Abstract.—Seventy-five shovelnose guitarfish, Rhinobatos productus, were collected between November 1988 and January 1991 near Long Beach, California, to determine age, growth, and sexual maturity. Thirteen guitarfish were kept in captivity and injected with Terramycin to provide a time mark for growth analysis. Later, vertebral centra were examined for opaque band formation, and there were positive results in two individuals. Outer margin analysis of centra from captive and field-collected guitarfish indicated that opaque bands formed between August and December. Guitarfish were aged to 11 years, and growth appeared to be best represented by a linear growth equation, TL = 43.33 + 6.90x, where TL =total length and x = estimated age in years. Analysis of reproductive tracts showed that female guitarfish matured at 99 cm (estimated age at seven years). Clasper length and width indicated that males matured at 90-100 cm (estimated age at eight years).

Age, growth, and sexual maturity of shovelnose guitarfish, *Rhinobatos productus* (Ayres)

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Recently, a Federal fishery management plan was initiated for some large coastal and pelagic species of sharks of the eastern seaboard of the United States (NMFS¹). Regulations on shark fisheries are important not only because they affect fisheries but because they affect fisheries but because they set an example to be followed by other coastal areas. Many species of elasmobranchs are highly migratory; thus regulations are necessary on a broader scale if they are to be effective management tools.

Elasmobranchs tend to have slow growth and low fecundity (Holden, 1973); thus, overexploitation of a species is possible. Fortunately, recent collection of age, growth, and reproductive data on elasmobranchs has helped provide some of the baseline information necessary to manage many species.

The shovelnose guitarfish, *Rhinobatos productus*, is a common coastal ray found in temperate waters along the Pacific coast of the United States from Baja California to San Francisco (Miller and Lea, 1972). Although not a highly prized commercial catch, it is edible and is often found in fish markets labeled as generic "shark steak" and sold on piers in Santa Barbara, California, as "fish n' chips." Guitarfish

is not sold as "guitarfish" on restaurant menus: however it may become a popular fare in the future as a substitute for shark. Furthermore, dried guitarfish are sold in large numbers as curios in shell shops from central California to Baja California. The majority of guitarfish sold for human consumption are the larger, mature individuals; however, curio and shell shops tend to sell all sizes, especially newborn pups. Congeners of Rhinobatos are particularly targeted for commercial sale in other areas of the world including Peru (Tresierra et al., 1989) and Brazil (Lessa and Vooren, 1986). Currently, in southern California, commercial landings of guitarfish are grouped under benthic shark species and not recorded as guitarfish.² Most literature on R. productus is contained in field guides and California Fish and Game publications (Roedel, 1953; Miller and Lea, 1972; Lane and Hill, 1975; Eschmeyer et al. 1983; Talent, 1982, 1985) usually with no more than brief mention of some of

¹ NMFS. 1993. Fishery management plan for sharks of the Atlantic Ocean. Prepared for the U.S. Dep. Commer., Natl. Mar. Fish. Serv., NOAA, 167 p.

² Vojkovich, M. 1994. Dep. Fish and Game, Long Beach, CA 90807. Personal commun.

its life history aspects, such as maximum size and food preferences. One particular aspect of guitarfish behavior is that large numbers of them are often found in shallow embayments, such as Elkhorn Slough and Mugu Lagoon, California, and Almejas Bay, Baja California, México. In these areas, they are easily captured with a seine net and are thus particularly susceptible to fishing pressure.

Because elasmobranchs tend to be exploited before regulatory measures are in effect (Pratt and Casey, 1990), it is necessary to determine age and growth relationships and size at sexual maturity of R. productus prior to increases in fishing pressure. The results of this study provide basic information for management of guitarfish, should it become more popular as a food item.

We have incorporated the following methods of age determination into this study of the age, growth, and sexual maturity of guitarfish: 1) a laboratory analysis of the vertebral bands and their outer margin state (translucent or opaque) in order to assign ages to individuals; 2) a study of growth in captivity to verify estimated growth from the laboratory analysis; and 3) a determination of age at sexual maturity. The main focus of this age and growth study is based on an examination of vertebral centra and their use in ageing guitarfish.

