

Abstract.—Little information exists on the biology of the demersal shark, *Squalus mitsukurii*. Recently, large numbers of this species were taken incidentally during research surveys conducted at Southeast Hancock Seamount in the central North Pacific Ocean. The information collected during 1985 to 1988 from these surveys is used to describe the life history, depth distribution, and biology of *S. mitsukurii*.

Bathymetric distributional patterns of female and male *S. mitsukurii* differed slightly, although bottom longline catches revealed a depth distribution extending from the summit (260 m) to 740 m for both sexes. Males generally were found deeper than females. In addition, the size of males generally increased with depth whereas no apparent trend was observed for females.

Reproductive parameters for both sexes are presented. Males tended to reach maturity at smaller sizes than did females. Gravid females had broods of up to six uterine embryos. Length of young close to parturition was 21–26 cm.

Tentative estimates of age and growth were made from dorsal spine increment counts. Maximum ages were 27 years for females and 18 years for males. Females exhibited more rapid growth than males after about age 9.

The diet of *S. mitsukurii* included both benthic and mesopelagic prey. Fishes, cephalopods, and crustaceans were the major components of the diet.

Comparison of the biological characteristics suggest that this species is probably typical of other slow-growing, low fecund members of the genus *Squalus*. The 50% decline in catch rates observed during this study suggests that the number of *S. mitsukurii* on the seamount declined dramatically, possibly as a result of overfishing.

Biology and population characteristics of *Squalus mitsukurii* from a seamount in the central North Pacific Ocean

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The discovery of large stocks of the pelagic armorhead, *Pseudopentaceros wheeleri*, on seamounts of the southern Emperor-northern Hawaiian Ridge by Soviet fishermen in 1967 signaled the inception of a large, intense foreign trawl fishery for this species during the early 1970's (Uchida and Tagami, 1984). During 1967–75, for example, nearly one million metric tons of pelagic armorhead were taken from this area by Japanese and Russian trawlers (Boehlert and Genin, 1987). By the mid-1970's, catch rates of pelagic armorhead had declined dramatically, and commercial fishing for the species effectively ceased by 1984. The National Marine Fisheries Service (NMFS) initiated research stock-surveys of the area in 1985, and in August 1986 a six-year fishing moratorium was enacted (NMFS, 1986).

Results from the NMFS surveys provided information to describe the population dynamics of *P. wheeleri* (Somerton and Kikkawa, 1992). However, the population biology of several other fish species which were caught incidentally in large numbers during the NMFS surveys was largely unknown. One example was the demersal shark, *Squalus*

mitsukurii, which represented the largest bycatch in the NMFS survey data (Somerton¹).

Little is known about the life history and population dynamics of *S. mitsukurii* (Compagno, 1984) in contrast to the more cosmopolitan congener *S. acanthias* which has been extensively studied (Compagno, 1984; Ketchen, 1986). *Squalus mitsukurii* is broadly distributed in the Pacific and Indian Oceans (Compagno, 1984; Parin, 1987). Specimens resembling *S. mitsukurii* have also been taken in the Atlantic although their taxonomic status is unclear (Compagno, 1984). *Squalus mitsukurii* is known to inhabit the waters around various islands and seamounts in addition to coastal waters (Parin, 1987; Taniuchi et al., 1993). Litvinov (1990) reported on several aspects of the biology of *S. mitsukurii* from 117 specimens taken from the Sala-y-Gomez Seamounts in the Southeast Pacific. Off southeast Africa, Bass et al. (1976) presented limited information on the life history of *S. mitsukurii*, which had earlier been identified as *S. blainvillei* (Bass et

¹ Somerton, D. National Marine Fisheries Service, Seattle, WA 98115. Personal commun., 1992.

al., 1986). Whether populations of *S. mitsukurii* from different geographic areas exhibit the high variability in life history characteristics reported for *S. acanthias* (Ketchen, 1972, 1986; Compagno, 1984; Nammack et al., 1985) is unclear. The aim of the present study was to provide information on the biology and population characteristics of *S. mitsukurii* using a larger number of specimens than had previously been available, and thus elucidate its role as a member of the unique fauna associated with seamounts in the central North Pacific Ocean.

Methods

Squalus mitsukurii specimens were collected aboard the NOAA ship *Townsend Cromwell* during nine cruises to Southeast (SE) Hancock Seamount from January 1985 to November 1988 (Table 1). The seamount is located on the northern Hawaiian Ridge in the central North Pacific Ocean at lat. 29°48'N and long. 179°04'E (Fig. 1). It has a circular, flat-topped summit with an area of about 4.5 km² at a depth of

260 m. The seamount flanks have an average slope of 0.22 and reach bottom depths of 5,200 m about 22 km away from the summit (Brainard, 1986). Water temperatures generally are 13°–15°C at 260 m depth (i.e. summit) and decrease to 4°–6°C by 750 m (Brainard, 1986).

Most *S. mitsukurii* were collected with bottom longline gear (Somerton and Kikkawa, 1992; Shiota²), although a few specimens were also taken by bottom trawl, handline, vertical longline, and one set with a 25-mm square mesh bottom gill net (Table 1). Only data from hook-caught specimens were used (except for the food habits portion of the study) to avoid any bias due to differences in gear selectivity. Sets were conducted primarily during daylight hours, between the summit depth and 744 m.

All specimens of *S. mitsukurii* from a set, or a random subsample from large catches, were processed. Fish were sexed and weighed to the nearest 10 g.

² Shiota, P. M. 1987. A comparison of bottom longline and deep-sea handline for sampling bottom fishes in the Hawaiian archipelago. Honolulu Lab., Southwest Fish. Cent. Natl. Mar. Fish. Cent. Admin. Rep. H-87-5, 18 p.

