark, *Carcharodon carcharias*, in south Australian waters. *Aust. J. Mar. Freshwater. Res.*, **43:** 1–11 (1992).

Cadenat, J. Note d'ichthyologie ouest-Africaine. XV—Sur un requin renard nouveau pour la faune d'Afrique occidentale Française *Alopias superciliosus* (Lowe) 1840. *Bull. Inst. Fondam. Afr. Noire*, **18:** 1257–1266 (1956).

Cadenat, J. Notes d'ichthyologie ouest-Africaine. XXVIII—*Deania cremouxi*, sp. nov. des côtes du Sénégal. *Bull. Inst. Fondam. Afr. Noire*, **22:** 312–324 (1960).

Cadenat, J. and J. Blache. *Requins de Méditerranée et d'Atlantique.* Faune tropicale, ORSTOM, Paris. 330 pp. (1981).

Cailliet, G. M. Elasmobranch age determination and verification: an updated review. pp. 157–165. **In:** *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries.* (H. L. Pratt, S. H. Gruber, and T. Taniuchi, Eds.). NOAA Tech. Rep. NMFS 90, U.S. Dept. of Comm., Washington, D.C. (1990).

Cailliet, G. M., L. K. Martin, J. T. Harvey, D. Kusher, and B. A. Welden. Preliminary studies on the age and growth of blue, *Prionace glauca*, common thresher, *Alopias vulpinus*, and shortfin mako, *Isurus oxyrinchus*, sharks from California waters. pp. 179–188. **In:** *Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfish, and Sharks.* (E. O. Prince and L. M. Pulos, Eds.). NOAA Tech. Rep. NMFS 8, U.S. Dept. of Comm., Washington, D.C. (1983).

Cailliet, G. M., H. F. Mollet, G. G. Pittinger, D. Bedford, and L. J. Natanson. Growth and demography of the Pacific angel shark (*Squatina californica*), based upon tag returns off California. *Aust. J. Mar. Freshwater Res.*, **43:** 1313–1330 (1992).

Cailliet, G. M., L. J. Natanson, B. A. Welden, and D. E. Ebert. Preliminary studies on the age and growth of the white shark, *Carcharodon carcharias*, using vertebral bands. *Memoirs South. Calif. Acad. Sci.*, **9:** 49–60 (1985).

Cailliet, G. M., K. G. Yudin, S. Tanaka, and T. Taniuchi. Growth characteristics of two populations of *Mustelus manazo* from Japan based upon cross-readings of vertebral bands. pp. 167–176. **In:** *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries.* (H. L. Pratt, S. H. Gruber, and T. Taniuchi, Eds.). NOAA Tech. Rep. NMFS 90, U.S. Dept. of Comm., Washington, D.C. (1990).

Capapé, C. Contribution à la biologie des Scyliorhinidae des côtes tunisiennes. I. *Scyliorhinus canicula* (Linné, 1758): répartition géographique et bathymétrique, sexualité, reproduction, fécondité. *Bull. Off. Natl. Pêch. Tunisie*, **1:** 83–101 (1977).

Capapé, C. Nouvelle description de *Centrophorus granulosus* (Schneider, 1801) (Pisces, Squalidae). Données sur la biologie de la reproduction et le régime alimentaire des spécimens des côtes tunisiennes. *Bull. Inst. Natl. Scient. Tech. Oceanogr. Pêche Salambô*, **1985:** 97–141 (1985).

Capapé, C., and J. P. Quignard. 1977. Contribution à la biologie des Triakidae des côtes tunisiennes. I. *Mustelus mediterraneus* Quignard et Capapé 1972: répartition géographique et bathymétrique, migrations et déplacements, reproduction, fécondité. *Bull. Off. Natl. Pêch. Tunisie*, **1:** 103–122 (1977).

Capapé, C., J. A. Tomasini, and J. L. Bouchereau. Observations sur la biologie de la reproduction de la petite roussette *Scyliorhinus canicula* (L. 1758) (Pisces, Scyliorhinidae) du Golfe du Lion (France Méridional). *Ichtyophysiol. Acta*, **14:** 87–109 (1991).

Carlson, J. K., E. Cortés, and A. G. Johnson. Age and growth of the blacknose shark, *Carcharhinus acronotus*, in the eastern Gulf of Mexico. *Copeia*, **1999:** 683–690 (1999).

Carlson, J. K. and G. R. Parsons. Age and growth of the bonnethead shark, *Sphyrna tiburo*, from northwest Florida, with comments on clinal variation. *Environ. Biol. Fish.*, **50:** 331–341 (1997).

Carrier, J. C. and C. A. Luer. Growth rates in the nurse shark, *Ginglymostoma cirratum*. *Copeia*, **1990:** 686–692 (1990).

Casey, J. G. and L. J. Natanson. Revised estimates of age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. *Can. J. Fish. Aquat. Sci.*, **49:** 1474–1477 (1992).

Casey, J. G. and H. L. Pratt, Jr. Distribution of the white shark, *Carcharodon carcharias*, in the western North Atlantic. *Mem. South. Calif. Acad. Sci.*, **9:** 2–14 (1985).

Casey, J. G., H. L. Pratt, Jr., and C. E. Stillwell. Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. *Can. J. Fish. Aquat. Sci.*, **42:** 963–975 (1985).

Castro, J. A. and J. Mejuto. Reproductive parameters of blue shark, *Prionace glauca*, and other sharks in the Gulf of Guinea. *Mar. Freshwater Res.*, **46:** 967–973 (1995).

Castro, J. I. *The Sharks of North American Waters*. College Station, TX: Texas A&M Univ. Press (1983).

Castro, J. I. The biology of the golden hammerhead, *Sphyrna tudes*, off Trinidad. *Environ. Biol. Fish.* **24:** 3–11 (1989).

Castro, J. I. The biology of the finetooth shark, *Carcharhinus isodon*. *Environ. Biol. Fish.*, **36:** 219–239 (1993).

Castro, J. I. The biology of the blacktip shark, *Carcharhinus limbatus*, off the southeastern United States. *Bull. Mar. Sci.*, **59:** 508–522 (1996).

Castro, J. I. The biology of the nurse shark, *Ginglymostoma cirratum*, off the Florida east coast and the Bahamas Islands. *Environ. Biol. Fish.*, **58:** 1–22 (2000)

Castro, J. I., C. M. Woodley, and R. L. Brudek. A preliminary evaluation of the status of shark species. FAO Fisheries Technical Paper No. 380, Rome, FAO. 72 pp. (1999).

Castro, J. I. and J. P. Wourms. Reproduction, placentation, and embryonic development of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae. J. Morphol.*, **218:** 258–280 (1993).

Castro, J. I., P. M. Bubucis, and N. A. Overstrom. The reproductive biology of the chain dogfish, *Scyliorhinus retifer. Copeia*, **1988:** 740–746 (1988).

Castro-Aguirre, J. L. Especies de la familia Scyliorhinidae (Elasmobranchii, Galeoidea), de la costa occidental de México, con especial referencia a *Cephalurus cephalus* (Gilbert). *An. Esc. Nac. Cienc. biol. Mex.*, **24:** 71–93 (1981).

Chen, C. T., T. Taniuchi, and Y. Nose. Some aspects of reproduction in the pointed-snout dogfish *Squalus japonicus* taken off Nagasaki and Choshi. *Bull. Jpn. Soc. Sci. Fish.*, **47:** 1157–1164 (1981).

Chen, C. T, T. C. Leu, and S. J. Joung. Notes on reproduction in the scalloped hammerhead, *Sphyrna lewini*, in northeastern Taiwan waters. *Fish. Bull.*, **86:** 389–393 (1988).

Chen, C. T, T. C. Leu, S. J. Joung, and N. C. L. Lo. Age and growth of the scalloped hammerhead, *Sphyrna lewini*, in northeastern Taiwan waters. *Pacific Sci.*, **44:** 156–170 (1990).

Chen, C. T, K. M. Liu, and Y. C. Chang. Reproductive biology of the bigeye thresher shark, *Alopias superciliosus* (Lowe, 1839) (Chondrichthyes: Alopiidae), in the northwestern Pacific. *Ichthyol. Res.*, **44:** 227–235 (1997).

Chiaramonte, G. E. Placentación en la "bacota", *Carcharhinus brachyurus* (Chondrichthyes: Carcharhinidae): tipificación, descripción macroscópica y otros aspectos reproductivos. *Mus. Arg. Cien. Nat. "Bernardino Rivadavia" e Inst. Nac. Invest. Cien. Nat., Nueva Serie*, **143:** 1–7 (1996).

Clark, E. The maintenance of sharks in captivity, with a report on their instrumental conditioning. pp. 115–149. **In:** *Sharks and Survival.* (P. W. Gilbert, Ed.). Boston: D.C. Heath and Co. (1963).

Clark, E. and K. von Schmidt. Sharks of the central Gulf coast of Florida. *Bull. Mar. Sci.*, **15:** 13–83 (1965).

Clark, M. R. and K. J. King. Deepwater fish resources of the North Island, New Zealand: results of a trawl survey, May 1985 to June 1986. New Zealand Fish. Tech. Rep. 11. 56 pp. (1989).

Cliff, G. Sharks caught in the protective gill nets off Kwazulu-Natal, South Africa. VIII. The great hammerhead shark (*Sphyrna mokarran*) (Ruppell). *S. Afr. J. Mar. Sci.*, **15:** 105–114 (1995).

Cliff, G. and S. F. J. Dudley. Sharks caught in the protective gill nets of Natal, South Africa. VI. The bull shark (*Carcharhinus leucas*) (Valenciennes). *S. Afr. J. Mar. Sci.*, **10:** 253–270 (1991a).

Cliff, G. and S. F. J. Dudley. Sharks caught in the protective gill nets of Natal, South Africa. V. The Java shark (*Carcharhinus amboinensis*) (Muller and Henle). *S. Afr. J. Mar. Sci.*, **11:** 443–453 (1991b).

Cliff, G. and S. F. J. Dudley. Sharks caught in the protective gill nets of Natal, South Africa. VI. The copper shark (*Carcharhinus brachyurus*) (Gunther). *S. Afr. J. Mar. Sci.*, **12:** 663–674 (1992).

Cliff, G., S. F. J. Dudley, and B. Davis. Sharks caught in the protective gill nets of Natal, South Africa. I. The sandbar shark (*Carcharhinus plumbeus*) (Nardo). *S. Afr. J. Mar. Sci.*, **7:** 255–265 (1988).

Cliff, G., S. F. J. Dudley, and B. Davis. Sharks caught in the protective gill nets of Natal, South Africa. II. The great white shark (*Carcharodon carcharias*) (Linnaeus). *S. Afr. J. Mar. Sci.*, **8:** 131–144 (1989).

Cliff, G., S. F. J. Dudley, and B. Davis. Sharks caught in the protective gill nets of Natal, South Africa. III. The shortfin mako shark (*Isurus oxyrinchus*) (Rafinesque). *S. Afr. J. Mar. Sci.*, **9:** 115–126 (1990).