Methods

Age and growth

Seventy-five guitarfish were collected between November 1988 and January 1991 from the waters between Seal and Redondo Beaches, California (Fig. 1). Guitarfish were captured by hook and line, gill net, otter trawl, long line, or beach seine, and then frozen. Lengths were measured with a tape measure to the nearest centimeter over the contour of the dorsal portion of the guitarfish and included total length (TL), disc width (DW), first dorsal fin length (1D), and second dorsal fin length (2D) (Fig. 2). The contour measurement over the dorsal portion provided a more precise measurement of the first and second dorsal fin lengths. This method will increase the total length measurement and should be taken into consideration if comparisons are made with lengths of guitarfish in this study.

The only portion of the guitarfish that is available in fish markets is the trunk and tail or loin region, which includes the two dorsal fins. Therefore, we included the measurement of the distance from the origin of the first dorsal fin to the origin of the second dorsal fin (2D) to facilitate future predictions of



Figure 1

Study sites where guitarfish, *Rhinobatos productus*, were collected along the coast of southern California. A = Redondo Beach, B = Palos Verdes, C = San Pedro, D = Long Beach, E = Belmont Shores, and F = Seal Beach.

total length from market fish. Damp weight was measured for all guitarfish with a spring balance. Ten vertebrae were removed from each guitarfish just anterior to the first dorsal fin for analysis. The larger vertebrae were located just posterior to the eyes; however, they were not used because removal of these vertebrae would have interfered with dissection of the female reproductive tract. Each guitarfish was assigned a code number and this became the only identifying feature for each guitarfish for the remainder of the study. Vertebrae were cleaned by placing them in a dermestid beetle colony. The beetles consumed almost all muscle and connective tissue; the only remaining tissue was a cone-shaped membrane (membrane elastica externa) on the centrum that was easily removed from the dry vertebrae with fine forceps. Cleaned and dried vertebral centra were viewed whole with a Wilde dissecting scope with transmitted light within a dark field. Ten vertebrae from each guitarfish were examined to determine consistency of band formation within an individual. If all vertebrae for an individual guitarfish contained the same number of bands, then two of those vertebrae were used for three separate readings. Those having variable band counts or unreadable vertebrae among the ten vertebrae were discarded. Opaque bands present beyond the birth mark were counted (Fig. 3). Rings within bands were not always discernible as separate rings; therefore, bands were determined to be the most useful increment. The birth mark was defined here as the centermost opaque portion (first band) of the centra. It was present in the smallest of the guitarfish and was in the same position in all larger specimens. This birth mark is similar in place-





Figure 3

Examples of band formations in the vertebra of a 125.5-cm guitarfish (\mathbf{A}) and a 28.8-cm guitarfish (\mathbf{B}). The birth mark (b) appeared in all three vertebrae. Band formations (c) were poor towards the outer edge of the centra of the larger individual (A), and this individual was not used in the age study. Poor band formations were indicative of individual guitarfish with deformed vertebral columns.

ment to that found by Cailliet et al. (1983) in the blue shark, *Prionace glauca*, and Casey et al. (1985) in the sandbar shark, *Carcharhinus plumbeus*. Diameters of vertebral centra were measured with an ocular micrometer at 12× magnification. Each vertebra was read three times, one month apart, and those vertebrae in which all three readings agreed were used in the final analysis. To determine periodicity of band formation, the condition of the outermost band was recorded as either translucent, opaque, or undetermined. Ages were assigned to guitarfish on the basis of the number of opaque bands.

Statistical analyses included least squares regression analysis to provide predictive equations for estimates of TL from centrum diameter, TL from band counts, TL from second dorsal fin length (2D), and age from TL. Regression parameters were obtained with SAS PC software (SAS, 1985). Male and female growth curves were constructed from von Bertalanffy's growth curve equation (von Bertalanffy, 1938):

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

where $L_t = \text{total length at time } t$;

 L_{∞} = maximum theoretical length of species;

k =growth constant;

 t_0 = theoretical age at zero length; and

t = estimated age.

The von Bertalanffy growth equation was fitted by using FISHPARM (FISHPARM software [Prager et al., 1989]) to estimate the growth constant k and was compared to a linear least squares regression by using the same data.

