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Life history of the Pacific electric ray, Torpedo Californica (Ayres), in central and southern California

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**LIFE HISTORY OF THE PACIFIC ELECTRIC RAY,
TORPEDO CALIFORNICA (AYRES),
IN CENTRAL AND SOUTHERN CALIFORNIA.**

**A Thesis Presented to
The Faculty of
Moss Landing Marine Laboratories
San Jose State University**

**In Partial Fulfillment
of the Requirements for the Degree
Master of Science**

**by
Julie Ann Neer
August 1998**

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LIFE HISTORY OF THE PACIFIC ELECTRIC RAY,
TORPEDO CALIFORNICA (AYRES),
IN CENTRAL AND SOUTHERN CALIFORNIA

Julie Ann Neer

Pacific electric rays were collected from central and southern California from July 1994 through January 1996 for an age and growth, reproduction, and demography study. Vertebral centra were used for ageing. Maximum age was an estimated 16 years. The von Bertalanffy growth model provided the best fit to the size-at-age estimate data, predicting an asymptotic total length of 1372 mm for females and 921 mm for males. Estimated size (and age) at sexual maturity was 600 mm TL (6 years) for males and 840 mm TL (11 years) for females, and an estimated fecundity of ~17 young per litter. Time of parturition could not be determined. Instantaneous mortality estimates (z) ranged from 0.048 to 0.277, depending on the longevity estimates. Best demographic estimates indicate that the Pacific electric ray population is probably at equilibrium or slightly increasing with a generation time of 12.7-14.7 years, and an r of 0.07-0.13.

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INTRODUCTION

Elasmobranchs (sharks, skates, and rays) are a diverse group of aquatic organisms occurring in many marine habitats, often occupying apex positions in ecosystems (Compagno 1990). Much of the recent research on elasmobranchs has been focused on commercially or recreationally important shark species, with coastal ray species receiving comparatively little attention (Zeiner and Wolf 1987; Martin and Cailliet 1988a, 1988b; Natanson 1993).

Electric rays (Family Torpedinidae) are cosmopolitan, aplacental viviparous elasmobranchs occurring in all major oceans of the world. Currently, there are two recognized genera containing ~14 species (Nelson 1994). The Pacific electric ray, *Torpedo californica* (Ayres), is the only representative of the family located off California (Eschmeyer et al. 1983). Considered common, the species ranges from Sebastian Viscaïno Bay, Baja California to Queen Charlotte Islands, British Columbia, occurring at depths between 3 and 274 m (Miller and Lea 1972). A small fishery exists for the acquisition of biological and biomedical research specimens (Love 1996).

Information regarding movement patterns of the Pacific electric ray is scarce. Limited telemetry studies indicate that Pacific electric rays begin active movements after dusk and are primarily nocturnal (Bray pers. comm.). Traditionally thought to be sluggish and passive hunters, *in situ* observations indicate that Pacific electric rays actively hunt for prey in the water column near

rocky reefs and kelp beds and move rapidly in both offensive and defensive situations (Bray and Hixon 1978; Bray pers. comm.). Catch records from southern California indicate summer inshore migratory patterns, and possible segregation by sex (R. Fay pers. comm.). Segregation of animals by size also may occur along the California coast, with smaller individuals located in the northern portion of the species range (D. Bray, R. Fay, C. Lowe pers. comm.).

Whereas information exists regarding the movement patterns and diet of the Pacific electric ray, few data exist concerning its life span, age structure, or growth rate. Longevity estimates determined from vertebral centra are available for only one species of electric ray (*Torpedo marmorata*; Mellinger 1971), indicating that *Torpedo* may have traits similar to other elasmobranchs studied (slow growth, long-lived; Holden 1974). Newborn growth rates also are available but only for captive *T. ocellata* (Michaelson et al. 1979). Age validation was not attempted for either species.

Age determination is important for understanding population dynamics of vertebrate species. For elasmobranchs, markings on the vertebral centra are most often used for age determination and various techniques have been developed to visually enhance the banding pattern observed on vertebrae (Cailliet et al. 1986b; Cailliet 1990). Few researchers, however, have validated the temporal component of banding patterns in elasmobranchs or teleosts (Beamish and McFarlane 1983; Cailliet 1990). The annual periodicity of growth zones of only seven elasmobranch

species have been partially validated, only two of which, *Raja clavata* and *Raja erinacea*, are batoids (Holden and Vince 1973; Cailliet 1990; Natanson 1993). Growth zones were deposited annually for these species. However, not all species studied have demonstrated annual band deposition. Natanson and Cailliet (1990) determined that growth zones in the vertebral centra of the Pacific angel shark (*Squatina californica*) were not related to a temporal component but rather perhaps to somatic growth. This conclusion, along with the finding that individuals of this species displayed six to seven bands in their vertebral centra at birth, emphasized the need for validation for each species studied and that all size classes must be represented for validation to be complete (Beamish and McFarlane 1983; Cailliet et al. 1986).

A variety of methods currently exists for verifying and validating the temporal component of growth zones in calcified structures of elasmobranchs. Commonly used methods include size frequency analysis, centrum edge analysis, tag-recapture studies, and laboratory and field growth studies (Cailliet 1990). Radiometric dating was attempted for four species of elasmobranchs off California by Welden et al. (1987) but was not successful due to a violation of two assumptions of the technique. Electron microprobe analysis was promising as an additional verification technique but has rarely been used (Cailliet and Radtke 1987).

Reproductive parameters of the Pacific electric rays are unknown. Studies of other electric ray species indicate fecundity of 4 to 18 young per female (Mellinger 1971; Michaelson et al. 1979; Villavicencio - Garayzar 1993).

Mellinger (1971) and Capape (1979) reported a 2 - 3 year reproductive cycle for female *T. marmorata*; with males having an annual cycle. Gestation estimates for the genus range from 4 to 12 months (Quignard & Capape 1974; Capape 1979; Abdel-Aziz 1994).

The population dynamics of the Pacific electric ray have not been investigated. Demographic analysis, using age-specific mortality and reproductive information, can be useful in understanding the population dynamics of a species. Its use in assessing the vulnerability of elasmobranch populations to exploitation has recently become very popular (Cortes 1994; Sminkey and Musick 1995, Au and Smith 1997).

