

Long-term Trends in Catch Composition from Elasmobranch Derbies in Elkhorn Slough, California

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Introduction

Elkhorn Slough is a shallow, seasonal estuary of about 1,200 ha at the center of Monterey Bay on the central California coast (Fig. 1). The slough extends approximately 11 km inland from Monterey Bay and is characterized by a main central channel with branching tidal creeks bordered by extensive tidal mudflats and salt marsh. A large portion of the southeastern part of Elkhorn Slough is the Elkhorn Slough National Estuarine Research Reserve (ESNERR). The reserve is managed by the Califor-

nia Department of Fish and Game and is one of 26 Federally protected estuaries that are part of the National Oceanic and Atmospheric Administration's National Estuarine Research Reserve System. The slough is a highly productive system which supports a diverse array of fishes, invertebrates, marine mammals, and birds.

In 1946, the Pajaro Valley Rod and Gun Club (PVRGC) initiated a late spring-early summer angling derby for elasmobranchs in Elkhorn Slough. The PVRGC was soon joined by the Castroville Rod and Gun Club (CRGC) and the Izaak Walton League (IWL), who sponsored additional annual "shark derbies" at about the same time of the year. The revenues from the derbies helped fund the activities of the clubs. Additionally, the fishermen believed these derbies could help control shark and ray populations that were suspected of reducing more lucrative shellfish and finfish populations in the slough.

While the attendance at each derby fluctuated over the years, the number of

boats was usually between 100 and 150, each carrying 2 or 3 fishermen. Many prizes were given away at each derby, including small boats, outboard motors, fishing and hunting equipment, and up to \$1,000 in cash at the later derbies. By the early 1980's, only the PVRGC continued to hold the annual angling derby. In addition to the angling derbies, an archery derby for elasmobranchs in Elkhorn Slough was initiated in the mid 1980's and continued until the mid 1990's, but it took only a small fraction of the elasmobranchs that were caught in the angling derbies. Until the early 1990's, little regulation of recreational shark fishing existed in California, and there were no bag limits.

Ichthyologists, most notably the late Earl S. Herald of the California Academy of Sciences in San Francisco, took an early interest in these derbies as a means of collecting data on estuarine elasmobranch populations. From 1951 to 1962, Herald and several colleagues monitored and collected data at the Elkhorn Slough shark derbies. Catch

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ABSTRACT—Long-term trends in the elasmobranch assemblage of Elkhorn Slough, Monterey Bay, California, were analyzed by documenting species composition and catch per unit effort (CPUE) from 55 sport fishing derbies that occurred during May, June, and July, from 1951 until 1995. The most abundant species (bat ray, *Myliobatis californica*; shovelnose guitarfish, *Rhinobatos productus*; and leopard shark, *Triakis semifasciata*) were also analyzed for size-weight relationships, trends in size class distribution, stage of maturity, and sex ratios. Changes in species composition over the course of the derbies included the near complete disappearance of shovelnose guitarfish by the 1970's and a slight increase

in the abundance of minor species (mainly smoothhounds, *Mustelus spp.*, and thornback, *Platyrrhinoidis triseriata*) starting in the mid 1960's. The relative abundance of bat rays in the catch steadily increased over the years while the relative abundance of leopard sharks declined during the last two decades. However the average number of bat rays and leopard sharks caught per derby declined during the last two decades. Fishing effort appeared to increase over the course of the derbies. There were no dramatic shifts in the size class distribution data for bat rays, leopard sharks, or shovelnose guitarfish. The catch of bat rays and leopard sharks was consistently dominated by immature individuals, while the

catch of shovelnose guitarfish was heavily dominated by adults. There was evidence of sexual segregation in either immature or mature fish in all the species. Female bat rays and shovelnose guitarfish were larger than their male counterparts and outnumbered males nearly 2:1. Female and male leopard sharks were more nearly equal in size and sex ratio. Changes in species composition are likely due to fishing pressure, shifts in the prevailing oceanographic conditions, and habitat alteration in Elkhorn Slough. The sex ratios, stage of maturity, and size class distributions provide further evidence for the theory that Elkhorn Slough functions as a nursery habitat for bat rays and leopard sharks.

composition and fishing effort were assessed, in addition to individual specimen size, weight, sex, stomach content, and stage of sexual maturity (Herald and Dempster, 1952; Herald, 1953; Herald et al., 1960). In 1963 and 1964, the PVRGC and CRGC collected similar data from their respective derbies along the above format.

Collection of data from the elasmobranch derbies was sporadic in the late 1960's. In 1971, scientists from the

Moss Landing Marine Laboratories (MLML), California Department of Fish and Game, California Academy of Sciences, Stanford University, and San Francisco State University resumed the data collection. By 1980, as part of their training in fisheries research, the task had become an annual routine for graduate students at the MLML Ichthyology Laboratory.

In order to minimize the impact of the derbies on the elasmobranchs of

Elkhorn Slough and to assist in various research projects, a tag-and-release program was initiated in 1988 through a cooperative effort between MLML, the PVRGC, Monterey Bay Aquarium, and the Elkhorn Slough Foundation. That tagging effort continued until the derbies ended. The 1990's saw increasing environmental awareness in the general public and protests from environmental groups regarding shark conservation in Elkhorn Slough, as well as waning interests on the part of the derby organizers and sponsors. As a result the final shark derby was held on 16 July 1995 and there have been none since.