Growth rate of guitarfish in captivity

The main purpose of the captivity study was to determine if Terramycin (manufactured by Pfizer Agricultural Division) produced a readable time mark in vertebral centra of guitarfish. The study was designed to maintain guitarfish in captivity for at least one year to determine the temporal periodicity of band formation and growth rate of guitarfish in captivity.

Over a two-year period, 13 guitarfish (five males and eight females) were taken live and placed in an outdoor saltwater tank at California State University, Long Beach, California. Before guitarfish were introduced into the tank, we repeatedly measured TL, DW, 1D, and 2D until we obtained consistent, repeatable measurements. Guitarfish were first weighed, and then injected with Terramycin (dosage=0.5 mg/kg). Terramycin was injected with tuberculin-type syringes in the epaxial musculature, within two centimeters of the skin surface. Guitarfish were fed every other day a diet of anchovy, mackerel, mud shrimp, ghost shrimp, and squid.

When a guitarfish died in captivity, it was used for vertebral and reproductive analysis. Vertebral growth (beyond the time mark) was measured with the aid of a Wilde dissecting scope and ultraviolet flashlight (Fig. 4). Because time marks could be seen only under ultraviolet light and the opaque band formation could not be seen under ultraviolet light, transmitted light was used immediately after the ultraviolet light to compare the time mark with the opaque band position. This method allowed determination of whether a translucent or opaque band had formed after the time mark.

Reproductive maturity

Thirty-six female guitarfish were dissected for examination of their reproductive tract. Mature individuals were categorized into one of three visual stages: Stage 1-shell gland not differentiated from uteri, uteri empty, small follicles present; Stage 2shell gland and characteristic diagonal white band pattern within it forming, large Graafian follicles present, uteri thick; and Stage 3-uteri full, large Graafian follicles present. Immature individuals had no visible egg follicles, uteri were thin and transparent, and shell glands consisted only of a slight bulge in the upper portion of the uteri. These stages were distinct; any female guitarfish, upon dissection, could be categorized by using these criteria. No dissections were made for male guitarfish. The maturity of male guitarfish was determined by measuring the clasper width and length and by comparing the clasper length to total length, as well as by visual examination.

Results

Age and growth

Growth of the vertebrae was proportional to the growth of the guitarfish, as evidenced by the significant positive relation between centrum diameter and total length for females and males (females: $r^2=0.98$, n=27, P=0.0001; males: $r^2=0.96, n=31, P=0.0001$; Fig. 5). The number of bands per vertebra correlated strongly (r=0.92, n=42, P=0.0001) with the diameter of the centra, indicating that individuals having more bands had larger centra. Similarly, the number of opaque bands present in any individual was higher in larger guitarfish; the regressions were significant for females and males (females: $r^2=0.95, n=19, P=0.0001$; males: $r^2=0.78, n=24, P=0.0001$). A Pearson correlation matrix analysis of total length, centrum



Figure 4

Comparison of Terramycin-injected guitarfish vertebrae (\mathbf{A} and \mathbf{C}) with control (\mathbf{B}). The guitarfish vertebral column (C) was removed from a 27-cm individual that had been injected with Terramycin one month prior to its death in captivity. Note the yellow Terramycin band on the outer edge of the vertebra (A), and the Terramycin incorporation on the entire outside of the vertebral column (C). The control vertebra (B) was from a 37-cm guitarfish sacrificed immediately after capture.

diameter, and number of opaque bands further emphasized the strong relation between the three variables for males and females combined (opaque bands and TL: r=0.92, n=43, P=0.0001; centrum diameter and TL: r=0.99, n=60, P=0.0001; for opaque bands and centrum diameter see above).