The lack of information about the Pacific electric ray, especially regarding its basic biology, emphasizes the need for further research. To address this problem, I investigated the following hypotheses regarding the natural history of the Pacific electric ray: 1) Pacific electric rays, like other elasmobranchs, are slow growing and long-lived; 2) the use of vertebrae as an ageing structure is valid and the temporal periodicity of the banding pattern is annual; 3) male Pacific electric rays reach sexual maturity at a younger and smaller size than females; and 4) females have a low fecundity.

METHODS

Specimen Collection

Pacific electric ray specimens were obtained between August 1994 and January 1996 off central (Monterey Bay) and southern (Los Angeles Basin) California (Figure 1).

Monterey Bay specimens were primarily collected from the 35' R/V Ed RICKETTS, using an 8.3-m otter trawl . Trawls were towed from 5 to 20 minutes, at an average speed of 1.5 knots. The trawls occurred at water depths of 10 to 100 m. The body of the trawl consisted of a 3.8 centimeter (cm) stretch mesh, and a cod end mesh of 1.3 cm stretch mesh. Additional Monterey Bay specimens were obtained from commercial bycatch and from additional trawling operations conducted by Moss Landing Marine Laboratories (MLML) personnel.

Southern California specimens were obtained from three sources. Rim Fay of Pacific BioMarine provided vertebrae and reproductive tracts of hand or net collected specimens. Chuck Winkler of the Southern California Marine Institute (SCMI) provided specimens after removal of the electric organs. Most of these specimens were obtained from trawls conducted by SCMI from the R/V YELLOWFIN. Several specimens were provided by scientists at the Southern California Edison power plant marine lab located at King Harbor, Redondo Beach, California. These specimens were obtained from the impingement screens of the plant's biological recirculation system.

In addition to the Pacific electric ray specimens collected during this study, I used specimens and data from the MLML Ichthyology Museum collection. All specimens were frozen after collection and stored at MLML until examination.

Age and Growth

External examinations were conducted for all specimens after thawing. When possible, rays were sexed, weighed to the nearest 0.1 kg, and four linear measurements were recorded (Figure 2). Measurements, to the nearest millimeter (mm), were: 1) disk width (DW); 2) total length (TL; snout to tip of intact tail); 3) predorsal length 1 (PDL1; snout to origin of first dorsal fin); and 4) predorsal length 2 (PDL2; snout to insertion of second dorsal fin). Outer clasper length was also recorded for males. A subsample of specimens was measured prior to freezing and remeasured upon thawing to examine the effect freezing had on specimen size. A paired t-test was used to test for significant differences in measurements.

Vertebrae were used for ageing. A section of the vertebral column was removed just posterior of the chondocranium to at least the insertion of the first dorsal fin. The neural arch and protective cartilage were removed, and the columns were labeled, bagged, and frozen for two weeks to six months. Vertebrae were prepared for reading following techniques outlined in Martin and Cailliet (1988a). Five to seven vertebral elements were removed from the first through 25th vertebrae. Excess cartilage was removed using a scalpel or pointer,

the centra placed in Clorox bleach solution (100%) for 30 seconds to five minutes depending on size (larger vertebrae requiring more time), then placed in two changes of fresh water for 24 - 48 hours. The vertebrae were allowed to air dry and stored dry in labeled vials.

The use of vertebrae as an ageing structure was assessed. One clean vertebral centrum was selected from each specimen. Individual centrum selection was subjectively based on the lack of chips or cracks along the centrum edge. Once selected, three linear measurements of centrum diameter (CD) were recorded nearest millimeter across the centrum face using an image analyzer (Bausch and Lomb Monozoom 7 microscope attached to a Macintosh IICX equipped with Macintosh IMAGE 1.37 software; Figure 3a). The greatest of the three measurements was used for all further analyses. Centrum diameter was plotted against DW and TL to determine which measurement had a better predictive relationship (determined by r^2 value) for determining fish size from centrum size.

Banding pattern consistency throughout the column was examined. Vertebrae were removed from four locations along the vertebral column of six specimens. Centra were cleaned and the number of bands observed on the centra recorded for all positions along the vertebral column. Specimens examined were all at least 400 mm TL because it is assumed that variation in

growth within an animal would most likely be observed in larger, and presumably older, individuals (Figure 3b).

Several techniques for enhancing the banding pattern on the vertebral centra were assessed. Techniques that have proven useful for other species, alizarin red staining (LaMarca 1966; Gruber and Stout 1983), silver nitrate impregnation (Stevens 1975; Cailliet et al. 1983), cedarwood oil staining (Cailliet et al. 1983), water immersion, and straight light microscopy (Cailliet et al. 1986a), did not significantly increase the readability of the banding pattern for Pacific electric rays. All of the above techniques were examined on both whole and thin-sectioned vertebrae. Techniques that had the most promise were x-radiography (Martin and Cailliet 1988a) and lead microtopography enhancement (Parsons 1983). The use of electron microprobe analysis also was investigated (Cailliet and Radtke 1987).

For the lead microtopography technique, one vertebra from each specimen was selected. The face of the centrum was lightly scraped with a No. 2 pencil, moving from the center of the vertebra toward the edge, to create a cone-shaped shaded area (Figure 4). The number of observed bands was recorded while viewing under an Olympus dissecting microscope using fiberoptic reflected light.

The x-radiography technique follows Martin and Cailliet (1988a). The vertebrae were halved through the center to create two identical cones, thus eliminate confusion caused by double images on the x-rays. The centra were x-rayed using a Hewlett Packard Faxitron series X system (Model No. 43805N) with Kodak Industrex M film (ready pack M-2). After exposure, the film was processed using standard Kodak Industrex processing techniques. X-radiographs were viewed on a dissecting microscope with transmitted light, and the number of bands observed recorded.

Specimen age was determined by the banding pattern observed on the vertebral face. Following Cailliet et al. (1983), the term “band” refers to the larger concentric marks, composed of groups of smaller “rings” observed on the vertebral face (Figure 4). Bands, or growth zones, could be classified into two categories; more and less calcified, appearing light or dark depending on the lighting source. One band pair, comprised of one zone from each category, was assumed to represent one year. Sixty-eight samples were initially aged to establish reading criteria.