Colman, J. G. A review of the biology and ecology of the whale shark. *J. Fish. Biol.*, **51:** 1219–1234 (1997).

Compagno, L. J. V. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. FAO Species Catalogue. Vol. 4, Parts 1 and 2. FAO Fish. Synopsis 125. FAO, Rome, Italy (1984).

Compagno, L. J. V. *Sharks of the Order Carcharhiniformes*. Princeton, NJ: Princeton Univ. Press (1988).

Cousseau, M. B. Taxonomía y biología del pez ángel, *Squatina argentina* Marini (Pisces, Squatinidae). *Physis*, **32:** 175–195 (1973).

Cross, J. N. Aspects of the biology of two scyliorhinid sharks, *Apristurus brunneus* and *Parmaturus xaniurus*, from the upper continental slope off southern California. *Fish. Bull.*, **86:** 691–702 (1988).

Davenport, S. and J. D. Stevens. Age and growth of two commercially important sharks (*Carcharhinus tilstoni* and *C. sorrah*) from northern Australia. *Aust. J. Mar. Freshwater Res.*, **39:** 417–433 (1988).

DeCrosta, M. A., L. R. Taylor, Jr., and J. D. Parrish. Age determination, growth, and energetics of three species of carcharhinid sharks in Hawaii. pp. 75–95. **In:** *Proceedings of the Second Symposium on Resource Investigations in the Northwest Hawaiian Islands, May 25–27, 1983*. Univ. Hawaii Sea Grant MR-84–01 (1984).

Devadoss, P. Observations on the length-weight relationship and food and feeding habits of spade nose shark, *Scoliodon laticaudus* Muller and Henle. *Indian J. Fish.*, **36:** 169–174 (1989).

Devadoss, P. Growth and population parameters of the spade nose shark, *Scoliodon laticaudus* from Calicut coast. *Indian J. Fish.*, **45:** 29–34 (1998).

Dudley, S. F. J. and G. Cliff. Sharks caught in the protective gill nets of Natal, South Africa. VII. The blactip shark (*Carcharhinus limbatus*) (Valenciennes). *S. Afr. J. Mar. Sci.*, **13:** 237–254 (1993).

Ebert, D. A. Aspects on the biology of hexanchid sharks along the California coast. pp. 437–449. **In:** *Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes* (T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuura, Eds.). Icthyological Society of Japan, Tokyo (1986).

Ebert, D. A. Life history of the sevengill shark, *Notorynchus cepedianus* Peron, in two northern California bays. *Calif. Fish and Game*, **75:** 102–112 (1989).

Ebert, D. A. Biology of the sevengill shark *Notorynchus cepedianus* (Peron, 1807) in the temperate coastal waters of southern Africa. *S. Afr. J. Mar. Sci.*, **17:** 93–103 (1996).

Ebert, D. A., L. J. V. Compagno, and P. D. Cowley. A preliminary investigation of the feeding ecology of squaloid sharks off the west coast of southern Africa. *S. Afr. J. Mar. Sci.*, **12:** 601–609 (1992).

Ferreira, B. P. and C. M. Vooren. Age, growth, and structure of vertebra in the school shark *Galeorhinus galeus* (Linnaeus, 1758) from southern Brazil. *Fish. Bull.*, **89:** 19–31 (1991).

Ford, E. A contribution to our knowledge of the life histories of the dogfishes landed at Plymouth. *J. Mar. biol. Assoc. U.K.*, **12:** 468–505 (1921).

Fourmanoir, P. Requins de la côte ouest de Madagascar. *Mem. Inst. Sci. Madagascar, série F*, **4:** 1–107 (1961).

Francis, M. P. A biological basis for the management of New Zealand moki (*Latridopsis ciliaris*) and smoothhound (*Mustelus lenticulatus*) fisheries. M.Sc. Thesis, Univ. of Canterbury, New Zealand (1979).

Francis, M. P. Von Bertalanffy growth rates in species of *Mustelus* (Elasmobranchii: Triakidae). *Copeia*, **1981:** 189–192 (1981).

Francis, M. P. Observations on a pregnant white shark with a review of reproductive biology. pp. 157–172. **In:** *Great White Sharks: The Biology of Carcharodon carcharias*. (A. P. Klimley and D. G. Ainley, Eds.). San Diego, CA: Academic Press (1996).

Francis, M. P. and K. P. Mulligan. Age and growth of New Zealand school shark, *Galeorhinus galeus*. *New Zealand J. Mar. Freshwater Res.*, **32:** 427–440 (1998).

Garrick, J. A. F. Studies on New Zealand Elasmobranchii: part XI. Squaloids of the genera *Deania*, *Etmopterus*, *Oxynotus*, and *Dalatias* in New Zealand waters. *Trans. R. Soc. New Zealand*, **88:** 489–517 (1960a).

Garrick, J. A. F. Studies on New Zealand Elasmobranchii: part XII. The species of *Squalus* from New Zealand and Australia; and a general account and key to the New Zealand Squaloidea. *Trans. R. Soc. New Zealand*, **88:** 519–557 (1960b).

Garrick, J. A. F. Sharks of the genus *Carcharhinus*. NOAA Tech. Rep. NMFS Circ. 445, U.S. Dept. of Comm., Washington, D.C. (1982).

Garrick, J. A. F., R. H. Backus, and R. H. Gibbs, Jr. *Carcharhinus floridanus*, the silky shark, a synonym of *C. falciformis*. *Copeia*, **1964:** 369–375 (1964).

Gauld, J. Reproduction and fecundity of the Scottish-Norwegian stock of spurdogs, *Squalus acanthias* (L.). Int. Counc. Explor. Sea CM 1979/H:54, Copenhagen, Denmark (1979).

Gauld, J. Records of porbeagles landed in Scotland, with observations on the biology, distribution and exploitation of the species. DAFS Scottish Fish. Res. Rep. 45. 15 pp. (1989).

Gilmore, R. G. Observations on the embryos of the longfin mako, *Isurus paucus*, and the bigeye thresher, *Alopias superciliosus*. *Copeia*, **1983:** 375–382 (1983).

Gilmore, R. G. Reproductive biology of lamnoid sharks. *Environ. Biol. Fish.*, **38:** 95–114 (1993).

Gilmore, R. G., J. W. Dodrill, and P. A. Linley. Reproduction and embryonic development of the sand tiger shark, *Odontaspis taurus* (Rafinesque). *Fish. Bull.*, **81:** 201–225 (1983).

Gohar, H. A. F. and F. M. Mazhar. The elasmobranchs of the northwestern Red Sea. *Publ. Mar. Biol. Stn. Ghardaqa, Red Sea*, **13:** 1–144 (1964).

Gómez Fermin, E. and A. K. M. Bashirulah. Relación longitud-peso y hábitos alimenticios de *Rhizoprionodon porosus* Poey 1861 (Fam. Carcharhinidae) en el oriente de Venezuela. *Bol. Inst. Oceanogr. Venezuela Univ. Oriente*, **23:** 49–54 (1984).

Govender, A., N. Kistnasamy, and R. P. van der Elst. Growth of spotted ragged-tooth sharks *Carcharias taurus* (Rafinesque) in captivity. *S. Afr. J. Mar. Sci.*, **11:** 15–19 (1991).

Gruber, S. H. and L. J. V. Compagno. Taxonomic status and biology of the bigeye thresher, *Alopias superciliosus*. *Fish. Bull.*, **79:** 617–640 (1981).

Gruber, S. H. and R. G. Stout. Biological materials for the study of age and growth in a tropical marine elasmobranch, the lemon shark, *Negaprion brevirostris* (Poey). pp. 193–205. **In:** *Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfish, and Sharks*. (E. O. Prince and L. M. Pulos, Eds.). NOAA Tech. Rep. NMFS 8, U.S. Dept. of Comm., Washington, D.C. (1983).

Gubanov, Y. P. The capture of a giant specimen of the mako shark (*Isurus glaucus*) in the Indian Ocean. *J. Ichthyol.*, **14:** 589–591 (1974).

Gubanov, Y. P. The reproduction of some species of pelagic sharks from the equatorial zone of the Indian Ocean. *J. Ichthyol.*, **18:** 781–792 (1978).

Guitart-Manday, D. Nuevo nombre para una especie de tiburón del género *Isurus* (Elasmobranchii: Isuridae) de aguas cubanas. Poeyana (Ser. A). 9 pp. (1966).

Hanchet, S. M. Reproductive biology of *Squalus acanthias* from the east coast, South Island, New Zealand. *New Zealand J. Mar. Freshwater Res.*, **22:** 537–549 (1988).

Hazin, F. H. V., K. Kihara, K. Otsuka, C. E. Boeckman, and E. C. Leal. Reproduction of the blue shark *Prionace glauca* in the southwestern Equatorial Atlantic Ocean. *Fish. Sci.*, **60:** 487–491 (1994).

Hazin, F. H. V, F. M. Lucena, T. S. A. L. Souza, C. E. Boeckman, M. K. Broadhurst, and R. C. Menni. Maturation of the night shark, *Carcharhinus signatus*, in the southwestern equatorial Atlantic Ocean. *Bull. Mar. Sci.*, **66:** 173–185 (2000).

Hickling, C. F. A contribution towards the life history of the spur-dog. *J. Mar. Biol. Assoc. U. K.*, **16:** 529–576 (1930).

Hixon, M. A. Term fetuses from a large common thresher shark, *Alopias vulpinus*. *Calif. Fish and Game*, **65:** 191–192 (1979).

Holden, M. J. and P. S. Meadows. The structure of the spine of the spur dogfish (*Squalus acanthias* L.) and its use for age determination. *J. Mar. Biol. Assoc. U. K.*, **42:** 179–197 (1962).

Holden, M. J. and P. S. Meadows. The fecundity of the spurdog (*Squalus acanthias* L.). *J. Cons., Cons. Int. Explor. Mer.*, **28:** 418–424 (1964).

Jensen, A. C. Life history of the spiny dogfish. *U.S. Fish Wild. Serv. Fish. Bull.*, **63:** 527–551 (1966).

Jones, B. C. and G. H. Geen. Reproduction and embryonic development of spiny dogfish (*Squalus acanthias*) in the strait of Georgia, British Columbia. *J. Fish. Res. Board Can.*, **34:** 1286–1292 (1977a).

Jones, B. C. and G. H. Geen. Age and growth of spiny dogfish (*Squalus acanthias*) in British Columbia. *Can. Fish. Mar. Serv. Tech. Rep.* 699 (1977b).

Jones, B. C. and G. H. Geen. Observations on the brown catshark, *Apristurus brunneus* (Gilbert), in British Columbia waters. *Syesis*, **10:** 169–170 (1977c).

Joung, S. J., C. T. Chen, E. Clark, S. Uchida, and W. Y. P. Huang. The whale shark, *Rhincodon typus*, is a livebearer: 300 embryos found in one 'megamamma' supreme. *Environ. Biol. Fish.*, **46:** 219–223 (1996).