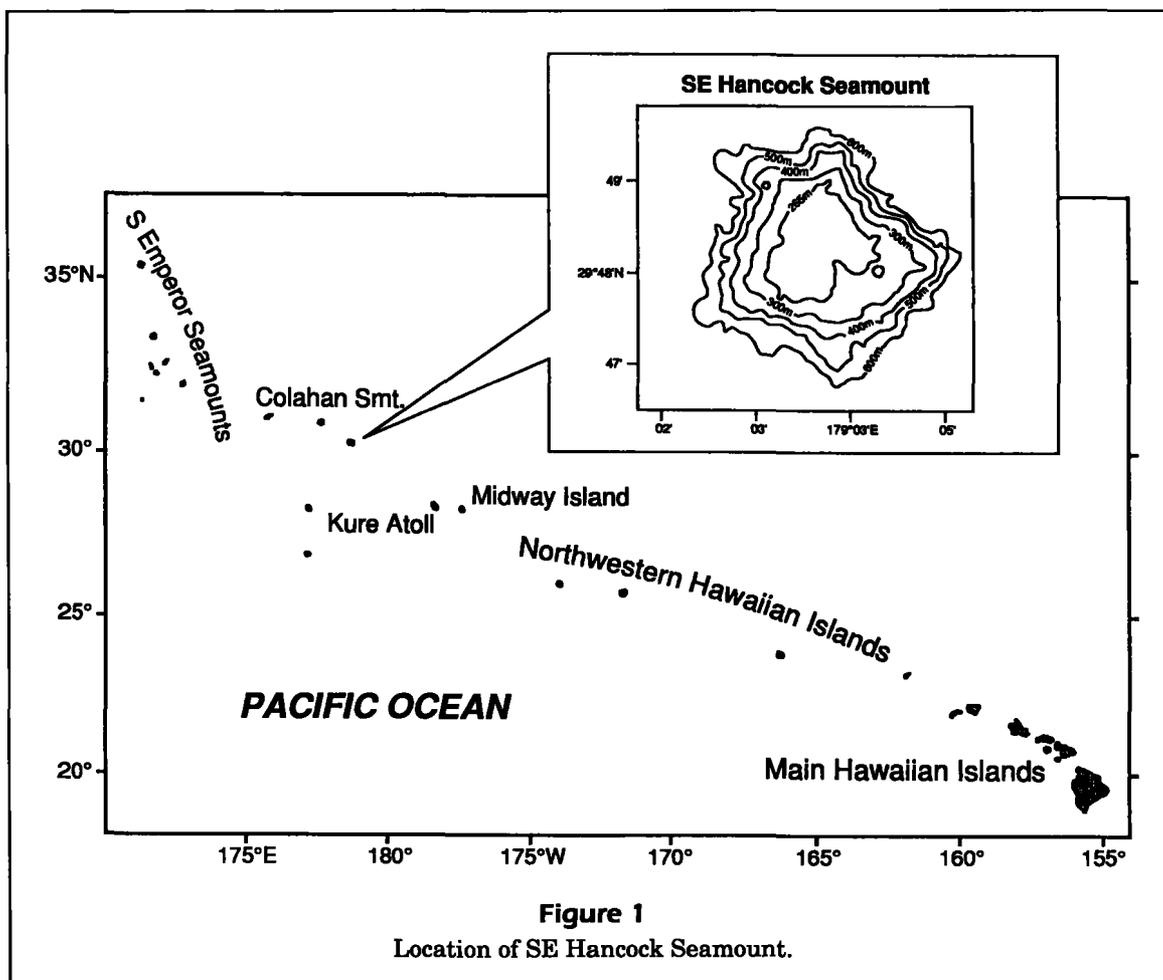


Figure 1
Location of SE Hancock Seamount.

Table 1

Catch by gear type, effort by bottom longline gear, and catch per unit of effort (CPUE; bottom longline catch per total number of hooks minus those with pelagic armorhead, *Pseudopentaceros wheeleri*) for *Squalus mitsukurii* from research operations at the SE Hancock Seamount during 1985–88. A dash indicates a particular gear type was not used on a cruise.

Date	Catch (no.)				Effort (no. hooks)			
	Bottom trawl	Handline	Vertical longline	Gill net	Bottom longline	Total	Total minus armorhead	CPUE
Winter 1985 (1/30–2/25)	1	66	—	—	335	2,001	1,607	0.208
Summer 1985 (6/19–7/16)	0	10	56	—	521	2,659	1,995	0.261
Summer 1986 (8/11–9/9)	8	—	—	42	506	6,568	4,208	0.120
Fall 1986 (10/31–11/12)	0	—	—	—	339	2,783	1,944	0.174
Spring 1987 (4/11–28)	20	5	—	—	218	3,218	2,243	0.097
Summer 1987 (8/8–25)	19	—	—	—	228	4,182	3,646	0.063
Winter 1988 (1/12–30)	4	—	—	—	253	3,546	2,842	0.089
Summer 1988 (7/13–8/21)	—	—	—	—	182	5,500	4,171	0.044
Fall 1988 (10/26–11/8)	—	—	—	—	219	4,067	2,921	0.075

Total length (TL) was determined to the nearest 1 mm by placing the shark on its side and measuring from the anterior tip of the snout to the posterior edge of the upper lobe of the caudal fin in the “natural” upright position. For some specimens, body length (STL) was measured from the anterior tip of the snout to the posterior edge of the upper lobe of the caudal fin after the lobe was depressed to a position in line with the body axis; fork length (FL) was also measured from the snout to the fork or middle of the caudal fin. Simple linear regression relationships among the three length measurements were determined to facilitate comparisons with other published studies. The relationships are $TL = 1.08 \times LF + 1.67$ ($r^2 = 0.99$, $n = 342$); $TL = 0.95 \times STL + 0.24$ ($r^2 = 0.99$, $n = 212$); $STL = 1.01 \times FL + 6.31$ ($r^2 = 0.91$, $n = 463$).

A nonlinear estimation procedure (Wilkinson, 1988) was used to fit individual length and weight (WT; in grams) data to the relationship, $WT = a \times TL^b$. Weight-length relationships between sexes were evaluated with analysis of covariance (ANCOVA) on the log-transformed data.

Catch per unit of effort (CPUE) for *S. mitsukurii* was determined by using only specimens taken by bottom longline for several reasons. The bottom trawl, handline, and gillnet gear did not have fishing effort comparable with the bottom longline, and the former data were too limited to construct individual time series for each gear. Furthermore, the vertical longline gear was used to define the vertical distribution of pelagic armorhead above the summit; therefore only a few hooks of uncertain number were on the summit and available to *S. mitsukurii*.

Finally, specimens from gear other than bottom longline accounted for only 8% of the total numbers caught. Therefore, it was unlikely that the exclusion of these data from the CPUE calculations would significantly bias our results. Fishing effort on *S. mitsukurii* was expressed in number of hooks set, minus hooks that caught pelagic armorhead. Pelagic armorhead respond more quickly to the bottom longline than do *S. mitsukurii* (Somerton³). Thus, excluding those hooks occupied by pelagic armorhead, although not removing all bias from the species-gear interaction, likely improved estimates of fishing effort on *S. mitsukurii* over the unadjusted value.

An estimate of the initial exploitable biomass of *S. mitsukurii* was made with the Leslie model (Ricker, 1975) in which a linear function was fitted to CPUE and cumulative catch data from all cruises. The function has a slope equal to catchability (q) and intercept equal to the product of q and the initial exploitable biomass. The model assumes that changes in CPUE over time are due to fishing and that other sources of losses and additions to the population are relatively minor or in balance (e.g. natural mortality and recruitment). The 95% confidence limit on the abundance estimate was calculated by using the method of Polovina (1986).