Vertebral centrum diameter at birth was estimated. All specimens less than 250 mm total length were assumed to be young-of-the-year (YOY). An average centrum diameter of YOY rays was determined and used as an estimate of centrum diameter at birth. This value was used as Age 0 (birth) for all band counts.

The lead microtopography technique was used for all specimens. All vertebrae were read by the author three times, with approximately two weeks between readings. The age estimates were recorded and an index of precision (APE) and percent error (D) were calculated to assess intrareader variability (Beamish and Fournier 1981; Chang 1982). Agreement of at least two of the three readings was necessary to determine the “final” age estimate for each specimen. If all three estimates differed, an additional reading was done and a final age estimate assigned. Lead-enhanced vertebrae were additionally aged once by a second reader. These age estimates were compared with the author’s final estimate and APE and D values were calculated. Percent agreement between readers also was assessed (Tanaka et al. 1990).

X-radiography was used for a subsample of specimens (n=70). X-rays were viewed under a dissecting microscope using transmitted fiberoptic lighting. X-rays of centra with a discernible banding pattern were read once by the author and age estimates assigned. These age estimates were compared with those obtained using the lead microtopography method using a paired t-test.

The electron microprobe analysis was conducted at the University of California - Santa Cruz using an ARISEMQ microprobe and the Probe for Windows software program. The vertebrae were embedded in epoxy resin, sectioned longitudinally through the core, and polished to a mirror finish to prevent analytical errors and diffraction of x-rays. The samples were then

carbon coated to further dampen diffraction of the x-rays and increase electron conductance. After standardization of the probe using an apatite standard, samples were analyzed for elemental calcium and phosphorus concentrations (expressed as weight percentages). Scans were initiated at the outer edge of the vertebral arms, and proceeded toward the center in 10-micrometer increments across one half of the centrum. The beam focused on a 2-micron² area and recorded counts for 10 seconds. The beam current was 10 mA, operating voltage 15 kV, and absorbed current 15 nA. Scans were then compared with the band patterns and counts with those prepared using standard techniques.

Centrum edge increment analysis was attempted to determine the timing of band deposition. At least one specimen was examined from every month during the study. The outermost band was characterized as either more or less calcified and a measurement of the band width was recorded.

Validation of the temporal component of the banding pattern was attempted. Validation studies often employ the use of oxytetracycline (OTC) as an internal marker (Smith 1984; Branstetter 1987; Kusher et al. 1992; Natanson 1993). Oxytetracycline, when injected into the body, is deposited in calcifying tissues such as vertebrae. The OTC mark will fluoresce under ultraviolet light, contrasting with the surrounding unmarked region of the vertebrae. Additional bands detected outside the OTC mark represent the known time period since

injection. Calcein, a similar internal marker, produces a more intense mark than that produced by OTC, and is visible under natural lighting conditions. It has been used as a fluorescent marker for juvenile and larval fish (Wilson et al 1987; Hales and Hurley 1991); however, its use on elasmobranchs has been limited (Gelsleichter et al. 1997).

Three laboratory growth studies using oxytetracycline (OTC) and calcein as internal markers were conducted at Moss Landing Marine Laboratories. Two 3-m diameter tanks with flow-through water systems were used to house the animals. The 3,985 L tanks were located outside, thereby subjecting the rays to a natural lighting regime. A sandy substrate was provided. All specimens in the validation study were obtained in otter trawls conducted in Monterey Bay.

The first validation study began 2 October 1994. Seven Pacific electric ray specimens were weighed, measured, and injected intramuscularly with 25 mg/kg OTC (Natanson and Cailliet 1990). All rays were then placed in one tank for the duration of the study. They were supplied live flatfish (Pleuronectidae, Bothidae, Cynoglossidae) and surfperch (Embiotocidae), allowing them to feed on their own schedule.

The second study began 21 July 1995. Eighteen rays were randomly allocated to one of two tanks (nine rays per tank). The rays were then allocated into one of three treatment groups: calcein, OTC, or control. AVID personal identification microchip tags (PIT) were injected subcutaneously into each animal

to identify individuals throughout the study. Animals were weighed and measured before treatment injection. The OTC treatment group received a dosage of 25 mg/kg (Natanson 1993). The calcein treatment group received a dosage of 5 mg/kg, following Gelsleichter et al. (1997), who recommended the lower dosage. The control group was injected with an "elasmo-ringer" solution utilized at Mote Marine Laboratory which attempts to mimic the osmolarity of serum (E. Cortes, pers comm). In addition to the food items mentioned above, these animals also were fed freshwater goldfish (*Carassius auratus*).

The third growth study began 17 October 1995. Nine rays were tagged with PIT tags and injected with 25 mg/kg of OTC. Weight and measurements were recorded. They were placed in one tank and fed live flatfish and surfperch. For all studies, the goal was to maintain the rays for a minimum of one year to assess the temporal deposition of the banding pattern on the vertebrae.

Growth models were fit to the age and length data using Fishparm, a non-linear curve-fitting software package (Saila et al. 1988). Gompertz, logistic, and von Bertalanffy models were fit and plotted. Mean square error (MSE) and r^2 values, provided by Fishparm, were used to determine which model had the best predictive value. Linear models also were constructed using Microsoft Excel (Microsoft Corp. 1994).

Differences in growth rates between males and females were assessed in two ways. Following Kappenman (1981), growth models were developed for the

sexes separately and combined and examined to determine which model best described the data. Differences in the confidence intervals of parameters derived for the von Bertalanffy growth function (L_{∞} , k , and t_0) also were compared between sexes using a t-test (Cailliet et al. 1990).

Estimates of possible longevities were obtained through four alternative methods: 1) longevity determined by the oldest fish aged in this study, 2) longevity estimated as $5 \ln 2/k$, representing the time it takes a fish to reach 95% of its asymptotic length (Cailliet et al. 1992; H. Mollet pers. comm.), 3) longevity estimated by extending a mean growth rate to the L_{∞} predicted by the von Bertalanffy model and converting to age, and 4) longevity derived by extending the growth coefficient k to the L_{∞} predicted by the von Bertalanffy model and converting to age.