Joung, S. J.and C. T. Chen. Reproduction in the sandbar shark, *Carcharhinus plumbeus*, in the waters off northeastern Taiwan. *Copeia*, **1995:** 659–665 (1995).

Kaganovskaia, S. A method of determining the age and the composition of the catches of the spiny dogfish (*Squalus acanthias* L.). *Vest. Dalnevost. Fil Akad. Nauk SSSR*, **1–3:** 139–141 (1933). (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. 281, 1960).

Kato, S. and A. H. Carvallo. Shark tagging in the eastern Pacific Ocean, 1962–65. pp. 93–109. **In:** *Sharks, Skates, and Rays*. (P. W. Gilbert, R. F. Mathewson, and D. P. Rall, Eds.). Baltimore, MD: John Hopkins Press (1967).

Ketchen, K. S. Size at maturity, fecundity, and embryonic growth of the spiny dogfish (*Squalus acanthias*) in British Columbia waters. *J. Fish. Res. Board Can.*, **29:** 1717–1723 (1972).

Ketchen, K. S. Age and growth of dogfish *Squalus acanthias* in British Columbia waters. *J. Fish. Res. Board Can.*, **32:** 43–59 (1975).

Killam, K. A. Reproductive biology, age and growth of the blacktip shark, *Carcharhinus limbatus* (Valenciennes) near Tampa Bay, Florida. M.Sc. Thesis, Univ. of South Florida, St. Petersburg, FL. 170pp. (1987).

Killam, K. A. and G. R. Parsons. Age and growth of the blacktip shark, *Carcharhinus limbatus*, near Tampa Bay, Florida. *Fish. Bull.*, **87:** 845–857 (1989).

King, K. J. and M. R. Clark. Sharks from the upper continental slope—are they of value? *Catch*, **14:** 3–6 (1987).

Kobayashi, H. Studies on deep-sea sharks in Kumano-nada region. *Bull. Fac. Fish. Mie Univ/ Miedai Suisan Kenpo*, **13:** 25–133 (1986).

Kohler, N. E., J. G. Casey, and P. A. Turner. Length-weight relationships for 13 species of sharks from the western North Atlantic. *Fish. Bull.*, **93:** 412–418 (1995).

Krefft, G. Neue und erstmalig nachgewiesene Knorpelfische aus dem Archibenthal des Südwesatlantiks, einschliesslich einer Discussion einiger *Etmopterus*-Arten südlicher Meere. *Arch. Fischereiwiss.*, **19:** 1–42 (1968).

Krogh, M. Spatial, seasonal and biological analysis of sharks caught in the New South Wales protective beach meshing programme. *Aust. J. Mar. Freshwater Res.*, **45:** 1087–1106 (1994).

Kunzlik, P. A. The basking shark. Scot. Fish. Inf. Pamphlet 14, Dept. Agric. Fish. Scot. (1988).

Kusher, D. I., S. E. Smith, and G. M. Cailliet. Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction. *Environ. Biol. Fish.*, **35:** 187–203 (1992).

Last, P. R. and J. D. Stevens. *Sharks and Rays of Australia*. Melbourne, Australia: CSIRO Div. of Fish. 513 pp. (1994).

Lenanton, R. C. J., D. I. Heald, M. Platell, M. Cliff, and J. Shaw. Aspects of the reproductive biology of the gummy shark, *Mustelus antarcticus* Günther, from waters off the south coast of Western Australia. *Aust. J. Mar. Freshwater Res.*, **41:** 807–822 (1990).

Lessa, R. and F. M. Santana. Age determination and growth of the smalltail shark, *Carcharhinus porosus*, from northern Brazil. *Mar. Freshwater Res.*, **49:** 705–711 (1998).

Lessa, R., V. Batista, and Z. Almeida. Occurrence and biology of the daggernose shark *Isogomphodon oxyrhynchus* (Chondrichthyes: Carcharhinidae) off the Maranhão coast (Brazil). *Bull. Mar. Sci.*, **64:** 115–128 (1999).

Litvinov, F. F. Ecological characteristics of the dogfish, *Squalus mitsukurii*, from the Sala-y-Gomez Seamounts. *J. Icthyol.*, **30:** 577–586 (1990).

Liu, K. M., P. J. Chiang, and C. T. Chen. Age and growth estimates of the bigeye thresher shark, *Alopias superciliosus*, in northeastern Taiwan waters. *Fish. Bull.*, **96:** 482–491 (1998).

Liu, K. M., C. T. Chen, T. H. Liao, and S. J. Joung. Age, growth, and reproduction of the pelagic thresher shark, *Alopias pelagicus*, in the northwestern Pacific. *Copeia*, **1999:** 68–74 (1999).

Lyle, J. M. Observations on the biology of *Carcharhinus cautus* (Whitley), *C. melanopterus* (Quoy and Gaimard) and *C. fitzroyensis* (Whitley) from Northern Australia. *Aust. J. Mar. Freshwater Res.*, **38:** 701–710 (1987).

McLaughlin, R. H. and A. K. O'Gower. Life history and underwater studies of a heterodont shark. *Ecol. Monogr.*, **41:** 271–289 (1971).

Menni, R. C. Distribución y biología de *Squalus acanthias*, *Mustelus schmitti* y *Galeorhinus vitaminicus* en el Mar Argentino en agosto-setiembre de 1978 (Chondrichthyes). *Rev. Mus. de La Plata (Nueva Serie) Sec. Zool.*, **13:** 151–182 (1985).

Menni, R. C. Shark biology in Argentina: a review. pp. 425–436. **In:** *Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes*. (T. Uyeno, R. Arai, T. Taniuchi and K. Matsuura, Eds.). Icthyological Society of Japan, Tokyo (1986).

Menni, R. C., A. E. Gosztonyi, and H. López. Sobre la ecología y biología de *Halaelurus bivius* (Condrichthyes, Scyliorhinidae). *Rev. Mus. Arg. Cien. Nat. Vol. ii(sesq)*, **3:** 71–88 (1979).

Mollet, H. F., G. Cliff, H. L. Pratt, Jr., and J. D. Stevens. Reproductive biology of the female shortfin mako *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic develpment of lamnoids. *Fish. Bull.*, **98:** 299–318 (2000).

Moreno, J. A. and J. Morón. Reproductive biology of the bigeye thresher shark *Alopias supercilious*. *Mar. Freshwater Res.*, **43:** 77–86 (1992).

Moulton, P. L., T. I. Walker, and S. R. Saddlier. Age and growth studies of gummy shark, *Mustelus antarcticus* Günther, and school shark, *Galeorhinus galeus* (Linnaeus), from southern Australian waters. *Aust. J. Mar. Freshwater Res.*, **43:** 1241–1267 (1992).

Nagasawa, K. Predation by salmon sharks (*Lamna ditropis*) on Pacific salmon (*Oncorhynchus* spp.) in the north Pacific Ocean. *N. Pac. Anadr. Fish Comm. Bull.*, **1:** 419–433 (1998).

Nair, K. P. Age and growth of the yellow dog shark *Scoliodon laticaudus* Muller and Henle from Bombay waters. *J. Mar. Biol. Ass. India*, **3:** 531–539 (1976).

Nakano, H. Age, reproduction and migration of blue shark in the North Pacific Ocean. *Bull. Nat. Res. Inst. Far Seas Res.*, **31:** 141–144 (1994).

Nammack, M. F., J. A. Musick, and J. A. Colvocoresses. Life history of spiny dogfish off the northeastern United States. *Trans. Am. Fish. Soc.*, **114:** 367–376 (1985).

Natanson, L. J. and G. M. Cailliet. Reproduction and development of the Pacific angel shark, *Squatina californica*, off Santa Barbara, California. *Copeia*, **1986:** 987–994 (1986).

Natanson, L. and G. M. Cailliet. Vertebral growth zone deposition in Pacific angel sharks. *Copeia*, **1990:** 1133–1145 (1990).

Natanson, L., J. G. Casey, and N. E. Kohler. Age and growth estimates for the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean. *Fish. Bull.*, **93:** 116–126 (1995).

Natanson, L. and N. E. Kohler. A preliminary estimate of age and growth of the dusky shark *Carcharhinus obscurus* from the southwest Indian Ocean, with comparisons to the western North Atlantic population. *S. Afr. J. Mar. Sci.*, **17:** 217–224 (1996).

Olsen, A. M. The biology, migration and growth rate of the school shark, *Galeorhinus australis* (macLeay) (Carcharhinidae) in southeastern Australia waters. *Aust. J. Mar. Freshwater Res.*, **5:** 353–410 (1954).

Olsen, A. M. Synopsis of biological data on the school shark, *Galeorhinus australis* (Macleay 1881). FAO Fish. Synop. 139. (1984).

Otake, T. and K. Mizue. Direct evidence for oophagy in thesher shark, *Alopias pelagicus. Jpn. J. Icthyol.*, **28:** 171–172 (1981).

Parker, H. W. and F. C. Stott. Age, size, and vertebral calcification in the basking shark, *Cetorhinus maximus* (Gunnerus). *Zool. Medel.*, **40:** 305–319 (1965).

Parsons, G. R. An examination of the vertebral rings of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae. Northeast Gulf Sci.*, **6:** 63–66 (1983).

Parsons, G. R. Growth and age estimation of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*: a comparison of techniques. *Copeia,* **1985:** 80–85 (1985a).

Parsons, G. R. Notes on the life history of the catshark, *Scyliorhinus meadi. Fish. Bull.*, **83:** 695–696 (1985b).

Parsons, G. R. Observations on the reproductive biology of the marbled catshark, *Galeus arae antillensis. Northeast Gulf Sci.*, **8:** 149–150 (1986).

Parsons, G. R. Age determination and growth of the bonnethead shark *Sphyrna tiburo*: a comparison of two populations. *Mar. Biol.*, **117:** 23–31 (1993a).

Parsons, G. R. Geographic variation in reproduction between two populations of the bonnethead shark, *Sphyrna tiburo. Environ. Biol. Fish.*, **38:** 25–35 (1993b).

Pauly, D. A critique of some literature data on the growth, reproduction and mortality of the lamnid shark *Cetorhinus maximus* (Gunnerus). Int. Counc. Explor. Sea CM 1978/H:17, Copenhagen, Denmark (1978).

Paust, B. and R. Smith. Salmon shark manual. Alaska Sea Grant Rep., Alaska Univ., Fairbanks. Sea Grant College Program. 430 pp. (1986).

Peres, M. B. and C. M. Vooren. Sexual development, reproductive cycle, and fecundity of the school shark *Galeorhinus galeus* off southern Brazil. *Fish. Bull.*, **89:** 655–667 (1991).

Pratt, H. L. Reproduction in the blue shark, *Prionace glauca. Fish. Bull.*, **77:** 445–457 (1979).