First and second dorsal spines were collected during the summer of 1986 for ageing *S. mitsukurii* with procedures outlined by McFarlane and Beamish (1987). All age results were based on the second

³ Somerton, D. National Marine Fisheries Service, Seattle, WA 98115. Personal commun., 1992.

dorsal spine which was considered most suitable for ageing (also see Litvinov, 1990). All ridges on the surface of the mantle covering the spine were counted by a single reader with a low-power dissecting scope and methods described by Ketchen (1975) and Beamish and McFarlane (1985). No ridges were grouped and counted as a single "annulus" as was done in several earlier studies (e.g. Holden and Meadows, 1962). Loss of increments due to abrasion of the tip of the spine has been reported for other species of *Squalus* (e.g. Ketchen, 1975), but this did not occur in the present study. For example, when a worn spine was observed, the worn area was confined to the region of the spine tip having a diameter of <3 mm. However, unworn spines having spine base diameters of ≤ 3 mm had not yet formed any increments (the spine base diameter of a late-term uterine embryo was 2.0 mm).

Validation of the annual nature of spine increment formation (following the methods described by McFarlane and Beamish [1986, 1987]) was not possible. Therefore increment counts from spines reported here must be considered as tentative estimates of age. Nonetheless, validation studies conducted on *S. acanthias* have verified that spine increments do represent annual marks (Beamish and McFarlane, 1985; Tucker, 1985).

Individual length-at-age data for each sex were fitted with a nonlinear estimation procedure (Wilkinson, 1988) to the von Bertalanffy growth model (Ricker, 1975):

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)} \right),$$

where L_t is length at age, L_∞ is asymptotic length, k is the growth coefficient, and t_0 is the theoretical age when $L_t = 0$.

Reproductive data were first collected from shark specimens during the summer of 1986. For females, counts were made of mature ovarian eggs (greater than about 2.5 cm diameter), candled embryos (i.e. gelatinous uterine capsules containing embryos in early stages of development), and embryos free in the uteri. Females possessing any or all of these reproductive products were considered sexually mature. Sex and TL of uterine embryos were also recorded. Ketchen (1972) determined that a period of rapid increase in clasper length indicates the onset of sexual maturity in male *S. acanthias*. A similar allometric growth phase between clasper length and TL was observed for *S. mitsukurii*. Thus, the right clasper length was measured to the nearest 1 mm from the body juncture to the clasper tip.

To determine the size at 50% sexual maturity for both sexes, data were fitted to the logistic function

by using an iteratively weighted (i.e. inverse of variance) nonlinear estimation procedure (Wilkinson, 1988) and evaluated at 50% (Somerton, 1980). The logistic equation is defined as

$$Y = 1/(1 + Ae^{BX}),$$

where Y is the proportion of animals sexually mature, X is the midpoint of a length class, and A and B are parameters defining the curve. Before the logistic equation was fitted to length data for males, the data were transformed to approximate the logistic pattern of growth. For example, clasper length (CL) plotted against fish TL (not shown) produced a roughly sigmoid curve, although at large and small fish sizes, clasper length continues to increase with size of the fish. To flatten the ends of the curve as required by the logistic equation, clasper length was expressed as a proportion of fish TL and normalized to values between 1 and 0 (i.e. with $a = CL/TL$, the quantity $Y' = (a - a_{\min}) / (a_{\max} - a_{\min})$ was plotted against fish TL).

To obtain information on feeding habits, the stomach contents from 251 *S. mitsukurii* caught on longlines and 42 fish caught in gill nets during the summer of 1986 were examined. Longline-caught fish ranged from 20.6 to 79.5 cm TL (mean length $\bar{L} = 50.4$ cm) and gillnet-caught fish ranged from 49.5 to 78.9 cm TL ($\bar{L} = 65.5$ cm). Samples from the bottom longline and gillnet gear were compared to examine the potential feeding bias that might occur if attraction to baited longlines varied as a function of stomach fullness for *S. mitsukurii*.

For most of the fish, stomachs were extracted upon capture and preserved in 10% formalin until examination in the laboratory. However, if time permitted, stomachs were examined at sea for the presence of food items; empty stomachs were noted and discarded (those with food items were saved). In the laboratory, samples were sorted, counted, and identified to the lowest possible taxon. Food items were sorted to taxa, blotted dry, and weighed to the nearest 0.1 g.

Stomach contents data were analyzed for frequency of occurrence, numerical abundance, and gravimetric proportions of prey items to quantitatively describe the diet and feeding habits of *S. mitsukurii* (Hyslop, 1980). Prey items that were attributed to the presence of the research vessel (i.e. bait, galley refuse, or processed fish offal) were not included in the analyses; stomachs containing only those items were considered empty. To examine diel feeding behavior, samples were grouped by time of capture: 0600–1200 ($n=39$), 1200–1800 ($n=86$), 1800–2400 ($n=64$), and 0000–0600 ($n=62$). Chi-square (χ^2) analyses of 2×2 contingency tables were used to test for

differences in stomach fullness (defined simply in terms of presence versus absence of food) between time blocks. Sunrise was at about 0545 h and sunset at 1930 h. The χ^2 test was similarly used to identify differences in stomach fullness between longline- and gillnet-caught fish from a single time block (1800–2400 h).

Results

Abundance

A total of 1,392 female, 1,539 male, and 7 unsexed, hook-caught *S. mitsukurii* were collected. CPUE was highest in 1985 and declined by more than 50% by spring 1987 (Table 1). The CPUE data plotted as a function of cumulative catch (*C*) appeared generally linear with a negative slope (Fig. 2); coefficients of the fitted model were $CPUE = -6.87 \times 10^{-5} \times C + 0.2498$ ($r^2=0.76$). The model estimate of the initial exploitable population was 3,641 fish ($\pm 1,954$). Based on this estimate, about 80% ($\pm 55\%$) of the initial population of *S. mitsukurii* had been removed by fishing.

Both sexes of *S. mitsukurii* were caught over the full depth range sampled. The median depth of occurrence for males was usually greater than that of females (Table 2).

Size

Female *S. mitsukurii* were on average longer and reached larger maximum sizes than males (Fig. 3). Maximum lengths recorded were 91 cm for females and 82 cm for males. Differences were also detected in length-weight data between female and male *S. mitsukurii* (ANCOVA, $P < 0.05$). Non-linear fits of length-weight growth curves between sexes diverged at about the size at 50% maturity for male sharks (see Reproduction). Length-weight parameter estimates were $a=1.718 \times 10^{-2}$, $b=2.687$ for males and $a=3.773 \times 10^{-3}$, $b=3.089$ for females.

The size of male sharks increased with depth. For example, for each cruise and sex, fish were divided into either a shallow or deep subgroup, depending on whether they were caught above or below the median depth of occurrence for that group on that cruise. Estimates of the median length for males from the deep group were

Table 2

Maximum and median depth (m) of occurrence for female and male *Squalus mitsukurii*, median length (cm) for each sex above and below median depth of occurrence, and statistical significance between median depths or lengths (Mann-Whitney *U*-test, * $P \leq 0.05$, ** $P \leq 0.001$).