Growth zones formed at approximately the same time each year, as was evident from examination of centra of two captive guitarfish. One of these guitarfish was injected with Terramycin in December 1989 and in July 1990 and was held in captivity for 13 months. The first Terramycin mark (closest to the focus of the centrum) was found at the peripheral edge of an opaque band (Fig. 6A). We do not know if the opaque band had formed prior to the injection or during the same month as the injection because the Terramycin may have diffused into the opaque band region. It was clear, however, that the mark was the same distance (0.07 cm) from the outer margin of the centrum as the peripheral edge of the opaque band. From the periphery of the opaque band to the outer margin of the centrum, a translucent band was present; and the outer margin of the centrum contained the other Terramycin mark. The predicted growth (0.029 cm) of this centrum (with the formula in Fig. 5) was lower than the actual growth of 0.07 cm and shows that individuals probably vary in growth, especially in more optimal laboratory conditions. A second guitarfish was first injected in October 1989 and again in July 1990. This guitarfish lived for 14 months and had completely formed one opaque band during this period (Fig. 6B). This opaque band was formed after the October injection, and a translucent band was present beyond the opaque band to the outer margin of the centrum. The outer margin of the centrum showed the second injection mark at the periphery of the translucent zone at the time of death in January 1991. For this guitarfish, the predictive equation (Fig. 5) estimated centrum growth to be 0.062 cm; it was actually 0.053 cm. In both guitarfish, opaque band formation occurred sometime between the months of October and December followed by translucent band formation. The remaining eleven guitarfish were held in captivity for six months or less. Eight of the eleven were injected with Terramycin and did not show any growth beyond the Terramycin mark on the vertebrae and each had grown less than one centimeter in total length. Three control guitarfish (no injections) lived 10, 50, and 72 days in captivity and showed no gain in length.

Analysis of the outer edges of the centra with regard to periodicity of band formation provides further evidence for opaque band formation between October and December. Eight out of 17 guitarfish collected between October and November had opaque outer margins, whereas none of the 34 other guitarfish collected during the other months (excluding August) had opaque outer margins. Three guitarfish caught in August showed opaque formation on the outer margins. A two-way test of independence indicated rejection of the null hypothesis that opaque band formation was independent of month (group 1=January-June, group 2=August-November; G(adjusted)=18.94, df=1, P=0.00003). Therefore, it appears that opaque bands form from late summer (August) into fall (November). There was no pronounced relation between outer margin width and months of the year, probably indicating variation of growth within individual guitarfish. Another way to



interpret these findings is to suggest that guitarfish lay down opaque bands bi-yearly (every other year). If this is the case, then the guitarfish were twice as old. However, the band formations found in the two captive guitarfish led us to assume that opaque bands were formed once per year.

Assigning ages under the assumption of the annual formation of one opaque and one translucent band, we found that both males and females ranged in age from one to 11 years. Females ranged from 25 to 130 cm TL. Males ranged from 23 to 114 cm TL. Percent agreement in band counts from three separate readings of two vertebrae from each guitarfish showed 73.8% in total agreement (43 guitarfish), 16.4% disagreement \pm 1 band (10 guitarfish), 6.5% disagreement \pm 2 bands (4 guitarfish), and 3.3% dis-



Examples of opaque band formation indicating seasonal formation of bands (no photograph was available). The diagrams of centra represent rays in the captive study that were injected twice with Terramycin. T_1 = first injection, T_2 = second injection, TZ = translucent zone, and D = centrum diameter. Gray areas indicate opaque band areas and are not to scale. Example A was held alive in captivity for 13 months, and example B was alive for 14 months.

agreement \pm 3 bands (2 guitarfish). Only bands in total agreement (from 43 guitarfish) were used in the final analysis.

The linear model best represented growth of combined sexes of guitarfish because the coefficient of determination was 0.90 for the linear regression, and 0.81 for the nonlinear von Bertalanffy curve (Fig. 7: Table 1). For females only, the linear regression and the von Bertalanffy curve produced similar values



for the coefficient of determination $(r^2=0.95)$, and $r^2=0.94$, respectively). For males, the linear regression also appeared to be a better predictor $(r^2=0.78)$ than the von Bertalanffy curve $(r^2=0.70)$; Table 1). Residuals for both the linear regression and the von Bertalanffy model (females and males) clustered evenly about both sides of the prediction lines. There was no reason to suggest any violation of homoscedasticity in either model.

If it is necessary to predict the total length of a specimen from fish markets using only the tail region of the guitarfish, the following equation is suggested (Fig. 8):



Predictive relationship for total length of guitarfish based on their second dorsal fin length.

Table 1

A comparison of linear regression parameters and von Bertalanffy parameters for male (n=24) and female (n=19) guitarfish and for combined sexes (n=43).