Reproduction and Demography

Male and female reproductive status was examined upon dissection. Male reproductive status was based on three criteria: 1) the relationship of clasper length to total length (Babel 1967; Chen et al. 1996); 2) clasper calcification (Yano 1993); and 3) vas deferens coiling (Pratt 1979). Outer clasper length was measured for all males (Figure 2). Clasper calcification was subjectively assigned a category based on ease of clasper bending. Degree of vas deferens coiling was visually assigned to one of the following categories: straight, wavy, or coiled, or a combination of two consecutive stages (straight/wavy, wavy/coiled).

The reproductive status of female specimens was based on three criteria: 1) number of ova (Pratt 1979), 2) diameter of ova (Pratt 1979), and 3) uterine width (Martin and Cailliet 1988b ; Timmons and Bray 1996). Fecundity was estimated using ova counts and the examination of a single pregnant female. Time of parturition in Monterey Bay was examined by plotting the size of YOY rays relative to their month of capture.

Ova and ovaries were frail and difficult to handle and examine. To alleviate this problem, the technique described by Martin and Cailliet (1988b) was used with minor modifications. Frozen organs were thawed in 70% isopropyl alcohol, then transferred to 35% isopropyl alcohol for 24 - 36 hours. This procedure imparts a tough, leathery consistency to the tissues. The organs were then drained of alcohol and refrozen. Frozen ova were then easily separated, counted, and measured. Total numbers of ova per female were obtained by counting all ova in both ovaries. Ovaries of specimens <700 TL were examined using microscopy. All ova present were measured along their longest axis to the nearest 0.1 mm using Vernier calipers.

Estimates of total instantaneous mortality (z) were obtained using a technique introduced by Hoenig (1983). He developed a general regression equation allowing for the prediction of total mortality from maximum age of a species. The equation, derived from 134 unexploited or lightly exploited stocks of fish, mollusc, and cetaceans, has the following form:

$$\ln(z) = 1.44 + (-0.982) \cdot \ln(t_{\max}),$$

Mortality estimates were calculated for the longevity estimates derived above.

The equation $l_x = (l_{x-1})(e^{-z})$ was used to calculate survivorship (l_x).

Survivorship curves, using the variation in longevity and corresponding mortality, were created by plotting l_x against fish age (x) over the life span of the fish (Cailliet 1992). The various longevity and mortality estimates provided a range of probable survivorship.

A life table was constructed to estimate the demographic parameters of generation time (G), net reproductive rate (R_0), and intrinsic rate of population increase (r). Several estimates of longevity and mortality (z) were considered when creating the table, providing for a range of reliable estimates for each parameter. Estimates of survivorship (l_x) and reproduction (m_x) are necessary for the calculation of the parameters of interest. It was assumed that once a female reached sexual maturity, the potential number of female offspring (m_x) remained constant and she reproduced annually throughout her lifetime. The fecundity estimate used in creating the life table was obtained by the examination of one pregnant female. The sex ratio at birth was assumed to be 1 to 1.

Non-annual reproduction also was considered. Demographic parameters were estimated using the most biologically realistic estimates of longevity and

mortality and a biennial reproductive cycle. For this scenario, it was assumed that 50% of all females reproduced every other year.

RESULTS

Specimen Collection

A total of 198 specimens was obtained from central and southern California between August 1994 and January 1996. Specimens of both sexes were represented in 12 of the 18 size classes obtained; males ranged from 186 to 842 mm total length (TL); females from 199 to 1020 mm TL (Figures 1 and 5).

Age and Growth

The total length-weight relationship was best described by a power curve of the form: $y = 0.00002x^{3.0213}$ ($r^2=0.99$) for females and $y = 0.00004x^{2.8753}$ ($r^2=0.98$) for males (Figure 6). Freezing did not significantly affect measurements of either disc width ($t_{\text{calc}} = 0.312$, $df = 19$, $P_{(2)} = 0.758$) or total length ($t_{\text{calc}} = 0.634$, $df = 19$, $P_{(2)} = 0.533$). A very strong ($r^2 = 0.96 - 0.99$) and significant ($p < 0.001$; Wilkinson et al. 1992) linear relationship existed between total length and all other measurements of body size (Figure 7).

Centrum diameter also was strongly and significantly ($p < 0.001$; Wilkinson et al 1992) correlated with total length ($r^2 = 0.93$) and disc width ($r^2 = 0.98$). Both measurements were predicted equally well from centrum diameter. Total

length was selected as the primary size measurement due to its slightly higher r^2 value of 0.98 (Figure 8).

The number of bands observed at several locations along a single vertebral column did not vary within an animal. Age estimates were consistent regardless of centrum position along the column. Vertebrae may thus be obtained from any location and used for ageing.

Average centrum diameter for YOY specimens ($n = 48$) was 2.14 ± 0.17 mm. This distance corresponded with an observed band in all samples examined and was used as Age 0 (birth) for all band counts.

The lead microtopography technique provided good resolution of the banding pattern and was used for all 198 specimens. Average percent error (APE) and percent error (D) among the author's first three readings were 6.5% and 4.9%, respectively. Age estimates among all three readings differed by only one year in 92% of the centra. Interreader variability was also low, with an APE and D of 8.5% each. The two readers agreed within one year on 81% of the centra and within two years on 93% of the centra read (Figure 9).

Age estimates determined from x-radiography differed significantly from those obtained using the lead microtopography technique ($t_{\text{calc}} = 4.822$, $df = 60$; $P_{(2)} = 0.00001$; Figure 10). The x-radiography technique was too variable and difficult to interpret to be used for estimating age for this species. All age estimates, therefore, were based on the lead microtopography technique.

The electron microprobe technique was unusable as an ageing technique for this species. No discernible bands, based on calcium and phosphorous concentrations, were observed in the graphical representations of the scan data (Figure 11).

Existing data from marginal increment analysis did not provide validation of the temporal component of the observed banding pattern. Likewise, specimens in captivity did not survive the minimum of one year required for validation. The greatest duration an animal was held in captivity was 157 days. Most specimens did not feed and subsequently starved to death. Additionally, several specimens died probably because of a large influx of freshwater associated with unusually heavy rains in January 1995, and six animals were removed by an unknown assailant. Several of the oxytetracycline injected vertebrae did show evidence of OTC deposition, with almost the entire centrum glowing under ultraviolet light.