Sampling period	Sex	Maximum depth	Median depth	Median length above/below median depth
Winter 1985	F	443	302**	66.0/61.0
	M	459	327	59.9/58.7
Summer 1985	F	744	309*	58.4/50.0
	M	744	327	52.6/58.5*
Summer 1986	F	556	260*	41.8/45.6
	M	454	269	43.5/50.9**
Fall 1986	F	468	291*	54.4/51.2
	M	494	298	52.1/54.1
Spring 1987	F	384	293	48.9/47.9
	M	518	269	46.8/54.2
Summer 1987	F	483	283	43.2/45.4*
	M	459	283	40.5/46.2**
Winter 1988	F	512	272	50.3/56.0*
	M	446	276	52.2/58.6*
Summer 1988	F	569	411	50.2/52.3
	M	569	448	46.0/55.2**
Fall 1988	F	430	274	56.0/50.9
	M	382	278	50.0/52.2

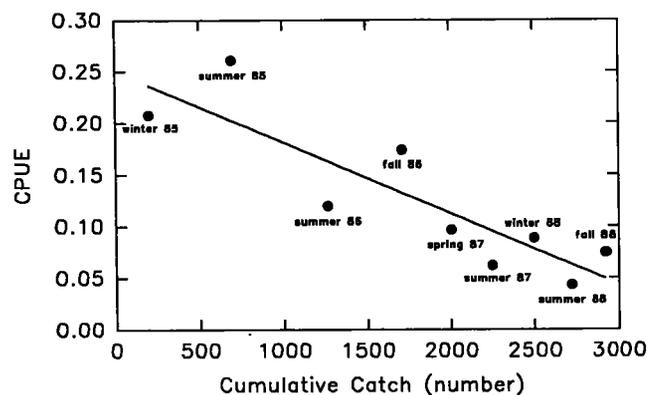
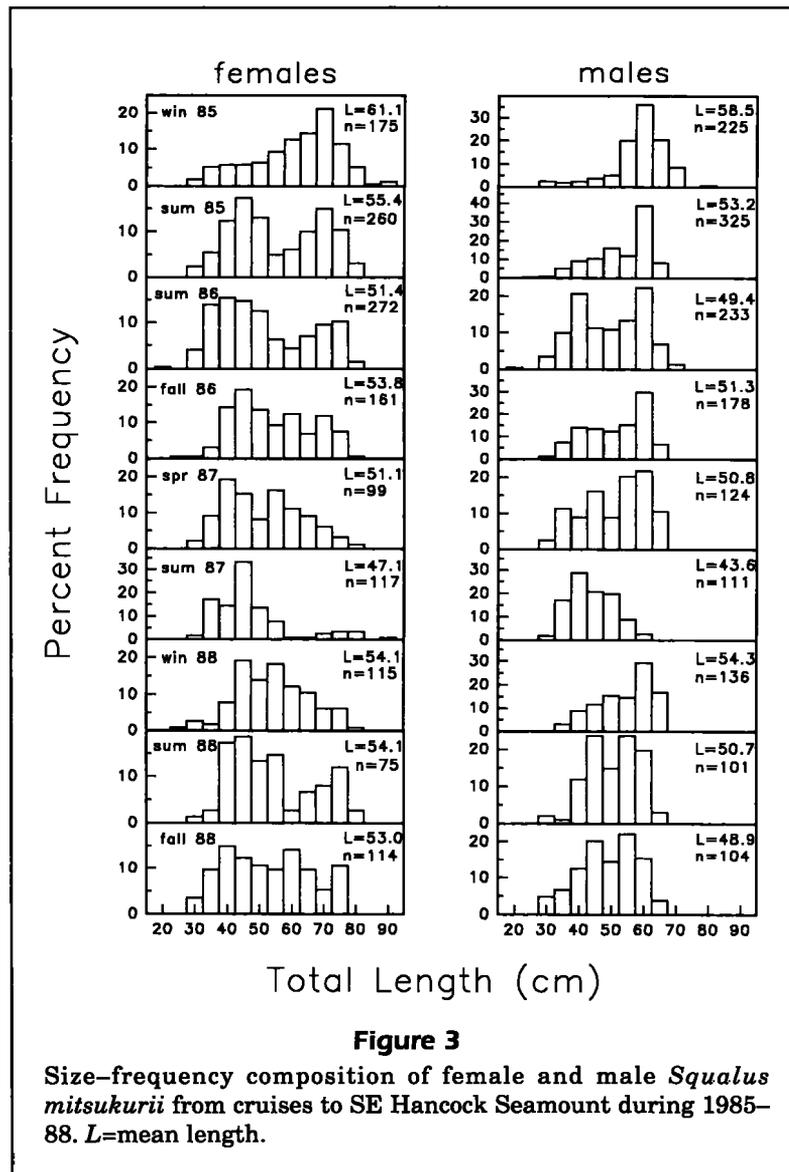


Figure 2

Catch per unit of effort (CPUE) for each sampling period (filled circles) and predicted CPUE based on the Leslie model (solid line), and plotted as a function of cumulative catch for *Squalus mitsukurii* from SE Hancock Seamount during 1985–88.



significantly greater than for the shallow group on five of nine cruises (Mann-Whitney U -test, $P < 0.05$) with similar, nonsignificant trends seen on three additional cruises (Table 2). These differences were greatest in summer. There was no apparent trend in size with depth for females (Table 2).

Age and growth

Spine increments were counted for 102 males (20.8–72.2 cm TL) and 105 females (20.6–79.5 cm TL). Increment counts ranged from 0 to 27 for female spines and 0 to 18 for male spines. Mean length at age for each sex was similar up to age 9; thereafter, females grew faster (Fig. 4). For both sexes, the mean length at time 0 was greater than that expected based on the estimated size at parturition for *S. mitsukurii* (see Reproduction).

Fitted growth curves for each sex differed considerably (Fig. 4). The L_{∞} estimate for females exceeded the observed maximum length from the catch data (i.e. 91 cm), although the L_{∞} estimate for males was much lower than the observed value of 82 cm.

Reproduction

Reproductive data were collected from a total of 258 female *S. mitsukurii* specimens during 1986–88. Gravid females examined during the four seasons ranged from 61 to 80 cm TL. The estimated size at 50% sexual maturity for females was 69 cm (Fig. 5). This size corresponds to an age of about 15 years. The largest infertile or sexually inactive female was 88 cm. No differences were found in the depth distributions of gravid and nongravid females greater than

60 cm in length (i.e. minimum observed size at maturity; Kolmogorov-Smirnov test, $P=0.069$).