Pratt, H. L. and J. G. Casey. Shark reproductive strategies as a limiting factor in directed fisheries, with a review of Holden's method of estimating growth-parameters. pp. 97–109. **In:** *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries.* (H. L. Pratt, S. H. Gruber, and T. Taniuchi, Eds.). NOAA Tech. Rep. NMFS 90, U.S. Dept. of Comm., Washington, D.C. (1990).

Quignard, J. P. and C. Capapé. Note sur les espèces méditerranéennes du genre *Mustelus. Rev. Trav. Inst. Pêches Marit.*, **36:** 15–29 (1972).

Randall, J. E. A fatal attack by the shark *Carcharhinus galapagensis* at Saint Thomas, Virgin Islands. *Carib. J. Sci.*, **3:** 201–205 (1963).

Randall, J. E. Contribution to the biology of the whitetip reef shark (*Triaenodon obesus*). *Pacific Sci.*, **31:** 143–164 (1977).

Relini Orsi, L. and M. Wurtz. Ricerche sull'alimentazione di *Etmopterus spinax* (Chondrichthyes, Squalidae). *Boll. Pesca Piscic. Idrobiol.*, **31:** 257–265 (1976).

Ripley, W. E. The soupfin shark and the fishery. *Calif. Div. Fish and Game, Fish. Bull.*, **64:** 7–37 (1946).

Rodriguez-Cabello, C., F. Velasco, and I. Olaso. Reproductive biology of lesser spotted dogfish *Scyliorhinus canicula* (L., 1758) in the Cantabrian Sea. *Sci. Mar.*, **62:** 187–191 (1998).

Sadowski, V. The hammerhead sharks of the littoral zone of Sao Paulo, Brazil, with the description of a new species. *Bull. Mar. Sci.*, **15:** 1–12 (1965).

Sadowski, V. Selachier aus dem litoral von Sao Paulo, Brasilien. *Beitr. Zur Neotrop. Fauna*, **V:** 1–88 (1967).

Saunders, M. W. and G. A. McFarlane. Age and length at maturity of the female spiny dogfish, *Squalus acanthias*, in the Strait of Georgia, British Columbia, Canada. *Environ. Biol. Fish.*, **38:** 49–57 (1993).

Schwartz, F. J. Occurrence, abundance, and biology of the blacknose shark, *Carcharhinus acronotus* in North Carolina. *Northeast Gulf. Sci.*, **7:** 29–47 (1984).

Seki, T., T. Taniuchi, H. Nakano, and M. Shimizu. Age, growth, and reproduction of the oceanic whitetip shark from the Pacific Ocean. *Fish. Sci.*, **64:** 14–20 (1998).

Setna, S. B. and P. N. Sarangdhan. Description, bionomics and development of *Scoliodon sorrakowah* (Cuvier). *Rec. Indian Mus.*, **46:** 25–53 (1948).

Setna, S. B. and P. N. Sarangdhan. A contribution to the systematics of *Scoliodon acutus* (Ruppell), *Hemipristis elongatus* (Klunzinger) and *Torpedo zugmayeri* Engelhart. *Rec. Indian Mus.*, **47:** 125–134 (1949)

Simpfendorfer, C. A. Reproductive strategy of the Australian sharpnose shark, *Rhizoprionodon taylori* (Elasmobranchii: Carcharhinidae), from Cleveland Bay, northern Queensland. *Aust. J. Mar. Freshwater Res.*, **43:** 67–75 (1992).

Simpfendorfer, C. A. Age and growth of the Australian sharpnose shark, *Rhizoprionodon taylori*, from north Queensland, Australia. *Environ. Biol. Fish.*, **36:** 233–241 (1993).

Simpfendorfer, C. A. and P. Unsworth. Reproductive biology of the whiskery shark, *Furgaleus macki*, off southwestern Australia. *Mar. Freshwater Res.*, **49:** 687–693 (1998).

Skomal, G. B. Age and growth of the blue shark, *Prionace glauca*, in the North Atlantic. M.Sc. Thesis, Univ. of Rhode Island. 103 pp. (1990).

Smale, M. J. Occurrence and feeding of three shark species, *Carcharhinus brachyurus*, *C. obscurus* and *Sphyrna zygaena*, on the eastern Cape coast of South Africa. *S. Afr. J. Mar. Sci.*, **11:** 31–42 (1991).

Smale, M. J. and L. J. V. Compagno. Life history and diet of two southern African smoothhound sharks, *Mustelus mustelus* (Linnaeus, 1758) and *Mustelus palumbes* Smith, 1957 (Pisces: Triakidae). *S. Afr. J. Mar. Sci.*, **18:** 229–248 (1997).

Smale, M. J. and A. J. J. Goosen. Reproduction and feeding of spotted gully shark, *Triakis megalopterus*, off the Eastern Cape, South Africa. *Fish. Bull.*, **97:** 987–998 (1999).

Sminkey, T. R. and J. A. Musick. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. *Copeia*, **1995:** 871–883 (1995).

Sminkey, T. R. and J. A. Musick. Demographic analysis of the sandbar shark, *Carcharhinus plumbeus*, in the western North Atlantic. *Fish. Bull.*, **94:** 341–347 (1996).

Smith, S. E. Timing of vertebral-band deposition in tetracycline-injected leopard sharks. *Trans. Am. Fish. Soc.*, **113:** 308–313 (1984).

Springer, S. Natural history of the sandbar shark, *Eulamia milberti*. *U.S. Fish Wildl. Serv., Fish. Bull.*, **61:** 1–38 (1960).

Springer, S. *Triakis fehlmani*, a new shark from the coast of Somalia. *Proc. Biol. Soc. Wash.*, **81:** 613–624 (1968).

Stevens, J. D. Vertebral rings as a means of age determination in the blue shark (*Prionace glauca* L.). *J. Mar. Biol. Assoc. U.K.*, **55:** 657–665 (1975).

Stevens, J. D. Observations on reproduction in the shortfin mako *Isurus oxyrinchus*. *Copeia*, **1983:** 126–130 (1983).

Stevens, J. D. Biological observations on sharks caught by sport fishermen off New South Wales. *Aust. J. Mar. Freshwater Res.*, **35:** 573–590 (1984a).

Stevens, J. D. Life history and ecology of sharks at Aldabra Atoll, Indian Ocean. *Proc. R. Soc. Lond. B*, **222:** 79–106 (1984b).

Stevens, J. D. and J. M. Lyle. Biology of three hammerhead sharks (*Eusphyra blochii*, *Sphyrna mokarran*, and *S. lewini*), from northern Australia. *Aust. J. Mar. Freshwater Res.*, **40:** 129–146 (1989).

Stevens, J. D. and K. J. McLoughlin. Distribution, size, and sex composition, reproductive biology and diet of sharks from northern Australia. *Aust. J. Mar. Freshwater Res.*, **42:** 151–199 (1991).

Stevens, J. D. and P. D. Wiley. Biology of two commercially important carcharhinid sharks from northern Australia. *Aust. J. Mar. Freshwater Res.*, **37:** 671–688 (1986).

Stillwell, C. E. and J. G. Casey. Observations on the bigeye thresher shark, *Alopias superciliosus* in the western North Atlantic. *Fish. Bull.*, **74:** 221–225 (1976).

Strasburg, D. W. Distribution, abundance and habits of pelagic sharks in the central Pacific Ocean. *Fish. Bull. Fish Wild. Ser. U.S.*, **58:** 335–361 (1958).

Tanaka, S. The structure of the dorsal spine of the deep sea squaloid shark *Centrophorus acus* and its utility for age determination. *Nippon Suisan Gakkaishi*, **56:** 903–909 (1990).

Tanaka, S., G. M. Cailliet, and K. G. Yudin. Differences in growth of the blue shark, *Prionace glauca*: technique or population? pp. 177–187. **In:** *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries.* (H. L. Pratt, S. H. Gruber, and T. Taniuchi, Eds.). NOAA Tech. Rep. NMFS 90, U.S. Dept. of Comm., Washington, D.C. (1990).

Tanaka, S. and K. Mizue. Age and growth of Japanese dogfish *Mustelus manazo* Bleeker in the East China Sea. *Bull. Jpn. Soc. Sci. Fish.*, **45:** 43–50 (1979).

Tanaka, S., Y. Shiobara, S. Hioki, H. Abe, G. Nishi, K. Yano, and K. Suzuki. The reproductive biology of the frilled shark, *Chlamydoselachus anguineus*, from Suruga Bay, Japan. *Jpn. J. Icthyol.*, **37:** 273–291 (1990).

Taniuchi, T. Reproduction of the sandbar shark, *Carcharhinus milberti*, in the East China Sea. *Jpn. J. Icthyol.*, **18:** 94–98–(1971).

Taniuchi, T., H. Kobayashi, and T. Otake. Occurrence and reproductive mode of the false cat shark, *Pseudotriakis microdon*, in Japan. *Jpn. J. Icthyol.*, **31:** 88–92 (1984).

Taniuchi, T., N. Kuroda, and Y. Nose. Age, growth, reproduction, and food habits of the star-spotted dogfish, *Mustelus manazo* collected from Choshi. *Bull. Jpn. Soc. Sci. Fish.*, **49:** 1325–1334 (1983).

Taniuchi, T. and H. Tachikawa. Geographical variation in age and growth of *Squalus mitsukurii* (Elasmobranchii: Squalidae) in the North Pacific. pp. 321–328. **In:** *Proceedings of the 5th Indo-Pacific Fish Conference, 3–8 November 1997, Nouméa-New Caledonia.* Société Française d'Ichtyologie, Paris, France (1999).

Taniuchi, T., H. Tachikawa, M. Shimizu, and Y. Nose. Geographical variations in reproductive parameters of shortspine spurdog in the North Pacific. *Nippon Suisan Gakkaishi*, **59:** 45–51 (1993).

Templeman, W. The life history of the spiny dogfish, *Squalus acanthias* and the vitamin A values of dogfish liver oil. Newfoundland Dept. Natl. Resour. Res. Bull. 15 (Fisheries) (1944).

Teshima, K. Studies on sharks—XII. Monthly change of the gonad index in male *Mustelus manazo* and *M. griseus*. *Jpn. J. Ichthyol.*, **24:** 285–289 (1978).

Teshima, K., Y. Kamei, M. Toda, and S. Uchida. Reproductive mode of the tawny nurse shark taken from the Yaeyama Islands, Okinawa, Japan, with comments on individuals lacking the second dorsal fin. *Bull. Seikai Natl. Fish. Res. Inst.*, **73:** 1–12 (1995).

Teshima, K., K. Mizue, and S. Koga. Studies on sharks—VII. Reproduction in female *Mustelus griseus*. *J. Shimonoseki Univ. Fish.*, **22:** 199–206 (1974).

Teshima, K., H. Yoshimura, and K. Mizue. Studies on sharks—II. On the reproduction of Japanese dogfish *Mustelus manazo* Bleeker. *Bull. Fac. Fish. Nagasaki Univ.*, **32:** 41–50 (1971).

Tester, A. L. Cooperative shark research and control program. Univ. Hawaii Final Rep. 1967–69. pp. 1–47 (1969).