Size at age estimate plots indicated a nearly linear relationship between age and total length in males and females, and both sexes combined (Figure 12). Gompertz, logistic, and von Bertalanffy growth models fit the data equally well (Table 1). Although the Gompertz model had a slightly better fit, (with the greatest r^2 and lowest MSE) the difference between it and the von Bertalanffy growth function (VBGF) was negligible. I used the VBGF to allow for comparisons with other elasmobranch species (Hoenig and Gruber 1990). In

addition, the L_{∞} predicted by the VBGF, 1373 mm for females and 921 mm for males, closely corresponds to the maximum reported length for the Pacific electric ray, 1372 mm (Eschmeyer et al. 1983).

Following Kappenman (1981), it was determined that von Bertalanffy models constructed for males and females separately described the data better than one model with both sexes combined. Females reach their asymptotic length at a slightly slower rate ($k = 0.07$) than males ($k = 0.13$). The 95% confidence intervals around the predicted L_{∞} values for males (921 ± 107.4 mm) and females (1373 ± 288.2 mm) did not overlap, another indication that growth in this species is best described separately for males and females, and that sexual dimorphism exists

Estimates of longevity varied widely with the method used. An estimate of 47 years was obtained using the 95% asymptotic length method and an estimate of 24 years was obtained by extending a mean growth rate to the L_{∞} predicted by the von Bertalanffy model and converting to age. By extending the growth coefficient k to the L_{∞} predicted by the von Bertalanffy model and converting to age, an estimate of 95 years was obtained. The longevity estimates of 47 and 95 years were determined to be biologically unrealistic. All three calculated estimates exceed the maximum age of 16 determined for specimens aged in the study.

Reproduction and Demography

Ninety-nine male Pacific electric rays were examined for sexual maturity. All indices indicated that males mature at 600 mm TL (Figures 13 and 14). An abrupt change in the clasper length - TL relationship occurs at ~600 mm TL. Eighty-three percent of males >600 mm TL displayed complete coiling of the vas deferens (n = 46) and 87% had calcified claspers (n = 39). Maturity is attained at approximately six years.

Female Pacific electric rays mature at approximately 840 mm TL. Uterine width starts to increase rapidly at 750 mm TL, with a maximum observed width of 50 mm in a 925 mm TL specimen (Figure 15). The observed number of ova per female and maximum ovum diameter also indicate maturity at 840 mm TL (Figures 16 and 17). A 1092 mm TL female with 8 mm eggs was probably obtained shortly after giving birth. Age at female sexual maturity is approximately 11 years.

Estimates of fecundity varied with stage of female development. Both ovaries were functional, having approximately the same number of ova in each. Total number of ova ranged from 0-55, the number increasing with increasing size of female rays (Figure 16). However, two distinct ovum size classes often were present in each ovary. A single pregnant female (1000 mm TL) was examined and contained 17 near-term embryos (7 females; 10 males), ranging

from 214 to 231 mm total length. The fecundity estimate presented here (17) agrees reasonably well with that observed for other electric rays (Table 2).

Parturition may occur in all months. No seasonal pupping time could be determined. Young-of-the-year specimens (<250 mm total length) were obtained year-round from Monterey Bay (Figure 18).

Estimates of total instantaneous mortality (z) ranged from 0.048 to 0.277, with increasing longevity resulting in decreased mortality (Table 3). The longevity estimate of 95 years is unrealistic for this species, therefore, no corresponding survivorship curve was constructed. Survivorship curves generated using the remaining three mortality estimates most closely approximate a type III curve (Figure 19).

Using the various longevity and mortality estimates, demographic estimates of generation time (G) ranged from 12.7 to 29.8 years. Net reproductive rate (R_0) estimates ranged from 1.4 to 104.5 for this species. Intrinsic rate of increase (r) estimates ranged from 0.02 to 0.26, indicating that the population is stable or increasing (Tables 3 and 4).

The possibility of non-annual reproduction was also examined. Using the most biologically realistic estimates of longevity and mortality (24 years, $z = 0.186$), a biennial reproductive cycle was simulated. This resulted in $r = 0.07$, in contrast to $r = 0.13$ under the annual reproduction assumption.

DISCUSSION

Specimen Collection

This species previously thought to segregate by size but this was not well defined. The bimodal size frequency distribution seen in Figure 5 most likely represents a sampling bias. The majority of specimens >500 mm TL were obtained from commercial collectors in southern California who selectively take larger individuals for their larger electric organs. The majority of <500 mm TL specimens were obtained from Monterey Bay. Larger individuals are taken in Monterey Bay as bycatch by commercial fishermen. However large rays were seldom retained because of limited holding space and fishing ground distance from port. In addition, large individuals have been observed from the Monterey Bay Aquarium Research Institute's ROV *Ventana* and from the DSV *Delta* during dives in the Monterey and surrounding submarine canyons (K.Schlining, M. Yoklavich, pers. comm.). These deepwater areas were not accessible to the sampling gear I utilized. Thus, probably no size frequency differences exist between central and southern California.

Age and Growth

Vertebrae provide a suitable structure for age determination in the Pacific electric ray. To be useful for ageing, the ageing structure must continue to grow proportionally to the size of the fish and age increments must be continually added to the structure. This was demonstrated for the Pacific electric ray by

examining the centrum diameter - total length relationship (Figure 8). Age increments appear to be continually added, with no evidence of reabsorption, based on size at age plots (Figure 12). Additionally, vertebrae may be useful for determining age estimates for this species because the position of the centrum along the vertebral column did not affect the age estimate. This factor is important when obtaining samples from unknown origin (such as fishermen or collectors).

Pacific electric ray vertebrae are very thin, fragile, deeply-coned structures. They are poorly calcified when compared to most other elasmobranch species previously studied. Most commonly used techniques for enhancing the vertebral banding pattern failed to be useful for this species. Of the three techniques that were most promising (lead microtopography, x-radiography, and electron microprobe analysis), only one proved useful, lead microtopography. A new copper substitution technique under development did not enhance the banding pattern, although it has worked well with other test species (J. Gelsleichter pers. comm.).