	Linear regression parameters			von Bertalanffy parameters			
	Y-intercept	Slope	r^2	L_{∞}	k	t _o	r^2
Female	34.02	8.29	0.95	594	0.016	-3.80	0.94
Male	47.00	6.32	0.78	142	0.095	-3.942	0.70
Female and male	43.33	6.90	0.90	228	0.047	-4.030	0.81

TL = 6.01 + 5.56(2D),

- where TL = estimated total length of the guitarfish; and
 - 2D = second dorsal length (when 2D >3.5 cm and <20 cm).

Reproductive maturity

The smallest sexually mature female guitarfish was 99 cm TL and was estimated to be seven years old, based on vertebral band counts. Developing ovaries were present in 26 specimens from 40 to 99 cm TL. These individuals showed no evidence of previous birthing or egg follicles: uteri were thin walled and shell glands were not distinguishable from surrounding oviducts. Immature female guitarfish accounted for the majority of specimens taken (27 of 36).

A well-developed shell gland (nidimental gland) was present in mature shovelnose. Females with full uteri contained a case as described by Cox (1963) for *Rhinobatos*. In four individuals with full uteri, no developing embryos were seen in any of the specimens. These specimens contained either four or five yolks within the right or left egg case and, with the exception of one specimen, had nine total yolks per mature female. These four fish were captured in February (one), April (one), and June (two).

Male guitarfish reached maturity between 90 and 100 cm TL. At maturity there was an abrupt increase in clasper length and claspers extended well beyond the pelvic fin (Fig. 9). Claspers of mature males were at least 13 cm in length, and clasper width at maturity was at least 1 cm. A well-developed spur was present on both claspers in mature males and was not present in immature males (Fig. 10). Immature male squaloid sharks also lack spines (Applegate, 1967). Twelve of the 38 sampled were mature and 26 were immature.

Discussion

Age and growth

The shovelnose guitarfish is best described as a slowgrowing species typified by linear growth after parturition. Our total estimated age range (one to 11 years) for R. productus was the same that Lessa (1982) found for R. horkelii. Her specimens were also in the same size range as R. productus (20 to 120 cm). Rossouw (1984) found ages 0 to 6 years in R. annulatus, and his largest specimen was 99.3 cm.

Age estimates in this study were based on the assumption that one opaque and one translucent band





are formed annually. One verification procedure, examination of individuals held in captivity, provided support for the outer margin analysis; however, this analysis was based on only two specimens. The second verification procedure, outer margin analysis of field-caught specimens, indicated that band formation was dependent on season; however, there was no correlation between width of the outer margin and month. Early band formations at the margin can be difficult to detect with whole centra. To avoid this difficulty we tried sectioning the centra; however, we were unable to obtain readable sectioned centra. Others, such as Tanaka (1990) and Gruber and Stout (1983) have had success in sectioning vertebrae to view band formations. Therefore, we do not consider our verification procedure to be complete. It is evident that guitarfish have linear growth which might be somatic and not correlated with age of the guitarfish, as was suggested by Natanson et al. (1984) for Squatina californica. Further studies should be attempted to answer this question. Specifically, we suggest more tagging and injection studies to validate laboratory data.

Reproductive maturity

We encountered a problem collecting large (>90 cm) females; it has been suggested by Baxter (1980) and Lane and Hill (1975) that individuals of this size are uncommon. Our largest female was 130 cm. In Almejas, Baja California Sur, México, Villavicencio-Garayzar (1993) reported that his largest captured female R. productus was 137 cm. Females in the present study were mature at ≥ 99 cm TL, whereas Villavicencio-Garayzar (1993) suggested that maturity of R. productus was at >70 cm TL. The youngest free-living guitarfish obtained was 23 cm TL, and it appears that the estimate of 15 cm (Eschmeyer et al., 1983) for newborn pups might be low. Melouk (1949) reported 16-cm specimens of R. halavi that still had sizable yolk attachments in utero. It is possible that Eschmeyer's measurements of 15 cm were taken from expelled premature pups. Expulsion of embryos can occur from stressed females (Pratt and Casey, 1990). Another possibility is that mortality is high in postpartum pups and many do not survive. Perhaps the smallest specimens that we sampled were first-year survivors. Rossouw (1984) suggested that the average length of Rhinobatos annulatus at birth was 23 cm TL and Dubois (1981) stated that embryos of R. productus at parturition were 23 cm. Villavicencio-Garayzar (1993) reported a free-swimming R. productus at 24 cm and suggested neonates are 20-24 cm. The first year class we collected (presumably represented as the smallest guitarfish we obtained) did not have any bands present beyond the birth mark. Many of the young guitarfish were captured by otter trawls in the Belmont Shores area in Long Beach, CA.; it appears that this is a nursery ground for guitarfish.