Uchida, S., M. Toda, K. Teshima, and K. Yano. Pregnant white sharks and full-term embryos from Japan. pp. 139–155. **In:** *Great White Sharks: The Biology of Carcharodon carcharias.* (A. P. Klimley and D. G. Ainley, Eds.). San Diego, CA: Academic Press (1996).

Vaske-Junior, T. and G. Rincon-Filho. Conteudo estomacal dos tubaroes azul (*Prionace glauca*) e anequim (*Isurus oxyrinchus*) em aguas oceanicas no sul do Brasil. *Rev. Bras. Biol.*, **58:** 445–452 (1998).

Walker, T. I. Fishery model of gummy shark for Bass Strait. pp. 422–438. *In*: *Proceedings of Resource Technology '94 New Opportunities Best Practice'*. (I. Bishop, Ed.). The Centre for Geographic Information Systems and Modelling, Univ. of Melbourne, Australia (1994).

Walker, T. I. Stock assessment of the school shark, *Galeorhinus galeus* (Linnaeus), off southern Australia by applying a delay-difference model. Report to Southern Shark Fishery Assessment Group, Mar. Fresh. Res. Inst., Queenscliff, Victoria. 28 pp. (1995).

Waller, G. N. H. and A. Baranes. Food of *Iago omanensis*, a deep water shark from the northern Red Sea. *J. Fish Biol.*, **45:** 37–45 (1993).

Walter, J. P. and D. A. Ebert. Preliminary estimates of age of the bronze whaler *Carcharhinus brachyurus* (Chondrichthyes: Carcharhinidae) from southern Africa, with a review of some life history parameters. *S. Afr. J. Mar. Sci.*, **10:** 37–44 (1991).

Wass, R. C. A comparative study of the life history, distribution and ecology of the sandbar shark and the gray reef shark in Hawaii. Doctoral Dissertation, Univ. Hawaii, Honolulu, 219 pp. (1971).

Watson, G. and M. J. Smale. Reproductive biology of shortnose spiny dogfish, *Squalus megalops*, from the Agulhas Bank, South Africa. *Mar. Freshwater Res.*, **49:** 695–703 (1998).

Watson, G. and M. J. Smale. Age and growth of the shortnose spiny dogfish, *Squalus megalops* from the Agulhas Bank, South Africa. *S. Afr. J. Mar. Sci.*, **21:** 9–18 (1999).

Wetherbee, B. M. Distribution and reproduction of the southern lantern shark from New Zealand. *J. Fish. Biol.*, **49:** 1186–1196 (1996).

Wetherbee, B. M., G. L. Crow, and C. G. Lowe. Biology of the Galapagos shark, *Carcharhinus galapagensis*, in Hawaii. *Environ. Biol. Fish.*, **45:** 299–310 (1996).

Wetherbee, B. M., G. L. Crow, and C. G. Lowe. Distribution, reproduction and diet of the gray reef shark *Carcharhinus amblyrhynchos* in Hawaii. *Mar. Ecol. Prog. Ser.*, **151:** 181–189 (1997).

Wheeler, J. F. G. Report on the Mauritius-Seychelles Fisheries Survey 1948–1949. Part I. The bottom fishes of economic importance. *Fish. Publ., London*, **1:** 1–57 (1953).

Wheeler, J. F. G. Notes on the three common species of sharks in the Mauritius-Seychelles area. *Proc. R. Soc. Arts Sci. Maurit.*, **2:** 146–160 (1962).

Wilson, C. D. and M. P. Seki. Biology and population characteristics of *Squalus mitsukurii* from a seamount in the central North Pacific Ocean. *Fish. Bull.*, **92:** 851–864 (1994).

Wintner, S. P. and G. Cliff. Age and growth determination of the blacktip shark, *Carcharhinus limbatus*, from the east coast of South Africa. *Fish. Bull.*, **94:** 135–144 (1996).

Wintner, S. P. and G. Cliff. Age and growth determination of the white shark, *Carcharodon carcharias*, from the east coast of South Africa. *Fish. Bull.*, **97:** 153–169 (1999).

Yamaguchi, A., T. Taniuchi, and M. Shimizu. Age and growth of the starspotted dogfish *Mustelus manazo* from Tokyo Bay, Japan. *Fish. Sci.*, **62:** 919–922 (1996).

Yamaguchi, A., T. Taniuchi, and M. Shimizu. Reproductive biology of the starspotted dogfish *Mustelus manazo* from Tokyo Bay, Japan. *Fish. Sci.*, **63:** 918–922 (1997a).

Yamaguchi, A., T. Taniuchi, and M. Shimizu. Geographic variation in growth of the starspotted dogfish *Mustelus manazo* from five localities in Japan and Taiwan. *Fish. Sci.*, **64:** 732–739 (1998).

Yano, K. Catch distribution, stomach contents, and size at maturity of two Squaloid sharks, *Deania calceus* and *D. crepidalbus*, from the southeast Atlantic off Namibia. *Bull. Jpn. Soc. Fish. Oceanogr.*, **55:** 189–196 (1991).

Yano, K. Reproductive biology of the slender smoothhound, *Gollum attenuatus*, collected from New Zealand waters. *Environ. Biol. Fish.*, **38:** 59–71 (1993).

Yano, K. and S. Tanaka. Some biological aspects of the deep sea squaloid shark *Centroscymnus* from Suruga Bay. *Jpn. Bull. Jpn. Soc. Fish.*, **50:** 249–256 (1984).

Yano, K., M. Toda, S. Uchida, and F. Yasuzumi. Gross anatomy of the viscera and stomach contents of a megamouth shark, *Megachasma pelagios*, from Hakata Bay, Japan, with a comparison of the intestinal structure of other planktivorous elasmobranchs. pp. 105–113. **In:** *Biology of the Megamouth Shark*. (K. Yano, J. Morrissey, Y. Yabumoto, and K. Nakaya, Eds.). Tokyo, Japan: Tokai Univ. Press (1997).

Yudin, K. G. and G. M. Cailliet. Age and growth of the gray smoothhound, *Mustelus californicus*, and the brown smoothhound, *M. henlei*, sharks from central California. *Copeia*, **1990:** 191–204 (1990).

APPENDIX

Life History Trait Information for 230 Populations from 164 Species of Sharks. All Size Data Are in Centimeters Total Length, Ages Are in Years, and K is the Growth Constant (yr^{-1}) from the von Bertalanffy Growth Equation. Data Are Given for Females and Males, or for Sexes Combined (All); Litter Size is Reported As the Mean and a Range. Longevity Is the Value Obtained Through Aging of Hard Parts, Tag-Recapture, or Captivity (Empirical or an Expected Theoretical Value (in Parentheses)[a]

Species	Maximum size			Litter size		Offspring	K			Size at maturity		Age at maturity			Longevity		
	Female	Male	All	Mean	Range	size	Female	Male	All	Female	Male	Female	Male	All	Female	Male	All
Carcharhiniformes																	
Carcharhinidae																	
Carcharhinus acronotus (EGM)	130	122	—	—	4-5	38-45	0.210	0.483	—	110	103	3	2.5	—	4.5 (17)	4.5 (7)	—
C. acronotus (NWA)	154	164	—	—	4-6	45-50	0.138	0.117	—	120	110	3-4	3	—	5 (25)	6 (30)	—
C. albimarginatus (SWI)	208	204	—	5.5	1-10	70-80	—	—	—	165-200	165-180	—	—	—	—	—	—
C. albimarginatus (NI)	261	235	—	—	1-10	80-82	—	—	—	200	170-180	—	—	—	—	—	—
C. altimus (NWA)	282	267	—	—	3-15	70-90	—	—	—	226	216	—	—	—	—	—	—
C. amblyrhynchoides (EI)	162	161	—	3	1-9	50-60	—	—	—	115	—	—	—	—	—	—	—
C. amblyrhynchos (CP1)	187	174	—	5	3-6	60	—	—	0.294	137	130-135	7	—	—	—	—	12 (12)
C. amblyrhynchos (CP2)	190	185	—	4.1	3-6	60	—	—	—	125	120-140	—	—	—	—	—	—
C. amblyrhynchos (EI)	178	150	—	3	2-3	63	—	—	—	135	—	—	—	—	—	—	—
C. amblyrhynchos (NI)	172	168	—	—	1-4	70	—	—	—	122-125	112-140	—	—	—	—	—	—
C. amboinensis (SWI1)	223	196	—	—	—	75	—	—	—	200	—	—	—	—	—	—	—
C. amboinensis (SWI2)	246	239	—	5.2	3-7	79	—	—	—	224	210	—	—	—	—	—	—
C. amboinensis (EI)	243	231	—	9	6-13	60-65	—	—	—	215	208	—	—	—	—	—	—
C. brachyurus (SWI1)	292	294	—	16	13-24	69	—	—	0.039	229	200	19.5	16	—	25 (90)	30 (90)	—
C. brachyurus (SWI2)	303	293	—	13	11-16	75	—	—	—	231	200	—	—	—	—	—	—
C. brevipinna (SWI)	266	233	—	—	6-15	65-75	—	—	—	212-266	176-200	—	—	—	—	—	—
C. brevipinna (EI)	276	260	—	—	8-13	70-80	—	—	—	210	195	—	—	—	—	—	—