The poor calcification may explain the difficulty of using the x-radiography technique. The x-rays were often washed out, displaying either poorly defined bands or no banding pattern at all. It is possible that this technique could work if the vertebrae were x-rayed on a suitably sensitive machine.

The electron microprobe technique might not be useful for ageing elasmobranchs. Although Cailliet and Radtke (1987) found it helpful in enhancing the banding pattern for the gray reef shark (*Carcharhinus amblyrhynchos*) and the common thresher shark (*Alopias vulpinus*), I was unable to gain any ageing information for this species. The technique also failed to produce useful information for the Australian sharpnose shark, *Rhizoprionodon taylori* (C. Simpfendorfer pers. comm.).

Pacific electric rays may not exceed approximately 16 years of age, the age estimate of the largest specimen obtained in this study. The largest individual was 1020 mm in total length, smaller than the maximum reported length of 1372 mm for females of the species (Eschmeyer et al. 1983). However, the asymptotic length of 1373 mm for females predicted by the von Bertalanffy growth model was consistent with the scientific literature and indicated that Pacific electric rays may reach approximately 24 years of age.

An estimated longevity of 24 years is comparable to that of other species in this family. Female *Torpedo marmorata* age estimates may have a lifespan of approximately 20 years and males may live to approximately 13 (Mellinger 1971). The lesser electric ray, *Narcine brasiliensis* may exceed 11 years for males and 15 years for females (Villavicencio - Garayzar and Cailliet, pers. comm.). The bat ray (*Myliobatis californica*; Myliobatidae), a similar elasmobranch occupying the same range, has a longevity of approximately 23

years (Martin and Cailliet 1988a). None of the above age estimates have been validated.

All estimates of longevity depend upon the accuracy of age estimates used to derive them. Unfortunately, age estimates for the Pacific electric ray could not be validated. Despite numerous attempts to keep these animals in captivity, and that other species such as the marbled (*T. marmorata*) and spotted (*T. ocellata*) electric ray have been successfully raised (Belbenoit 1979; Michaelson et al. 1979; J. O'Sullivan, Monterey Bay Aquarium, pers. comm.), we were unable to maintain Pacific electric rays in captivity for growth validation studies. Tag and recapture methods require sufficient specimens for release and tag returns. This was not the case in this study as all captured rays were necessary for an adequate sample size for age estimation. Centrum edge analysis was attempted, as specimens were captured from every month, however, most specimens were young-of-the-year and demonstrated no distinctive seasonal edge characteristics.

Despite the lack of validation of my age estimates, I feel confident in my conclusions for several reasons. The sample size used in this study ($n = 198$) is large for elasmobranchs, the specimens covered almost the entire size range of the species, and both sexes were well represented (Figure 5). In addition, the low APE and D values provide some verification of the age estimates (Figure 9)

and the von Bertalanffy growth model parameter estimates seem sensible when compared to other elasmobranch species (Figure 12; Cortes and Parsons 1996).

Reproduction and Demography

The onset of male sexual maturity occurs at approximately 6 years of age or 65% of the predicted total length obtained by males. Males of the marbled electric ray, *T. marmorata*, reach sexual maturity at 5 years (Mellinger 1971). The use of an internal reproductive measure (vas deferens coiling) in addition to the commonly used total length-clasper length relationship strengthens the conclusion that male Pacific electric rays reach maturity at approximately 600 mm total length.

Female Pacific electric rays reach sexual maturity at approximately 62% of their reported maximum size or 11 years of age. This estimate agrees with that for the marbled electric ray, *T. marmorata*, which reaches maturity at 10 to 15 years; 55 - 68% of its maximum size (Mellinger 1971; Capape 1979; Abdel-Aziz 1994). The estimate for the spotted electric ray, *T. ocellata* is slightly lower at 41 - 53% of maximum total length (Quignard and Capape 1974).

The Pacific electric ray is similar to other elasmobranchs in having low fecundity (Natanson 1984; Timmons and Bray 1997). The fecundity estimate reported here, 17 young per female, is the highest reported for the family (Table 2). Although this estimate is based on only one pregnant female, it is realistic when fecundity estimates for each species are examined in relation to their

maximum lengths (Table 2). An increase in fecundity with body size has been observed for several species of sharks (Smith and Abramson 1990).

Mortality estimates (z) were dependent on the longevity estimates used to generate them. The values ranged from approximately 0.048 to 0.277. All estimates fit within the range published by Hoenig (1983); however, the lowest two estimates (0.048 and 0.096) fall at the extreme end of the range presented. The mortality estimates of 0.277 and 0.186 seem most biologically realistic for the Pacific electric ray. The sampling biases discussed above precluded me from plotting a meaningful catch curve. Additional samples in the middle size classes would be helpful to redefine and possibly verify the mortality estimates presented here.

The demographic parameters calculated using the two most biologically realistic estimates of longevity (16 and 24) and mortality fit well within the range of values presented for other elasmobranch species (Cortes 1995). The case of the Pacific angel shark, *Squatina californica*, is especially interesting (Cailliet et al. 1992). The parameter estimates derived for *S. californica* ($R_0 = 2.25$; $G = 14.5$; and $r = 0.056$) and the Pacific electric ray ($R_0 = 5.99$; $G = 14.7$; and $r = 0.13$), are similar. Both species co-occur over much of their range and have similar behavioral patterns (i.e. ambush predators during the day). The greatest values of r (0.22 and 0.26) generated for the Pacific electric ray, indicating that the population is increasing rapidly, seemed unrealistic. This is not surprising as

the longevity estimates used to calculate them (0.096 and 0.048) also were unrealistic.

Simulating a biennial reproductive cycle did not greatly affect the demographic parameter estimates, mainly influencing r and R_0 (Table 5). Although direct evidence of such a cycle was not discovered during this study, *T. marmorata* have a 2 - 3 year breeding cycle (Mellinger 1971; Capape 1979). The possibility of a non-annual cycle might also explain the small numbers of females collected with mature ova and the capture of YOY individuals year round.

CONCLUSIONS

Pacific electric rays appear to be similar to other elasmobranchs in being long-lived, having a low fecundity, and having a late age at sexual maturity. Demographic estimates indicate that the central and southern California population may be at equilibrium or slightly increasing. More detailed information regarding parturition season, reproductive cycles, and natural mortality is needed to refine the estimates presented here. Validation of my age estimates also needs to be accomplished.