Estimates of fecundity for female *S. mitsukurii* were similar regardless of the reproductive stage used. Gravid females had similar mean numbers of large ovarian eggs (3.8, SE=0.10, $n=95$), candled embryos (3.7, SE=0.15, $n=40$), and uterine embryos (3.6, SE=0.15, $n=57$); numbers for any developmental stage ranged from 1 to 6. Fecundity increased significantly with the size of the female (Table 3, Spearman's $r=0.44, 0.40, 0.46$; $P<0.05$).

The size range of uterine embryos (65 female, 51 male, and 73 unsexed) for *S. mitsukurii* was 6.6–25.9 cm TL ($\bar{L}=17.8$ cm, SD=5.57). A very large (30.5 cm TL) male embryo from winter 1988 was excluded because its length could not be verified. Bimodal size-frequency distributions of the uterine embryos were evident for samples from all periods (Fig. 6). All gravid females had one of two size classes of uterine embryos. Further, the total numbers of uterine embryos within all but fall 1988 samples were apportioned approximately equally between the "small" and "large" size classes ($\chi^2, P>0.05$).

No well-defined parturition season was detected either from a large increase in catches of small (i.e. 21–26 cm), free-living fish (Fig. 3) or by the absence of large, near-term embryos in females (Fig. 6). However, the smallest uterine embryos were found in fall and winter and were absent in spring and summer (Fig. 6), which is indicative of a reasonably well-defined seasonal production cycle for young. Specimens as small as 21 cm were captured from longline gear in summer 1986. This confirms that 21–26 cm long embryos would be close to parturition. The only significant correlation between numbers of "large," "small," or total uterine embryos, candled embryos, or large ovarian eggs was a positive association between numbers of uterine embryos and large ovarian eggs (Pearson's $r=0.62, P<0.05$).

Size at sexual maturity for male *S. mitsukurii* was estimated indirectly from 812 specimens. The estimated size at 50% sexual maturity was 48 cm (Fig. 5). This corresponds to a tentative age of about 4 years based on the von Bertalanffy growth equation.

Feeding

Overall, 101 of the 293 (34.5%) stomachs examined contained prey. Stomach contents averaged 2.0 prey items (SD=1.4) and weighed 4.5 g (SD=9.3 g). Fishes, cephalopods, and crustaceans were the

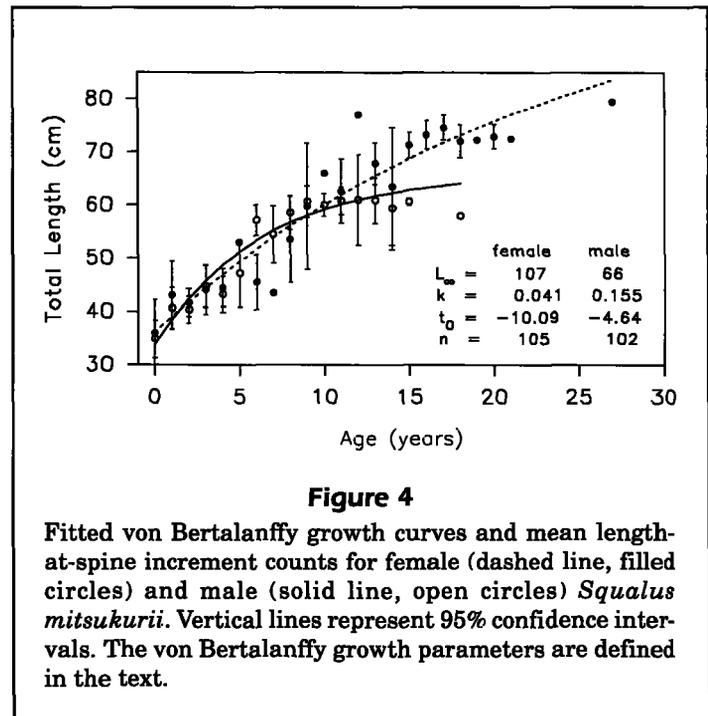


Figure 4

Fitted von Bertalanffy growth curves and mean length-at-spine increment counts for female (dashed line, filled circles) and male (solid line, open circles) *Squalus mitsukurii*. Vertical lines represent 95% confidence intervals. The von Bertalanffy growth parameters are defined in the text.

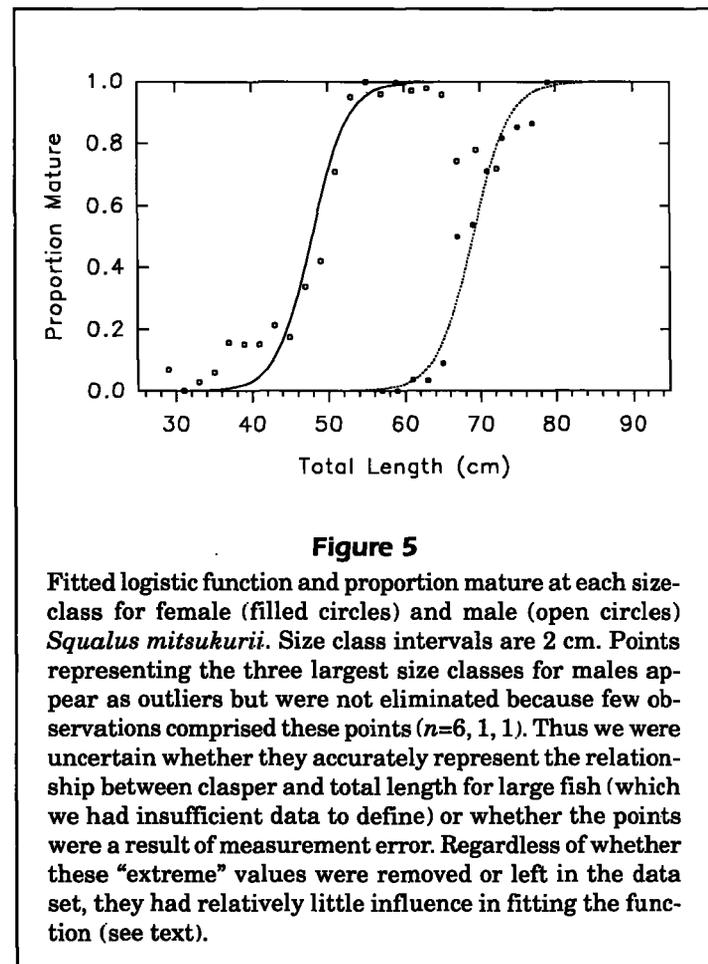


Figure 5

Fitted logistic function and proportion mature at each size-class for female (filled circles) and male (open circles) *Squalus mitsukurii*. Size class intervals are 2 cm. Points representing the three largest size classes for males appear as outliers but were not eliminated because few observations comprised these points ($n=6, 1, 1$). Thus we were uncertain whether they accurately represent the relationship between clasper and total length for large fish (which we had insufficient data to define) or whether the points were a result of measurement error. Regardless of whether these "extreme" values were removed or left in the data set, they had relatively little influence in fitting the function (see text).