Our estimates of nine offspring per female were also the mean number of offspring found by Villavicencio-Garayzar (1993) for *Rhinobatos* productus in Almejas, Baja California Sur, México. He found that *R. productus* females had a minimum of six pups and a maximum of 16. Additionally, Villavicencio-Garayzar (1995) found that *Zapterix* exasperata females contained a minimum of 4 and a maximum of 11 embryos (the most common numbers of embryos per individual were between 6 and 9).

Males showed the same size at maturity as males sampled by Dubois (1981). His males were all mature when TL exceeded 92 cm. No males in his study had clasper lengths in the range of 11 to 15 cm, indicating a definite size break in clasper length between immature and mature males. Our male guitarfish showed this same break between clasper lengths of 11 and 13 cm, and all males in our study were mature when TL exceeded 100 cm. Our smallest mature male was 91 cm. Both of our studies indicated a lack of individuals with clasper lengths in the 10-13 cm range, and Martin and Cailliet (1988) found a similar break in clasper lengths (between approximately 22–37 cm) in Myliobatis californica. This indicated to us that sexual maturity occurred within a distinct size range (TL) for males. Visual examinations of the claspers confirmed maturity; they were well developed and occasionally contained semen. Villavicencio-Garayzar (1993) found male Rhinobatos productus with sperm in their vasa deferentia at 63, 68, and 69 cm TL, but did not indicate a length at first maturity. For Zapterix exasperata, Villavicencio-Garavzar (1995) found males at 69 cm with semen.

Information from this research will provide a starting point for persons who may be interested in regulating guitarfish catch in the future. The information on size at first maturity for both males and females and the equation for estimating total length of guitarfish from tails sold to markets by fisherman will be useful management tools. Although the age estimates of the guitarfish are preliminary, total length (TL) at sexual maturity is most valuable. This information provides a starting point for evaluation of possible future size limitations for catches of guitarfish. We suggest further studies in order to attempt to age guitarfish over its entire population range.

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Literature cited

- Applegate, S. P.
 - 1967. A survey of shark hard parts. In P. W. Gilbert, R. F. Mathewson, and D. P. Rall (eds.), Sharks, skates, and rays. Johns Hopkins Press, Baltimore, MD, 624 p.
- Baxter, J. L.
 - 1980. Inshore fishes of California. Dep. Fish Game, Sacramento, CA, 72 p.

Cailliet, G. M., L. K. Martin, P. Kusher, P. Wolf, and B. A. Welden.

1983. Techniques for enhancing vertebral bands in age estimation of California elasmobranchs. In Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks, p. 157–165. U.S. Dep. Commer., NOAA Tech. Report. NMFS 8.

Casey, J. G., H. L. Pratt Jr., and C. E. Stillwell.

- **1985.** Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. Can. J. Fish. Aquat. Sci. 42:963–975.
- Cox, K.W.
 - 1963. Egg-cases of some elasmobranchsand a cyclostome from Californian waters. Calif. Fish Game 49:271-289.
- Dubois, A. J.
 - 1981. Studies on fishes in Mugu Lagoon, California. M.A. thesis, Univ. Calif. Santa Barbara, Santa Barbara, CA, 95 p.

Eschmeyer, W. N., E. S. Herald, and H. Hammann.

1983. A field guide to Pacific coast fishes of North America from the Gulf of Alaska to Baja California. Peterson Field Guide Series, Houghton Mifflin Co., Boston, MA, 336 p.

Gruber, S. H., and R. G. Stout.

1983. Biological materials for the study of age and growth in a tropical marine elasmobranch, the lemon shark, *Negaprion brevirostris* (Poey). Summary of round table discussions on age validation. In Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks, p. 193-205. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8.

Holden, M. J.

1973. Are long-term sustainable fisheries for elasmobranchs possible? Rapp. P.-V. Reun. Cons. Int. Explor. Mer 164:360-367. Lane, D. E., and C. W. Hill.