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Table 1. Summary of coefficient of variation (r^2) and mean square error (MSE) values for growth models examined. VBGF = von Bertalanffy Growth Function

Model	VBGF		Gompertz		Logistic		Linear	
	r^2	MSE	r^2	MSE	r^2	MSE	r^2	MSE
Female	0.97109	2086.46	0.97152	2055.34	0.9705	2128.92	0.9577	na
Male	0.94492	2866.58	0.94716	2750.38	0.94776	2718.83	0.9124	na
Sexes combined	0.94919	3045.39	0.94921	3043.84	0.94787	3124.11	0.9313	na

Table 2. Fecundity information for several species of electric rays (Torpedinidae and Narcinidae).

Species	Max Total Length (cm)	Number of Young	Size at Birth (cm)	Source
<i>Torpedo torpedo</i> common electric ray	41	2 - 12	8 - 10	Abdel-Aziz 1994
<i>Torpedo marmorata</i> marbled electric ray	62	4 - 18	10 - 13	Mellinger 1971
<i>Torpedo ocellata</i> spotted electric ray	----	6 - 11	7	Michaelson et al. 1979
<i>Narcine brasiliensis</i> lesser electric ray	76	4 - 12	11-12	Villavicencio- Garayzar 1993
<i>Torpedo californica</i> Pacific electric ray	102	17	18-22*	present study

*estimated size from young-of-the-year samples

Table 3. Summary of demographic parameters (net reproductive rate (R_0), generation time (G), intrinsic rate of increase (r), and finite rate of increase (e^r)), calculated for the Pacific electric ray for the four longevity and resulting mortality estimates obtained in this study.

Longevity Estimate	Demographic Parameters				
	Mortality Estimate	R_0	G	r	e^r
16	0.277	1.35	12.73	0.02	1.02
24	0.186	5.99	14.77	0.13	1.13
47	0.096	31.25	19.82	0.22	1.24
95	0.048	104.53	29.81	0.26	1.30

Table 4. Life table for Pacific electric rays for two variations in longevity and resulting instantaneous mortality (z): A) 16 years, z = 0.277; and B) 24 years, z = 0.186 used to calculate the best possible demographic estimates of generation time (G), net reproductive rate (Ro), intrinsic rate of change (r), and finite rate of population increase (e^r) for annual reproduction.

A. z = 0.277; 16 years									
n	age int.	x	mean TL (mm)	growth	lx	mx	lx*mx	lx*mx*x	
49	0 to 1	0	228		1.000	0.00	0.00	0.00	
29	1 to 2	1	267	38.8	0.758	0.00	0.00	0.00	
16	2 to 3	2	319	51.9	0.575	0.00	0.00	0.00	
3	3 to 4	3	401	81.8	0.436	0.00	0.00	0.00	
4	4 to 5	4	457	55.8	0.330	0.00	0.00	0.00	
1	5 to 6	5	650	67.5	0.250	0.00	0.00	0.00	
10	6 to 7	6	592	67.5	0.190	0.00	0.00	0.00	
8	7 to 8	7	651	59.4	0.144	0.00	0.00	0.00	
24	8 to 9	8	707	55.7	0.109	0.00	0.00	0.00	
13	9 to 10	9	697	22.9	0.083	0.00	0.00	0.00	
19	10 to 11	10	752	55.0	0.063	0.00	0.00	0.00	
7	11 to 12	11	771	19.4	0.048	8.50	0.40	4.44	
4	12 to 13	12	808	36.6	0.036	8.50	0.31	3.67	
7	13 to 14	13	842	34.0	0.027	8.50	0.23	3.02	
3	14 to 15	14	872	30.0	0.021	8.50	0.18	2.46	
0	15 to 16	15	na		0.016	8.50	0.13	2.00	
1	16+	16	1020	74.2	0.012	8.50	0.10	1.62	
			average growth	50.0		Ro =	1.35	17.21	
						G =	12.73		
						r =	0.02		
						e ^r =	1.02		

Table 4 (cont).

B. $z = 0.186$; 24 years

n	age int.	x	mean TL (mm)	growth	lx	mx	lx*mx	lx*mx*x
49	0 to 1	0	228		1.000	0.00	0.00	0.00
29	1 to 2	1	267	38.8	0.830	0.00	0.00	0.00
16	2 to 3	2	319	51.9	0.689	0.00	0.00	0.00
3	3 to 4	3	401	81.8	0.572	0.00	0.00	0.00
4	4 to 5	4	457	55.8	0.475	0.00	0.00	0.00
1	5 to 6	5	650	67.5	0.395	0.00	0.00	0.00
10	6 to 7	6	592	67.5	0.328	0.00	0.00	0.00
8	7 to 8	7	651	59.4	0.272	0.00	0.00	0.00
24	8 to 9	8	707	55.7	0.226	0.00	0.00	0.00
13	9 to 10	9	697	22.9	0.187	0.00	0.00	0.00
19	10 to 11	10	752	55.0	0.156	0.00	0.00	0.00
7	11 to 12	11	771	19.4	0.129	8.50	1.10	12.08
4	12 to 13	12	808	36.6	0.107	8.50	0.91	10.95
7	13 to 14	13	842	34.0	0.089	8.50	0.76	9.85
3	14 to 15	14	872	30.0	0.074	8.50	0.63	8.80
0	15 to 16	15	na		0.061	8.50	0.52	7.83
1	16 to 17	16	1020	74.2	0.051	8.50	0.43	6.94
0	17 to 18	17	1070	50.0	0.042	8.50	0.36	6.12
0	18 to 19	18	1120	50.0	0.035	8.50	0.30	5.38
0	19 to 20	19	1170	50.0	0.029	8.50	0.25	4.71
0	20 to 21	20	1220	50.0	0.024	8.50	0.21	4.12
0	21 to 22	21	1270	50.0	0.020	8.50	0.17	3.59
0	22 to 23	22	1320	50.0	0.017	8.50	0.14	3.12
0	23 to 24	23	1370	50.0	0.014	8.50	0.12	2.71
0	24+	24	1420	50.0	0.012	8.50	0.10	2.35
						Ro =	5.99	88.55
						G =	14.77	
						r =	0.12	
						e ^Λ _T =	1.13	

Table 5. Life table for Pacific electric rays using the most biologically realistic estimate of longevity and mortality (z): 24 years, $z = 0.186$ to calculate the best possible demographic estimates of generation time (G), net reproductive rate (R_0), intrinsic rate of increase (r), and finite rate of population increase (e^{*r}) for a biannual reproductive cycle.