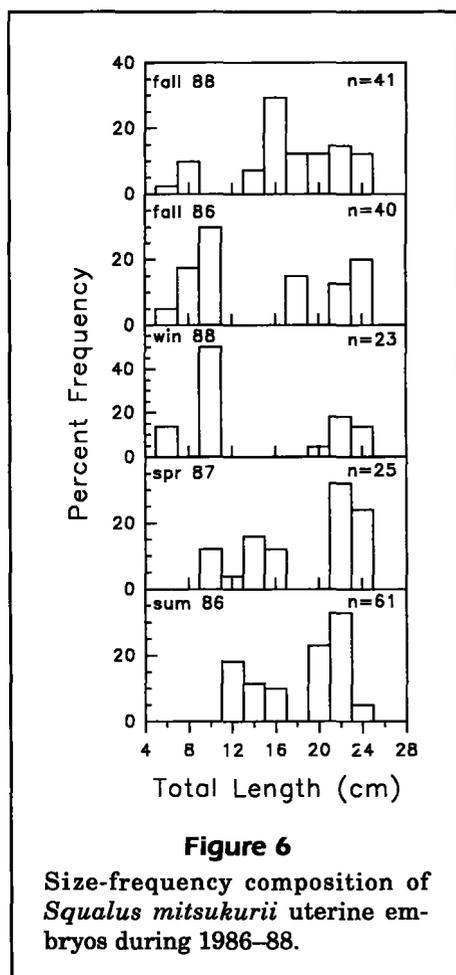
Table 3

Mean length, standard deviation (SD), and number of gravid *Squalus mitsukurii* specimens as a function of number of large ovarian eggs and candled and uterine embryos.

Maternal statistics	Number of eggs or candled or uterine embryos					
	1	2	3	4	5	6
Large ovarian eggs						
Mean length	68.0	71.1	70.1	72.3	74.4	75.1
SD	—	2.49	3.97	2.96	3.18	2.91
Number	1	4	33	35	18	4
Candled embryos						
Mean length	70.5	74.6	72.0	74.0	76.1	76.2
SD	—	5.30	4.03	2.17	2.58	—
Number	1	2	14	17	5	1
Uterine embryos						
Mean length	73.1	68.1	72.4	74.4	76.1	79.5
SD	3.76	1.63	3.89	2.24	2.09	—
Number	4	2	21	18	11	1

major components of the diet (Table 4). Fishes were found in 63.7% of the stomachs with prey and numerically accounted for 36.8% of the total prey while making up 74.5% of the total aggregate weight. Micronektonic stomiiform and myctophid fishes, and filefishes (family Monacanthidae) were the most commonly identified fishes; however, most fishes were in an advanced stage of digestion and thus unidentifiable to a lower taxon. Crustaceans were present in 32.3% of the stomachs and represented 30.3% of the prey organisms, but only 3.6% of the total aggregate weight. In particular, euphausiids and the lophogastrid mysid *Gnathophausia longispina*, were commonly found. Cephalopods, predominantly digestion-resistant squid beaks and eye lenses, were present in 45.1% of the stomachs, representing 26.4% of the total prey items and 19.9% of the prey weight. Remaining prey items included pelagic tunicates, coelenterates, and unidentified remains.

Gut fullness was evaluated as a function of diel feeding activity and gear type. For longline data, no significant difference was found between the two daytime ($\chi^2=0.001$, $P>0.1$) or two nighttime blocks ($\chi^2=3.822$, $P>0.1$). However, when longline data from daytime blocks were pooled and compared with pooled nighttime blocks, the proportion of empty stomachs was significantly greater during the night (87%) than during the day (46%; $\chi^2=26.250$, $P<0.001$). Longline-caught fish had a significantly greater proportion of empty stomachs than did fish caught by bottom gill net ($\chi^2=5.081$, $P<0.05$).

**Figure 6**

Size-frequency composition of *Squalus mitsukurii* uterine embryos during 1986-88.

Discussion

Size and abundance

Squalus mitsukurii was the second most abundant species sampled by bottom longline gear at SE Hancock Seamount in 1985-88 (Somerton⁴). However, the large apparent decline in catch rates for *S. mitsukurii* during this period suggests that the research fishing may have had a major impact on stock size which is (i.e. in 1988) at only 20% of its 1985 value. It is likely that populations of this species, like other elasmobranchs (Holden, 1974), are particularly sensitive to overfishing. In addition, seamount populations of *S. mitsukurii* may be at further risk to overexploitation because of the limited habitat

⁴ Somerton, D. National Marine Fisheries Service, Seattle, WA 98115. Personal commun., 1992.

Table 4
Diet composition (as identified to lowest possible taxon) for 101 *Squalus mitsukurii* at SE Hancock Seamount.

Taxa	Total no.	% no.	Total weight (g)	% weight	Frequency	% frequency
Coelenterata	1	0.5	0.5	0.1	1	1.0
Cephalopoda	41	20.7	11.2	2.5	35	34.6
Sepiolidae	2	1.0	7.5	1.7	2	2.0
<i>Iridoteuthis iris</i>	1	0.5	2.1	0.5	1	1.0
Histioteuthidae	1	0.5	1.1	0.2	1	1.0
Enoploteuthidae						
<i>Enoploteuthis</i> sp.	1	0.5	25.0	5.5	1	1.0
Ommastrephidae	5	2.5	22.5	5.0	5	4.9
Octopoda	3	1.5	21.0	4.6	3	3.0
Crustacea	2	1.0	1.5	0.3	1	1.0
Mysidacea						
<i>Gnathophausia longispina</i>	13	6.6	1.9	0.4	10	9.9
Amphipoda						
<i>Phronima</i> sp.	1	0.5	0.3	0.1	1	1.0
Euphausiacea	11	5.6	0.8	0.2	6	5.9
<i>Thysanopoda aequalis</i>	1	0.5	0.1	<0.1	1	1.0
<i>Thysanopoda</i> sp.	17	8.6	1.6	0.3	8	7.9
<i>Euphausia gibboides</i>	1	0.5	0.1	<0.1	1	1.0
<i>Euphausia</i> sp.	2	1.0	0.2	<0.1	2	2.0
Decapoda						
Sergestidae	7	3.5	1.1	0.2	7	6.9
Penaeidae						
<i>Gennadas propinquus</i>	1	0.5	0.1	<0.1	1	1.0
<i>Gennadas tinayrei</i>	1	0.5	0.1	<0.1	1	1.0
<i>Gennadas</i> sp.	2	1.0	0.4	0.1	2	2.0
Caridea	1	0.5	5.0	1.1	1	1.0
Oplophoridae	1	0.5	0.1	<0.1	1	1.0
Reptantia	1	0.5	3.0	0.7	1	1.0
Pisces	39	19.7	83.3	18.4	38	37.6
Leptocephalus	1	0.5	1.5	0.3	1	1.0
Stomiiformes	5	2.5	12.5	2.8	5	4.9
Sternoptychidae						
<i>Maurolicus muelleri</i>	1	0.5	1.3	0.3	1	1.0
Melanostomiidae	3	1.5	57.3	12.7	3	3.0
Aulopiformes						
Paralepididae	1	0.5	0.3	0.1	1	1.0
Myctophiformes						
Myctophidae	4	2.0	9.5	2.1	4	4.0
<i>Lampanyctus</i> sp.	1	0.5	13.0	2.9	1	1.0
Beryciformes						
Berycidae						
<i>Beryx splendens</i>	1	0.5	56.4	12.5	1	1.0
Perciformes						
Apogonidae						
<i>Epigonus</i> sp.	2	1.0	4.3	0.9	2	2.0
Callanthiidae						
<i>Grammatonotus laysanus</i>	2	1.0	59.9	13.2	2	2.0
Echeneidae	1	0.5	2.1	0.5	1	1.0
Emmelichthyidae	2	1.0	32.2	7.1	2	2.0
Pleuronectiformes						
Bothidae	1	0.5	0.7	0.1	1	1.0
Tetraodontiformes						
Monacanthidae	11	5.6	4.5	1.0	8	7.9
Tunicata						
Pyrosomatidae						
<i>Pyrosoma</i> sp.	3	1.5	3.2	0.7	3	3.0
Salpidae	1	0.5	0.1	<0.1	1	1.0
Unidentified remains	8	4.0	5.4	1.2	8	7.9