Species	Maximum size			Litter size		Offspring	K			Size at maturity		Age at maturity			Longevity		
	Female	Male	All	Mean	Range	size	Female	Male	All	Female	Male	Female	Male	All	Female	Male	All
C. cautus (NEI)	119	101	—	2.9	1-5	40	—	—	—	91	84	—	—	—	—	—	—
C. dussumieri (EI)	88	87	—	2	1-3	38-40	—	—	—	70	70	—	—	—	—	—	—
C. falciformis (NWGM)	305	272	—	—	10-15	70-75	—	—	0.153	>225	210-220	7-9	6-7	—	14	13	(23)
C. falciformis (SGM)	308	314	—	11	2-12	76	0.091	0.098	0.101	232-245	225	12	10	—	22 (38)	20 (35)	---
C. falciformis (NWA)	330	—	—	—	6-14	75	—	—	—	234	218	—	—	—	—	—	—
C. falciformis (WI)	283	244	—	11	9-14	74-78	—	—	—	248	—	—	—	—	—	—	—
C. falciformis (SWP)	250	225	—	7	5-8	—	—	—	—	200	210-215	—	—	—	—	—	—
C. fitzroyensis (NEI)	135	126	—	3.7	1-7	50	—	—	—	100	88	—	—	—	—	—	—
C. galapagensis (CP)	300	267	—	8.7	4-16	80	—	—	0.172	215-245	205-239	6.5-9	6-8	—	—	—	15 (20)
C. isodon (NWA)	160	144	—	4	2-6	48-58	—	—	—	135	130	—	—	—	—	—	—
C. leucas (NGM)	—	—	285	8	5-10	60-80	—	—	0.076	>225	210-220	18	14.5	—	24	21	(46)
C. leucas (SWI)	—	—	300	9	6-12	79	—	—	—	233-246	233-246	—	—	—	—	—	—
C. limbatus (NWGM)	—	—	176	4.8	3-6	—	—	—	0.274	150-155	130	7-8	4-5	—	9.3	5.8	(13)
C. limbatus (EGM)	191	175	—	4.9	3-6	52-60	0.197	0.276	—	158-162	133-135	6-7	4-5	—	10 (18)	9 (13)	—
C. limbatus (NWA)	202	189	—	4	2-6	55-60	—	—	—	156	142-145	—	—	—	—	—	—
C. limbatus (SWI)	247	246	—	6	-11	67	0.210	0.200	0.210	206-211	199-204	7	6	—	11 (17)	10 (17)	(17)
C. longimanus (NWA)	—	—	>260	—	10-15	65-75	—	—	—	175	—	—	—	—	—	—	—
C. longimanus (SWA)	>250	>235	—	—	—	—	—	—	0.099	180-190	180-190	—	—	6-7	17	14	(35)
C. longimanus (SWI)	>270	>245	—	—	—	60-65	—	—	—	180-190	>198	—	—	—	—	—	—
C. longimanus (SWP)	270	251	—	6.8	4-8	—	—	—	—	200	—	—	—	—	—	—	—
C. longimanus (CP/WP)	272	240	—	8.2	1-14	63-77	—	—	0.103	175-189	175-189	4-5	4-5	—	—	—	11 (34)
C. macloti (EI)	108	96	—	2	1-2	40-45	—	—	—	70-75	74	—	—	—	—	—	—
C. melanopterus (WI)	140	130	—	3.7	2-5	50	—	—	—	110	105	—	—	—	—	—	—
C. melanopterus (EI)	125	112	—	3.8	3-4	48	—	—	—	97	95	—	—	—	—	—	—
C. obscurus (NWA)	371	360	—	—	10-12	85-100	0.039	0.038	—	284	279	21	19	—	39 (89)	39 (91)	—
C. obscurus (SWI)	389	324	—	9.9	6-14	80-90	—	—	0.047	260-300	280	17-24	20.5	—	34	—	(74)
C. perezi (CARIB)	—	—	295	4	4-6	-73	—	—	—	200	160	—	—	—	—	—	—
C. plumbeus (CP)	190	172	—	5.5	1-8	60-75	—	—	—	144	131	—	—	—	—	—	—
C. plumbeus (NWA1)	234	226	—	8.4	4-12	61-65	0.059	0.059	0.057	—	—	15-16	15-16	—	24 (59)	20 (59)	24 (61)

APPENDIX (CONTINUED)

Species	Maximum size			Litter size		Offspring	K			Size at maturity		Age at maturity			Longevity		
	Female	Male	All	Mean	Range	size	Female	Male	All	Female	Male	Female	Male	All	Female	Male	All
C. plumbeus (NWA2)	233	—	—	—	—	—	0.086	0.087	0.089	—	—	15-16	15-16	—	22 (40)	18 (40)	22 (39)
C. plumbeus (NWA3)	—	—	—	—	—	—	0.040	0.050	—	—	—	12	13	—	21 (87)	15 (69)	—
C. plumbeus (NWA4)	—	—	—	—	—	—	—	—	0.046	—	—	—	—	29-30	32	40	(75)
C. plumbeus (NWA5)	234	226	—	9	1-14	61-64	—	—	—	183	180	—	—	—	—	—	—
C. plumbeus (SWI1)	195	188	—	8	—	60-65	—	—	—	173	163	—	—	—	—	—	—
C. plumbeus (SWI2)	203	193	—	7.2	4-10	68	—	—	—	170	168	—	—	—	—	—	—
C. plumbeus (NI)	220	213	—	8.3	6-11	—	—	—	—	177	180	—	—	—	—	—	—
C. plumbeus (EI)	208	204	—	6	3-8	60	—	—	—	155	156	—	—	—	—	—	—
C. porosus (NWA)	134	117	—	6	—	30	—	—	—	84	75-78	—	—	—	—	—	—
C. porosus (SWA)	120	105	—	7	2-7	30	—	—	0.101	70	71	6	6	—	12	12	(34)
C. sealei (SWI)	92	90	—	—	1-2	35-45	—	—	—	—	70-80	—	—	—	—	—	—
C. signatus (NWA)	—	—	>275	—	12-18	65	—	—	—	178-179	—	—	—	—	—	—	—
C. sorrah (EI)	152	131	—	3.1	1-8	52	0.340	1.170	—	95	90	2-3	1-2	—	7 (10)	5 (3)	—
C. tilstoni (EI)	180	—	—	3	1-6	60	0.140	0.190	—	115	110	3-4	3-4	—	12 (25)	8 (18)	—
C. wheeleri (WI1)	172	168	—	2.4	1-4	70	—	—	—	125	112-140	—	—	—	—	—	—
C. wheeleri (WI2)	182	158	—	3.3	2-4	65-70	—	—	—	—	110-120	—	—	—	—	—	—
Galeocerdo cuvier (NWA)	—	—	>450	55	30-70	70-85	—	—	0.107	315-320	310	10	10	—	16	15	(32)
G. cuvier (NWGM)	—	—	>450	—	—	—	—	—	0.184	—	—	8	7	—	11	9	(19)
G. cuvier (SWI)	410	370	—	35	23-46	—	—	—	—	340	>290	—	—	—	—	—	—
G. cuvier (SWP)	428	350	—	31	6-56	80-90	—	—	—	287	—	—	—	—	—	—	—
Isogomphodon oxyrhynchus (SWA)	145	125	—	6	3-7	43	—	—	—	115	103	—	—	—	—	—	—
Loxodon macrorhinus (EI)	88	80	—	2	1-2	40-46	—	—	—	57	64	—	—	—	—	—	—
Negaprion acutidens (WI)	240	242	—	9	6-12	55-60	—	—	—	220	220	—	—	—	—	—	—
N. brevirostris (GM/NWA)	—	—	320	—	8-12	60-65	0.060	0.055	0.057	240	225	12.7	11.6	—	18 (58)	20 (63)	(61)
Prionace glauca (NEP)	—	—	310	—	40-80	40-50	0.251	0.175	0.223	—	—	—	—	—	(14)	9 (20)	(16)
P. glauca (NEA)	—	—	300	—	—	—	—	—	0.110	—	—	6-7	—	—	—	—	(32)
P. glauca (NWP)[b]	—	—	—	—	—	36	0.144	0.129	—	140-160	130-160	5-6	4-5	—	(24)	(27)	—
P. glauca (NWA)	327	340	—	—	—	—	0.150	0.160	0.170	221	215	4-5	6	—	13 (23)	16 (22)	(20)
P. glauca (ECA)	—	—	318	37	4-75	—	—	—	—	221	—	—	—	—	—	—	—

Species	Maximum size			Litter size		Offspring	K			Size at maturity		Age at maturity			Longevity		
	Female	Male	All	Mean	Range	size	Female	Male	All	Female	Male	Female	Male	All	Female	Male	All
P. glauca (SWP)	316	312	—	32	4-57	40-50	—	—	—	218	—	—	—	—	—	—	—
P. glauca (SWI)	320	—	—	—	—	48-50	—	—	—	208	—	—	—	—	—	—	—
P. glauca (EI)	323	—	—	34	11-49	43	—	—	—	220	—	—	—	—	—	—	—
Rhizoprionodon acutus (SWI)	102	89	—	4.7	2-8	30-35	—	—	—	70-80	68-72	—	—	—	—	—	—
R. acutus (EI)	98	89	—	3	1-6	34-38	—	—	—	75	75	—	—	—	—	—	—
R. lalandii (SWA)	77	64	—	—	1-4	33-34	—	—	—	54	45-50	—	—	—	—	—	—
R. oligolinx (ALL)	70	61	—	—	3-5	21-26	—	—	—	32-41	29-38	—	—	—	—	—	—
R. porosus (ALL)	108	85	—	—	2-6	31-39	—	—	—	80	60	—	—	—	—	—	—
R. taylori (SWP)	>78	>69	—	4.5	1-10	22-26	1.013	1.337	—	>54	>56	1	1	—	7 (3)	6 (3)	—
R. taylori (EI)	66	55	—	5	1-8	25-30	—	—	—	45	43	—	—	—	—	—	—
R. terraenovae (GM1)	107	105	—	5	1-7	30-35	—	—	0.359	85-90	80-85	4	3	—	—	—	6 (10)
R. terraenovae (GM2)	107	103	—	—	—	—	—	—	0.450	—	—	2.8-3.9	2.4-3.4	—	—	—	7 (8)
Scoliodon laticaudus (NI)	69	58	—	—	1-14	14	0.358	0.406	—	33-35	24-36	1.6	1.2	—	(10)	(9)	7
Triaenodon obesus (CP)	>158	>168	—	2	1-5	52-60	—	—	—	105-109	104-105	—	—	—	—	—	—
Sphyrnidae																	
Eusphyra blochii (EI)	176	169	—	11.8	6-25	45-47	—	—	—	120	108	—	—	—	—	—	—
Sphyrna lewini (NWGM)	310	300	—	—	30-40	45-50	—	—	0.073	250	180	15	9-10	—	17	12	(47)
S. lewini (EI)	346	301	—	16.5	13-23	45-50	—	—	—	200	140-160	—	—	—	—	—	—
S. lewini (WP)	324	305	—	26	12-38	47	0.249	0.222	—	210	198	4.1	3.8	—	14 (14)	11 (16)	—
S. mokarran (EI)	409	332	—	15.4	6-33	65	—	—	—	210	225	—	—	—	—	—	—
S. mokarran (SWI)	459	374	—	—	—	—	—	—	—	337	309	—	—	—	—	—	—
S. tiburo (GM/Florida Bay)	104	82	—	9.3	—	27.4	0.370	0.530	—	80-85	68-70	2.4-3.0	2	—	7 (9)	6 (7)	—
S. tiburo (GM/Tampa Bay)	116	89	—	8.9	3-15	34.7	0.340	0.580	—	85-90	80	2.0-2.4	2	—	7 (10)	5 (6)	—
S. tiburo (GM/Northwest Florida)	124	109	—	—	—	—	0.280	0.690	—	—	—	2.4	2	—	6 (12)	5 (5)	—
S. tudes (CARIB)	120	121	—	—	5-12	30	—	—	—	98	80	—	—	—	—	—	—
S. zygaena (ALL)	>304	>256	—	—	29-37	50-61	—	—	—	210-240	210-240	—	—	—	—	—	—
Triakidae																	
Furgaleus macki (SEI/SWP)	132	135	—	—	9-16	20	—	—	—	110	109	—	—	—	—	—	—

APPENDIX (CONTINUED)