1975. The marine resources of Anaheim Bay. Calif. Fish Game. Fish Bull. 165:1–195.

- Lessa, R. P.
 - **1982.** Biologie et dynamique des populations de *Rhinobatos horkelii* (Müller and Henle, 1841) du Plateau Continental du Rio Grande do Sul (Bresil). Ph.D. diss., Dep. Oceanography, Universite de Bretagne Occidentale, 238 p.

Lessa, R. P., and C. M. Vooren.

1986. Migration and reproductive cycle of the guitarfish *Rhinobatos horkelii* (Mueller et Henle, 1842) from the Brazilian coast (abstract only). *In* T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuura (eds.), Indo-Pacific fish biology: proceedings of the second international conference on Indo-Pacific fishes, 29 July-3 August 1985, p. 929.

Martin, L. K., and G. M Cailliet.

1988. Aspects of the reproduction of the Bat Ray, *Myliobatis* californica, in Central California. Copeia 1988 (3):754–762. Melouk, M. A.

1949. The external features in the development of the Rhinobatidae. In H. A. F. Gohar, Bey (ed.), Publications of the Marine Biological Station Ghardaqa (Red Sea) No. 7. Fouad 1 Univ. Press, Cairo.

Miller, D. J., and R. N. Lea.

1972. Guide to the coastal marine fishes of California. Calif. Fish Game. Fish Bull. 157:1-249.

- Natanson, L. J., G. M. Cailliet, and B. A. Welden.
 - 1984. Age, growth and reproduction of the Pacific angel shark (Squatina californica) from Santa Barbara, California. Am. Zool. 24(3):130.

Prager, M. H., S. B. Saila, and C. W. Recksiek.

1989. FISHPARM: a microcomputer program for parameter estimation of nonlinear models in fishery science. Tech. Rep. 87-10, Dep. Oceanography, Old Dominion Univ., Norfolk, VA, 18 p.

Pratt, H. L., Jr., 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. In H. L. Pratt Jr., S. H. Gruber, and T. Taniuchi (eds.), Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries, p. 97–109. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 90.
- Roedel, P. M.
 - 1953. Common ocean fishes of the southern California coast. Calif. Fish Game.Fish Bull. 91:1–184.
- Rossouw, G. J.
 - 1984. Age and growth of the sand shark, *Rhinobatos annulatus*, in Algoa Bay, South Africa. J. Fish Biol. 25(2):213– 222.
- SAS (SAS, Inc.)

1985. SAS/statistical user's guide, 3rd ed. SAS, Inc., Cary, NC, 99 p.

- Talent, L. G.
 - 1982. Food habits of the gray smoothhound, *Mustelus californicus*, the brown smoothhound, *Mustelus henlei*, the guitarfish, *Rhinobatos productus*, and the bat ray, *Myliobatis californica*, in Elkorn Slough, California. Calif. Fish Game 68(4):224-234.

1985. The occurrence, seasonal distribution, and reproductive condition of elasmobranch fishes in Elkhorn Slough, California. Calif. Fish Game. 71(4):210–219.

Tanaka, S.

1990. Age and growth studies on the calcified structures of newborn sharks in laboratory aquaria using tetra-

cycline. In H. L. Pratt Jr., S. H.Gruber, and T. Taniuchi (eds.), Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries, p. 189–202. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 90.

Tresierra, A., Z. Culquichicon, and T. Alvarado.

1989. Artisanal fishing at Constante cove (Piura, Peru): status quo and perspectives. Simp. Int. Recursos vivos Pesquerias Pacifico Sudeste, Vina del Mar (Chile), 9 May 1988. In Rev. Com. Perm. Pac. Sur, p. 485–494. Villavicencio-Garayzar, C. J.

- 1993. Biología reproductiva de *Rhinobatos productus* (Pisces: Rhinobatidae), en Bahía Almejas, Baja, California Sur, México. Rev. Biol. Trop. 41(3):777–782.
- **1995.** Biología reproductiva de la Guitarra Pinta, *Zapterix exasperata* (Pisces: Rhinobatidae), en Bahía Almejas, Baja California Sur, México. Cienc. Mar. 21(2):141–153.

von Bertalanffy, L.

1938. A quantitative theory of organic growth (inquiries on growth laws. 2). Hum. Biol. 10:181–213.