area. In the case of SE Hancock Seamount, for example, the summit diameter is only about 2.4 km. Assuming recruitment is entirely dependent on the seamount population (i.e. little or no immigration from elsewhere), relatively little fishing effort is required to seriously deplete the stock.

It is not possible to verify whether the assumptions that are required by the Leslie model were met in the present study. The model assumes that changes in population abundance (i.e. CPUE) are due to fishing removals whereas other losses such as emigration and natural mortality are balanced by additions such as immigration and recruitment of young to the exploited population. The model has generally been applied over shorter time periods in other studies where the assumptions are more readily satisfied (Polovina, 1986; Somerton and Kikkawa, 1992). The fact that our model data were taken over a period of about four years may have introduced some noise into the results. Nevertheless, studies have indicated that members of the genus *Squalus* do exhibit low levels of natural mortality (Wood et al., 1979) and fecundity (see Reproduction below). Whether *S. mitsukurii* move among seamounts is unknown. Unfortunately, results from tagging studies with *S. acanthias* (McFarlane and Beamish, 1986 and references therein) are of limited usefulness to our work since they were not conducted over relatively isolated seamounts found in deep oceanic waters. However, tagging work on *S. acanthias* within the Strait of Georgia suggests that most recoveries were made within the areas of release although some long distance movements were also recorded (McFarlane and Beamish, 1986). Thus, while our application of the Leslie model to data taken over a period of several years may be somewhat unusual, there is no existing evidence that invalidates our assumption that the losses and additions to the seamount shark population were generally in balance over this time period.

Bottom longlines rather than trawls were the primary sampling gear used during the NMFS surveys. The few numbers of *S. mitsukurii* taken earlier in the commercial trawl fishery (Sasaki⁵) may have been the result of the different gear types. Other studies have reported the reduced effectiveness of trawls, relative to bottom longline gear, in catching *S. mitsukurii* (Litvinov, 1990).

The decreasing catch rates of *S. mitsukurii* at SE Hancock Seamount suggest a decline in the population size. However, a concomitant decrease in mean length was not observed for either sex (Fig. 3). This

may have occurred because there were large removals from the population with little or no recruitment from smaller (younger) size classes. It is interesting that no size class(es) appeared to progress through the population during the period of study.

Little has been reported concerning the bathymetric distribution patterns of *S. mitsukurii* from other regions. Although *S. mitsukurii* at the seamount and in other regions have a similar maximum depth of occurrence (Compagno, 1984), it is unknown whether *S. mitsukurii* females and males from other populations exhibit depth distributions similar to those at SE Hancock Seamount (Table 2). Sexes of the closely related species *S. acanthias* generally show the opposite trend; males were found at shallower depths than were females (Compagno, 1984).

The largest specimens of *S. mitsukurii* from our study attained sizes similar to the maximum generally reported for other areas. Off South Africa, maximum lengths for *S. mitsukurii* of 81 cm for males and 95 cm for females were reported by Bass et al. (1976). The maximum size we report agrees with that from an earlier study (Taniuchi et al., 1993) at SE Hancock (88–92 cm; $n=72$ specimens) but not that from another locality in the western North Pacific (112–116 cm).

Age and growth

Unvalidated estimates of age based on the second dorsal spine increment counts from 63 fish have been reported for *S. mitsukurii* from the SE Pacific Ocean (Litvinov, 1990). In that study, the maximum age for males was 14 years and for females was 16 years. In the present study maximum ages were somewhat higher: 18 years for males and 27 years for females.

Although tentative, our estimates of age based on spine increment counts suggest that *S. mitsukurii*, like *S. acanthias* (McFarlane and Beamish, 1987), is long-lived. However, maximum ages for *S. mitsukurii* were generally less than those for *S. acanthias*. Maximum ages for *S. acanthias* are quite variable. In the NE Pacific Ocean, ages may exceed 80 years (McFarlane and Beamish, 1987), in the Atlantic Ocean, ages to 40 years have been reported (Nammack et al., 1985), and in the Black Sea, maximum ages may be only 20 years (Kirnosova, 1989). Whether *S. mitsukurii* is a shorter-lived species than *S. acanthias* will require the evaluation of additional samples. Fishing on *S. mitsukurii* at SE Hancock Seamount may have removed much of the older segment of the population before we collected our age sample in the summer of 1986. Thus, the largest fish we aged was only 80 cm, whereas the largest fish caught was 91 cm. This suggests that *S. mitsukurii* may live longer.

⁵ Sasaki, T. National Research Institute of Far Seas Fisheries, Shimizu, Japan. Personal commun., 1992.

The von Bertalanffy growth model was fit to age-length data for *S. mitsukurii*. Increases in \bar{L} with age occurred for both sexes, although few larger, presumably older, specimens in the age sample may have prevented a reliable evaluation of growth over the entire age spectrum. Nonetheless, the growth model seemed to represent observed patterns fairly well over younger ages and smaller sizes for each sex. Rather perplexing is the fact that observed and predicted \bar{L} values at age 0 (Fig. 4) were larger than the observed size at parturition (see below). Possibly the birth of age-0 fish occurs at times other than when our age sample was taken (August–September). If this is the case, the formation of the first increment may not have occurred although the fish had grown in length. Alternatively, young-of-the-year fish may not lay down an increment until their second winter, or we may have simply missed the first increment which is often poorly defined, as with *S. acanthias* (Saunders⁶).