Species	Maximum size			Litter size		Offspring	K			Size at maturity		Age at maturity			Longevity		
	Female	Male	All	Mean	Range	Size	Female	Male	All	Female	Male	Female	Male	All	Female	Male	All
Furgaleus macki (SEI)	150	142	—	9	4-28	22-27	—	—	—	126	121	—	—	—	—	—	—
Galeorhinus galeus (SWA)	155	148	—	23	4-41	30	0.075	0.092	—	118-128	107-117	14-17.5	10.5-13	—	36 (46)	36 (38)	—
G. galeus (NEP)	195	185	—	—	—	—	—	—	—	150-180	135-175	—	—	—	—	—	—
G. galeus (SWP1)	174	171	—	28.4	17-41	28-35	—	—	0.124	>135	120-132	12	8-10	—	53	41	—
G. galeus (SWP2)	168	175	—	—	—	—	0.086	0.154	0.086	135-140	125-135	13-15	12-17	—	>25 (40)	(23)	(40)
Gogolia filewoodi (WP)	74	—	—	2	—	22	—	—	—	—	—	—	—	—	—	—	—
Hemitriakis japanica (WP)	>120	110	—	—	8-22	20-21	—	—	—	81-102	85	—	—	—	—	—	—
H. leucoperiptera (CWP)	96	—	—	12	—	>21	—	—	—	—	—	—	—	—	—	—	—
Hypogaleus hyugaensis (SWI)	122	127	—	11	—	32-35	—	—	—	114	112	—	—	—	—	—	—
Iago garricki (SWP)	65	—	—	—	4-5	23	—	—	—	—	—	—	—	—	—	—	—
I. omanensis (RED SEA/NWI)	67	43	—	—	2-10	>17	—	—	—	>40	>30	—	—	—	—	—	—
Mustelus antarcticus (SEI/SWP)	164	130	—	—	1-31	30-36	0.123	0.253	—	120-130	93	8	—	—	16 (28)	13 (14)	—
M. asterias (MED)	150	—	—	—	—	28-30	—	—	—	80	—	—	—	—	—	—	—
M. californicus (NEP)	163	116	—	—	2-5	20-30	0.218	0.350	0.168	70	57-65	2-3	1-2	—	9 (16)	6 (10)	(21)
M. canis (NWA)	150	110	—	—	4-20	34-39	—	—	—	95-100	70-80	—	—	—	—	—	—
M. dorsalis (EP)	64	—	—	4	—	21-23	—	—	—	43	43	—	—	—	—	—	—
M. griseus (NWP)	101	87	—	—	5-16	28	—	—	—	80	62-71	—	—	—	—	—	—
M. henlei (NEP)	100	79.5	—	—	3-5	28	0.225	0.285	0.224	51-63	52-66	2-3	3	—	13 (15)	7 (12)	(15)
M. lenticulatus (SWP)	137	114	—	—	2-23	30	—	—	—	90-100	80-90	—	—	—	—	—	—
M. manazo (NWP/Choshi)	—	—	—	4.9	1-22	30	0.070	0.100	—	62-64	62-64	5	4	—	9 (50)	9 (35)	—
M. manazo (NWP/Nagasaki)	96	96	—	—	—	—	0.200	0.220	—	—	—	—	—	—	(17)	(16)	—
M. manazo (NWP/Aomori)	135	104.5	—	—	—	—	0.122	0.163	—	—	—	—	—	—	17 (28)	9 (21)	—
M. manazo (NWP/Tokyo Bay)	107	95	—	6	2-13	20-30	0.113	0.155	—	70-82	69-78	3-4	3-5	—	10 (31)	8 (22)	—
M. manazo (NWP/Maizuru)	116	84	—	—	—	—	0.161	0.280	—	—	—	—	—	—	13 (22)	6 (12)	—
M. manazo (NWP/Shimonoseki)	104	104	—	—	—	—	0.149	0.158	—	—	—	—	—	—	10 (23)	6 (22)	—
M. manazo (NWP/Taiwan)	86.5	71	—	5.1	2-14	—	0.124	0.233	—	60	55	2	2	—	9 (28)	5 (15)	—
M. mento (SEP/SWA)	—	—	130	7	—	30	—	—	—	86-90	—	—	—	—	—	—	—
M. mosis (NI/NWI/SWI)	—	106	—	—	6-10	—	—	—	—	82	63-67	—	—	—	—	—	—
M. mustelus (SEA/SWI)	165	145	—	11.5	2-23	42.5	—	—	—	125-140	95-130	—	—	—	—	—	—
M. norrisi (GM/CARIB/SWA)	—	—	100	—	7-14	30	—	—	—	65	58	—	—	—	—	—	—

Species	Maximum size			Litter size		Offspring	K			Size at maturity		Age at maturity			Longevity		
	Female	Male	All	Mean	Range	size	Female	Male	All	Female	Male	Female	Male	All	Female	Male	All
M. palumbes (SEA/SWI)	113	101	—	6.9	3-15	34	—	—	—	80-100	75-85	—	—	—	—	—	—
M. punctulatus (MED)	191	182	—	—	—	38-43	—	—	—	100	90	—	—	—	—	—	—
M. schmitti (SWA)	109	87	—	6.2	2-13	28	—	—	—	62	60	—	—	—	—	—	—
M. whitneyi (SEP)	87	—	—	—	5-10	25	—	—	—	74	68	—	—	—	—	—	—
Scylliogaleus quecketti (SWI)	102	89	—	2.6	2-4	34	—	—	—	74-80	>70	—	—	—	—	—	—
Triakis megalopterus (SWI)	207.5	152	—	9.7	5-15	43.5	—	—	—	145	132	—	—	—	—	—	—
T. scyllium (NWP)	—	—	150	—	10-20	—	—	—	—	99-108	—	—	—	—	—	—	—
T. semifasciata (NEP)	180	160	—	—	7-36	20	0.073	0.089	—	105-135	100-105	10-15	7-13	—	(47)	24 (39)	—
Pseudotriakidae																	
Pseudotriakis microdon (SWI)	295	269	—	—	2-4	70-85	—	—	—	212	200	—	—	—	—	—	—
Hemigaleidae																	
Hemigaleus microstoma (EI)	110	103	—	8	1-19	30	—	—	—	65	60	—	—	—	—	—	—
Hemipristis elongatus (EI)	184	177	—	6	2-11	52	—	—	—	110-120	110	—	—	—	—	—	—
Paragaleus pectoralis (SEA)	117	114	—	—	1-4	47	—	—	—	75-90	76	—	—	—	—	—	—
Proscylliidae																	
Ctenacis fehlmanni (NWI)	46	—	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—
Eridacnis barbouri (NWA/CARIB)	—	—	34	2	2	>10	—	—	—	28	27	—	—	—	—	—	—
E. radcliffei (ALL)	24	23	—	—	1-2	11	—	—	—	15-16	18-19	—	—	—	—	—	—
E. sinuans (SWI)	37	>30	—	2	2	15-17	—	—	—	—	29-30	—	—	—	—	—	—
Gollum attenuatus (SWP)	109	107	—	—	—	41	—	—	—	70	70	—	—	—	—	—	—
Proscyllium habereri (NWP/WP)	65	57	—	2	2	—	—	—	—	51	42	—	—	—	—	—	—
Scyliorhinidae																	
Apristurus brunneus (NEP)	56	62.5	—	2	2	7	—	—	—	42.5-47	45-50	—	—	—	—	—	—
A. japonicus (NWP)	63	65-71	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. kampae (EP)	52	—	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—
A. macrorhynchus (NWP)	66	—	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—

APPENDIX (CONTINUED)

Species	Maximum size			Litter size		Offspring	K			Size at maturity		Age at maturity			Longevity		
	Female	Male	All	Mean	Range	size	Female	Male	All	Female	Male	Female	Male	All	Female	Male	All
A. maderensis (NEA)	67	68	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—
A. parvipinnis (GM/CARIB)	52	48	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—
A. platyrhynchus (ALL)	—	—	80	2	2	—	—	—	—	—	—	—	—	—	—	—	—
A. riveri (GM/CARIB)	40-41	43-46	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—
Asymbolus vincenti (SEI/SWP)	—	—	61	2	2	—	—	—	—	—	—	—	—	—	—	—	—
Atelomycterus macleayi (SEI/SWP)	—	—	60	2	2	10	—	—	—	—	—	—	—	—	—	—	—
A. marmoratus (ALL)	—	—	70	2	2	—	—	—	—	—	—	—	—	—	—	—	—
Cephaloscyllium sufflans (SWI)	109	89	—	2	2	20-22	—	—	—	71-82	—	—	—	—	—	—	—
C. umbratile (NWP)	114.5	114	—	—	—	—	—	—	—	92-94	86-88	—	—	—	—	—	—
C. ventriosum (ALL)	—	—	>100	2	2	14-15	—	—	—	—	—	—	—	—	—	—	—
Cephalurus cephalus (CEP)	—	—	28	2	2	10	—	—	—	19	19	—	—	—	—	—	—
Galeus arae arae (ALL)	43	36	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—
G. eastmani (NWP)	40	36	—	2	2	—	—	—	—	36-37	31-32	—	—	—	—	—	—
G. melastomus (EA/MED)	90	61	—	—	?-13	—	—	—	—	39-45	34-42	—	—	—	—	—	—
G. nipponensis (NWP)	65.6	—	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—
G. polli (ECA/SEA)	42	39	—	—	4-10	12	—	—	—	—	—	—	—	—	—	—	—
G. sauteri (NWP)	45	38	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—
Halaelurus boesemani (ALL)	47	48	—	—	?-8	>7	—	—	—	—	—	—	—	—	—	—	—
H. buergeri (NWP)	49	43	—	—	2-?	—	—	—	—	—	36	—	—	—	—	—	—
H. canescens (SEP)	68	65	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—
H. hispidus (NI)	29	26	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—
H. lineatus (SWI)	52	56	—	—	?-16	—	—	—	—	—	32-38	—	—	—	—	—	—
H. lutarius (WI/SWI)	39	34	—	2	2	10	—	—	—	—	—	—	—	—	—	—	—
H. natalensis (SWI)	47	45	—	—	12-18	—	—	—	—	37-38	39-41	—	—	—	—	—	—
Haploblepharus edwardsii (SWI)	60	59	—	2	2	10	—	—	—	>41	42-51	—	—	—	—	—	—
H. fuscus (SWI)	73	69	—	2	2	—	—	—	—	59	53	—	—	—	—	—	—
Holohalaelurus punctatus (SWI)	26	34	—	2	2	—	—	—	—	22-23	24	—	—	—	—	—	—
H. regani (SEA/SWI/WI)	41	61	—	2	2	—	—	—	—	38-39	50-54	—	—	—	—	—	—
Parmaturus xaniurus (NEP)	57	52	—	2	2	—	—	—	—	42.5-47	37.5-42	—	—	—	—	—	—
Poroderma africanum (SWI)	93	101	—	2	2	14-15	—	—	—	65-72	58-76	—	—	—	—	—	—