(e^r) for a biannual reproductive cycle.								
z = .186		n	age int.	x	lx	mx	lx^mx	lx^mx^x
49	0 to 1	0	1.000	0.00	0.00	0.00	0.00	0.00
29	1 to 2	1	0.830	0.00	0.00	0.00	0.00	0.00
16	2 to 3	2	0.689	0.00	0.00	0.00	0.00	0.00
3	3 to 4	3	0.572	0.00	0.00	0.00	0.00	0.00
4	4 to 5	4	0.475	0.00	0.00	0.00	0.00	0.00
1	5 to 6	5	0.395	0.00	0.00	0.00	0.00	0.00
10	6 to 7	6	0.328	0.00	0.00	0.00	0.00	0.00
8	7 to 8	7	0.272	0.00	0.00	0.00	0.00	0.00
24	8 to 9	8	0.226	0.00	0.00	0.00	0.00	0.00
13	9 to 10	9	0.187	0.00	0.00	0.00	0.00	0.00
19	10 to 11	10	0.156	0.00	0.00	0.00	0.00	0.00
7	11 to 12	11	0.129	8.50	1.10	12.08	0.00	0.00
4	12 to 13	12	0.107	0.00	0.00	0.00	0.00	0.00
7	13 to 14	13	0.089	8.50	0.76	9.85	0.00	0.00
3	14 to 15	14	0.074	0.00	0.00	0.00	0.00	0.00
0	15 to 16	15	0.061	8.50	0.52	7.83	0.00	0.00
1	16 to 17	16	0.051	0.00	0.00	0.00	0.00	0.00
0	17 to 18	17	0.042	8.50	0.36	6.12	0.00	0.00
0	18 to 19	18	0.035	0.00	0.00	0.00	0.00	0.00
0	19 to 20	19	0.029	8.50	0.25	4.71	0.00	0.00
0	20 to 21	20	0.024	0.00	0.00	0.00	0.00	0.00
0	21 to 22	21	0.020	8.50	0.17	3.59	0.00	0.00
0	22 to 23	22	0.017	0.00	0.00	0.00	0.00	0.00
0	23 to 24	23	0.014	8.50	0.12	2.71	0.00	0.00
0	24 to 25	24	0.012	0.00	0.00	0.00	0.00	0.00
				Ro =	3.27	46.90		
				G =	14.32			
				r =	0.08			
				e^r =	1.09

Figure 1. Collection locations and length frequencies of Pacific electric ray specimens for this study.

Figure 2. Linear measurements recorded for Pacific electric ray specimens. TL = total length; DW = disc width; PDL #1 = predorsal 1; PDL #2 = predorsal 2; and CL = clasper length. All measurements were in millimeters.

a.

b.

5 mm

anterior
↑

Figure 3. Diagram of Pacific electric ray vertebrae. a) Centrum diameter measurements. b) Change in vertebral shape with size/age.

Figure 4. Illustration of Pacific electric ray vertebral face with lead microtopographic enhancement of the banding pattern. Numbers represent estimated years since birth.

Figure 5. Size frequency histogram of Pacific electric ray specimens collected from southern and central California between August 1994 and January 1996.

Figure 6. Total length - weight relationships for female (a) and male (b) Pacific electric rays.

Figure 7. Total length relationships with disk width, first predorsal length (PDL #1), and second predorsal length (PDL #2) recorded for Pacific electric ray specimens.

Figure 8. Total length (a) and disc width (b) versus centrum diameter.

Figure 9. Precision of age determination for Pacific electric rays. Histograms represent differences (as the percentage of paired band counts differing by 0, 0.5, 1, 2, etc. years) within Reader 1 (author) and the author and second reader. The proportions of counts which agreed within a certain number of band counts are listed under "percent agreement", while D, S, and APE represent "percent error", its standard deviation, and "average percent error", respectively. The letter n represents the number of samples (centra) aged during this study, while the number beside each bar represents the number of comparative readings of those centra.

Figure 10. Comparison of age estimates between the lead microtopography and x-radiography techniques. The 45° line represents a line of agreement between the two techniques (N = 61).

Figure 11. Graphical representation of the electron microprobe analysis for the one Pacific electric ray specimen. Each point represents 10 microns. An age estimate of 8 years was determined for this sample using the lead microtopography technique.

Figure 12a. Von Bertalanffy growth curve for female Pacific electric rays. Parameters are listed in the insert.

Figure 12b. Von Bertalanffy growth curve for male Pacific electric rays. Parameters are listed in the insert.

Figure 13. Relationship of total length to outer clasper length for the Pacific electric ray, with categories of clasper calcification (n=92). Sexual maturity occurs at 600 mm TL.

Figure 14. Relationship of total length to outer clasper length for the Pacific electric ray, with categories of vas deferens coiling (n=99). Sexual maturity occurs at 600 mm TL.

Figure 15. Relationship of total length to maximum uterine width for the Pacific electric ray (n=56). Sexual maturity is reached at ~840 mm TL.

Figure 16. Relationship of total length to number of ova for Pacific electric rays ($n=36$). Total numbers of ova per female were obtained by counting all ova in both ovaries. Ovaries of specimens <700 mm TL were examined using microscopy. Sexual maturity is reached at ~840 mm TL.

Figure 17. Relationship of total length to maximum ovum diameter for Pacific electric rays ($n=36$). All ova present were measured to the nearest 0.1 mm using vernier calipers. Sexual maturity is reached at ~840 mm TL.

Figure 18. Size of Monterey Bay specimens by month of capture, indicating no parturition season (n = 63). Specimens were included only when month of capture was known.

Figure 19. Simulated survivorship curves for three longevity estimates and their corresponding mortality coefficients.

IMAGE EVALUATION TEST TARGET (QA-3)

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