Reproduction

Our results provide some insight into the gestation period for *S. mitsukurii*. The bimodal uterine size distributions that we observed during all seasons, and which exhibited no clearly dominant mode, are consistent with the two-year gestation period of the closely related species *S. acanthias* (Compagno, 1984; Ketchen, 1986; but see Kirnosova, 1989). To confirm the gestation period, however, information is needed on the growth rate of uterine embryos and the time required for the smaller size class to replace the larger size class.

Slight differences in reproductive traits of *S. mitsukurii* were detected between specimens collected at SE Hancock Seamount and from other areas. The minimum size at sexual maturity was 65 cm for females and 55 cm for males off South Africa (Bass et al., 1976), which was similar for females but larger than that of males (<48 cm) in our study. Only the female minimum size at maturity (85 cm) was reported for the SE Pacific (Litvinov, 1990). The value exceeded that of our study. In the North Pacific, Taniuchi et al. (1993) reported larger minimum lengths at maturity for both sexes than those reported here. Their reported minimum lengths at maturity, which included data from 72 fish from SE Hancock Seamount and which were expressed in 4-cm intervals, ranged from 68–72 cm to 96–99 cm for females and 48–52 cm to 68–72 cm for males.

Length and age at maturity for male *S. acanthias* are relatively high in the North Pacific (e.g. 72 cm, 14 years; Ketchen, 1975) compared with other areas, such as the Northwest Atlantic (e.g. 60 cm, 6 years; Nammack et al., 1985) and South Pacific (e.g. 58 cm, 6 years; Hanchet, 1986). For *S. mitsukurii* males from the central North Pacific, however, our estimated age at maturity is quite low (ca. four years). Thus, unlike *S. acanthias*, it seems doubtful that younger ages at maturity will be found in other regions (e.g. South Pacific), assuming our preliminary estimates of age are not seriously in error.

There were no apparent geographical differences in fecundity for *S. mitsukurii*. The reported number of large ovarian eggs (two to five) for females in the southeast Pacific (Litvinov, 1990) agrees with our study. A mean of 6.4 embryos per gravid female (range, 4–10) was reported off southeast Africa (Bass et al., 1976) compared with 3.6 from our study. However, the data from South Africa were taken from larger (76–95 cm) females. Likewise, litter sizes ranged from 2 to 15 (present study 1–6) from relatively large specimens collected in the western North Pacific (Taniuchi et al., 1993). When compared over sizes similar to those in the present study, however, litter sizes were nearly identical (2–6 versus 1–6). Thus, it is probable that the difference between our results and the latter two studies can be attributed to the positive relationship between parent length and fecundity reported in our study (Table 3) and by Taniuchi et al. (1993).

The lengths of near-term embryos from the South African specimens were at least 22 cm (Bass et al., 1976), and those from the southeast Pacific were 29–30 cm (Litvinov, 1990). Although our estimated near-term embryo lengths were similar to those from South Africa, those from the southeast Pacific were larger, possibly because of a positive relationship between the length of the parent and those of the near-term embryos.

Feeding

Squalus mitsukurii fed on a variety of benthic and particularly mesopelagic fishes, crustaceans, and cephalopods at SE Hancock Seamount. Other diet studies have also concluded that *S. mitsukurii* consume a variety of prey types. In the Indian Ocean, for example, *S. mitsukurii* consumed teleosts (57%), cephalopods (33%), and crustaceans (10%) (Bass et al., 1976). On seamounts in the Southeast Pacific, prey included fishes, crustaceans, and cephalopods (Litvinov, 1990). Along the west coast of South Africa, a species tentatively described as *S. mitsukurii* fed predominately on fishes and cephalopods (Ebert et al., 1992).

⁶ Saunders, M. Pacific Biological Station, Nanaimo, B.C. Personal commun., 1991.

In diet studies of the related temperate species *S. acanthias* (Bonham, 1954; Holden, 1966; Jones and Geen, 1977), consumed prey diversity was often lower than that of *S. mitsukurii* at SE Hancock with a large variation in the dominant prey species by season and location. These studies typically found that *S. acanthias* feed on the most abundant prey items available (normally teleost fishes), although other pelagic organisms (primarily euphausiids) were important, particularly for smaller sharks (Jones and Geen, 1977). *Squalus acanthias* often inhabit shelf areas that may maintain large influxes of a few different pelagic species that opportunistic predators such as squalids can exploit (Brodeur and Percy, 1992). *Squalus mitsukurii* at SE Hancock Seamount fed on a great diversity of mesopelagic prey typical of oceanic environments (Boehlert and Genin, 1987; Reid et al., 1991).

Because *S. mitsukurii* specimens in our feeding study were taken from gear set on the bottom, finding benthic prey, such as pleuronectiforms, crabs, or octopods, in the diet was not surprising. Based on results from our vertical longline sets and midwater trawling, however, *S. mitsukurii* did not appear to move high enough above the summit to feed on mesopelagic prey. Rather, these prey species (e.g. stomiiform fishes, lophogastrid mysids) were likely consumed by *S. mitsukurii* as the fauna were advected over or around the seamount. A similar mechanism may exist for other resident fish predators at SE Hancock (Seki and Somerton, 1994). Various studies have documented the importance of current-topographical interactions to biological processes in these environments (reviewed in Boehlert and Genin, 1987), as well as the exploitation of oceanic prey species by demersal predators as the former are advected over banks (Isaacs and Schwartzlose, 1965; Genin et al., 1988) or concentrate in submarine canyons (Pereyra et al., 1969). Over other seamounts, mesopelagic micronekton prey have been found to be an important, if not principal, forage base for resident fish populations (Parin and Prut'ko, 1985).

A high proportion of *S. mitsukurii* stomachs were classified as empty in our study (65%). The occurrence of numerous empty stomachs for squalid species has often been attributed to a combination of intermittent feeding behavior and partial regurgitation of food items (Bonham, 1954; Holden, 1966; Bowman, 1986). Whether the use of hook-and-line gear is biased towards actively feeding fish with empty stomachs is unknown. Holden (1966) discounted this hypothesis after he found a greater proportion of empty guts from trawl-caught rather than line-caught *S. acanthias*. However, the greater frequency of empty stomachs from longline-caught rather than

gillnet-caught fish in our study suggest further consideration of this hypothesis. It is possible that the rapid recovery of longlines to the surface may have increased the likelihood of food regurgitation or stomach flushing. However, we did not observe direct evidence of regurgitation, although the high frequency of empty stomachs filled with water suggests that undetected regurgitation may have occurred (see Bowman, 1986). Whether the preponderance of empty guts in this study actually reflects some aspect of feeding behavior or is simply an artifact of the sampling process requires further work.

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