Species	Maximum size			Litter size		Offspring	K			Size at maturity		Age at maturity			Longevity		
	Female	Male	All	Mean	Range	size	Female	Male	All	Female	Male	Female	Male	All	Female	Male	All
P. pantherinum (SWI)	73	84	—	2	2	—	—	—	—	58-61	54-59	—	—	—	—	—	—
Schroederichthys bivius (SEP/SWA)	70	82	—	2	2	—	—	—	—	40	53	—	—	—	—	—	—
S. maculatus (CARIB)	34	33	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—
Scyliorhinus canicula (MED)	>60	60	—	2	2	8-9	—	—	—	44	39	—	—	—	—	—	—
Scyliorhinus canicula (NEA)	—	—	100	2	2	9-11	—	—	0.126	54	—	—	—	—	—	—	9 (28)
S. capensis (SWI)	85	95	—	2	2	<30-31	—	—	—	68-70	66-78	—	—	—	—	—	—
S. retifer (NWA/GM/CARIB)	59	58	—	2	2	11	—	—	—	52	50	—	—	—	—	—	—
S. stellaris (NEA/MED/EA)	—	—	-162	2	2	16	—	—	—	—	—	—	—	—	—	—	>19
S. torazame (NWP)	>39	48	—	2	2	>8	—	—	—	—	—	—	—	—	—	—	—
Lamniformes																	
Lamnidae																	
Carcharodon carcharias (NEP)	640	550	—	—	8-10	91-152	—	—	0.058	457	426	9-10	—	—	—	—	15 (60)
C. carcharias (SWI)	500	—	—	—	—	—	—	—	0.065	—	—	—	—	—	—	—	—
Isurus oxyrinchus (SWP)	340	270	—	—	4-14	70	—	—	—	280	195	—	—	—	—	—	—
I. oxyrinchus (NEP)	—	—	351	—	—	—	—	—	0.072	180-280	—	7-8	—	—	17	—	(48)
I. oxyrinchus (NWA)	375	298	—	—	9-18	70-80	0.203	0.266	—	280	—	7	—	—	11.5 (17)	4.5(13)	—
I. oxyrinchus (SWI)	333	271	—	—	9-14	—	—	—	—	266	194-206	—	—	—	—	—	—
Lamna nasus (NWA)	—	—	365	—	2-5	70-72	—	—	0.116	200-250	150-200	7.5	—	—	19	—	(30)
Alopiidae																	
Alopias pelagicus (NWP)	375	353	—	2	2	158-190	0.085	0.118	—	282-292	267-276	8.0-9.2	7.0-8.0	—	16 (41)	14 (29)	—
A. vulpinus (NEP)	—	—	630	4	2-4	117-155	0.158	0.215	0.108	315	333	3-4	4-5	—	(22)	(16)	15 (32)
A. superciliosus (NEA)	444	410	—	2	2-4	>100	—	—	—	341	276	—	—	—	—	—	—
A. superciliosus (NWP)	422	357	—	2	2	135-140	0.092	0.088	—	332-341	270-288	12.3-13	9-10	—	20 (38)	19 (39)	—
Odontaspididae																	
Carcharias taurus (NWA)	318	250	—	2	2	100	0.142	0.174	0.143	220-230	190-195	6	4-5	—	10.5 (25)	7.5 (20)	16 (19)

APPENDIX (CONTINUED)

Species	Maximum size			Litter size		Offspring	K			Size at maturity		Age at maturity			Longevity		
	Female	Male	All	Mean	Range	size	Female	Male	All	Female	Male	Female	Male	All	Female	Male	All
Cetorhinidae																	
Cetorhinus maximus (ALL)	—	—	980	6	—	150	—	—	0.110	500	—	5	—	—	—	—	(32)
Pseudocarchariidae																	
Pseudocarcharias kamoharai (SWI)	105	98	—	4	—	40-43	—	—	—	89-102	74	—	—	—	—	—	—
Orectolobiformes																	
Ginglymostomidae																	
Ginglymostoma cirratum (NWA)	≥ 285	—	—	—	21–50	28–30	—	—	—	223-231	214	—	—	—	—	—	>25
Rhincodontidae																	
Rhincodon typus (WP)	—	—	1900	—	300	>64	—	—	—	>560	—	—	—	—	—	—	—
Hexanchiformes																	
Hexanchidae																	
Notorhynchus cepedianus (NEP)	296	243	—	79	-96	35-45	0.107	0.174	—	218-244	155	11-21	4.3-5	—	(32)	(20)	—
Hexanchus griseus (NEP)	482	—	—	—	22-108	60-70	—	—	—	421	325	—	—	—	—	—	—
H. vitulus (SWI)	178	157	—	—	—	43	—	—	—	142	123	—	—	—	—	—	—
Chlamydoselachidae																	
Chlamydoselachus anguineus (NWP)	196	165	—	6	2-10	55	—	—	—	140-150	110	—	—	—	—	—	—
Squaliformes																	
Squalidae																	
Centrophorus acus (WP)	161	132	—	—	—	40	—	0.173	—	—	—	—	10	—	—	(20)	—
C. granulosus (NEA/MED)	128	96	—	1	1	33-35	—	—	—	90	80	—	—	—	—	—	—
C. lusitanicus (SWI)	160	>128	—	—	1-6	—	—	—	—	—	—	—	—	—	—	—	—
C. scalpratus (SWI)	98	86	—	2	—	33-37	—	—	—	—	73	—	—	—	—	—	—
Dalatias licha (SWI)	159	121	—	—	10-16	-33	—	—	—	117-134	—	—	—	—	—	—	—

Species	Maximum size			Litter size		Offspring	K			Size at maturity		Age at maturity			Longevity		
	Female	Male	All	Mean	Range	size	Female	Male	All	Female	Male	Female	Male	All	Female	Male	All
Deania calcea (SWP)	—	—	120	—	—	—	—	—	—	100	78	—	—	—	—	—	—
D. profundorum (ECA)	76	>67	—	—	5-7	—	—	—	—	70	50-55	—	—	—	—	—	—
Etmopterus granulosus (SWP)	79	70	—	12.7	9-15	17-20	—	—	—	64-69	55-58	—	—	—	—	—	—
E. spinax (MED)	—	—	45	—	—	—	—	—	—	35	25	—	—	—	—	—	—
Euprotomicrus bispinatus (SWI)	26.5	22	—	8	—	6-10	—	—	—	22-24	17	—	—	—	—	—	—
Isistius brasiliensis (SWI)	50	39	—	—	—	—	—	—	—	38-44	31.4-37	—	—	—	—	—	—
Squalus acanthias (NEP1)	—	—	—	—	2-17	—	0.048	0.070	—	93.5	72	23	14	—	64 (72)	38 (50)	—
S. acanthias (NEP2)	130	103	—	—	—	—	0.044	—	—	94	—	35.5	—	—	81 (79)	—	—
S. acanthias (NEP3)	130	103	—	7.1	—	26	0.036	0.070	—	93.5	78.5	29	19	—	(96)	(50)	—
S. acanthias (NWA)	110	90	—	6.6	1-15	27	0.106	0.148	—	80	59.5	12.1	6	—	40 (33)	35 (23)	—
S. acanthias (NEA)	—	—	—	—	2-15	—	0.110	0.210	—	83	60	11	5	—	21 (32)	19 (17)	—
S. acanthias (SWP)	111	90	—	5	1-16	18-30	—	—	—	71.5	58	—	—	—	—	—	—
S. acanthias (SWA)	95.5	78	—	7	3-14	28	—	—	—	70	63	—	—	—	—	—	—
S. japonicus (WP)	76	64	—	3.9	2-8	—	—	—	—	56-58	50	—	—	—	—	—	—
S. megalops (SEA)	74	>55	—	3	2-4	23-24	—	—	—	55	42	—	—	—	—	—	—
S. megalops (SEA/SWI)	78	57	—	—	2-4	23-28	0.033	0.089	—	49	40	15	9	—	32 (105)	29 (39)	—
S. mitsukurii (SEP)	104	102	—	—	2-5	29-30	—	—	—	85	—	—	—	—	16	14	—
S. mitsukurii (NWP/Choshi)	114	94	—	8.8	4-15	—	—	—	—	96-99	68-72	19-22	11-12	—	—	—	—
S. mitsukurii (NWP/Masseiba)	102	—	—	7.1	6-9	—	—	—	—	—	—	—	—	—	—	—	—
S. mitsukurii (NWP/Ogasawara Isl.)	98	74	—	4.5	2-9	—	—	—	—	72-76	52-56	15-17	10	—	—	—	—
S. mitsukurii (SWI)	>95	>81	—	6.4	4-9	22-26	—	—	—	>69	58-60	—	—	—	—	—	—
S. mitsukurii (CP)	91	82	—	3.6	1-6	21-26	0.041	0.155	—	69	48	15	4	—	27 (85)	18 (22)	—
Squatiniformes																	
Squatinidae																	
Squatina africana (SWI)	108	—	—	—	7-11	28-34	—	—	—	90-93	75-78	—	—	—	—	—	—
S. argentina (SWA)	130	125	—	6	4-8	25	—	—	—	70-80	70-80	—	—	—	—	—	—
S. californica (NEP)	—	—	152	6	1-11	25-26	0.164	0.143	0.148	101-103	90-100	8-13	—	—	(20)	(24)	22 (23)
S. tergocellata (SWI)	140	102.5	—	4.5	2-9	32-33	—	—	—	115-125	81-91	—	—	—	—	—	—

APPENDIX (CONTINUED)

Species	Maximum size			Litter size		Offspring size	K			Size at maturity		Age at maturity			Longevity		
	Female	Male	All	Mean	Range		Female	Male	All	Female	Male	Female	Male	All	Female	Male	All
Heterodontiformes																	
Heterodontidae																	
Heterodontus portusjacksoni (SWP)	123	105	—	—	10-16	23-24	—	—	—	90	70-80	11-14	8-10	—	—	—	—

[a] *The geographical location for each set of life-history data is in parentheses next to each species name: GM=Gulf of Mexico; EGM=Eastern Gulf of Mexico; SGM=Southern Gulf of Mexico; NWGM=Northwestern Gulf of Mexico; NWA=Northwestern Atlantic; SWA=Southwestern Atlantic; NEA=Northeastern Atlantic; EA=Eastern Atlantic; ECA=Eastern Central Atlantic; SEA=Southeastern Atlantic; SWI=Southwestern Indian; WI=Western Indian; NWI=Northwestern Indian Ocean; NI=Northern Indian; NEI=Northeastern Indian; EI=Eastern Indian; SEI=Southeastern Indian; NP=Northern Pacific; NWP=Northwestern Pacific; WP=Western Pacific; CWP=Central Western Pacific; SWP=Southwestern Pacific; SEP=Southeastern Pacific; CP=Central Pacific (Hawaiian Islands); NEP=Northeastern Pacific; CARIB=Caribbean; MED=Mediterranean; RED SEA=Red Sea; ALL=Complete species range. Numbers or text following geographic abbreviations indicate different studies or populations, respectively. A complete list of literature sources is included before this appendix.*

[b] *Lengths are precaudal lengths.*