Seven species of elasmobranchs are typically found in Elkhorn Slough. These include: bat ray, *Myliobatis californica*; shovelnose guitarfish, *Rhinobatos productus*; leopard shark, *Triakis semifasciata*; gray smoothhound, *Mustelus californicus*; brown smoothhound, *Mustelus henlei*; thornback, *Platyrhinoideis triseriata*; and round stingray, *Urobatis halleri*. In addition, the Pacific electric ray, *Torpedo californica*; spiny dogfish, *Squalus acanthias*; and big skate, *Raja binoculata*, have been found in Elkhorn Slough. All but Pacific electric rays were caught during the derbies. A number of studies have been conducted on the feeding ecology (Ackerman, 1971; Talent, 1976; Talent, 1982; San Filippo, 1995; Barry et al., 1996; Kao, 2000), reproduction (Ackerman, 1971; Talent, 1985; Martin and Cailliet, 1988a), and age and growth (Ackerman, 1971; Martin and Cailliet, 1988b; Yudin and Cailliet, 1990; Kusher et al., 1992) of these elasmobranchs in Elkhorn Slough.

Elasmobranch species composition and seasonal patterns of occurrence in Elkhorn Slough have been documented by Barry (1983), Talent (1985), Yoklavich et al. (1991), and San Filippo (1995) although Talent (1985) was the only one to focus on the entire elasmobranch assemblage. Talent (1985) found that leopard sharks and bat rays were the two most common species, comprising 56% and 20% of the catch, respectively, and were commonly caught year-round though in slightly lower numbers in the winter.

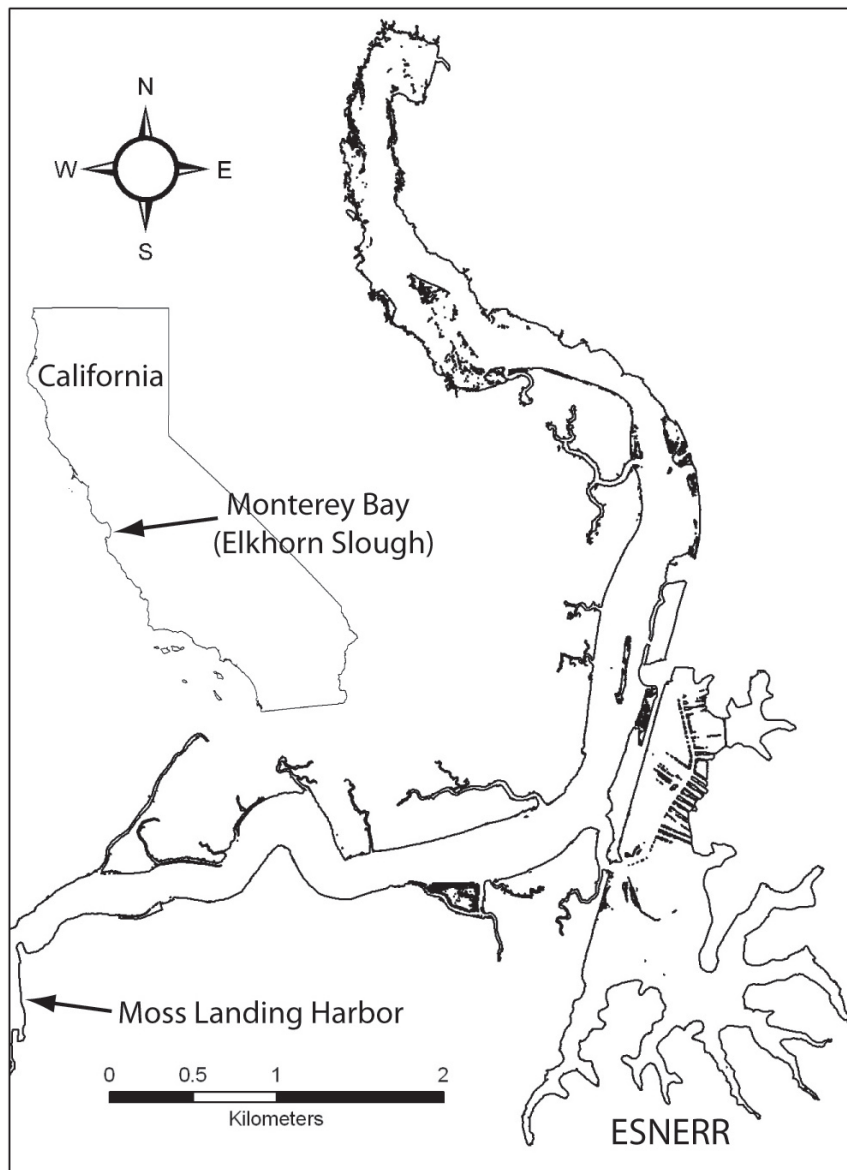


Figure 1.—Elkhorn Slough, California. ESNERR is the Elkhorn Slough National Estuarine Research Reserve.

Talent (1985) believed that the bat ray catch was not necessarily representative of their abundance in the slough, due to the difficulties of catching bat rays in his sampling gear (gill nets). Other species had more pronounced seasonal occurrences and were caught in lower numbers. Gray smoothhounds (9%) and round stingrays (6%) were most abundant during the winter. Shovelnose guitarfish (5%) were most abundant during the fall, and brown smoothhounds (3%) were most abundant during the spring.

Barry (1983) found that in shallow marsh habitats of the slough leopard sharks and bat rays were the only elasmobranchs caught in significant numbers, especially during the spring and summer, and that they were primarily juveniles with fewer reproductively active adults. Yoklavich et al. (1991) also found that leopard sharks and bat rays were the only two elasmobranchs caught in significant numbers, and that juvenile and reproductively mature adult leopard sharks and bat rays were most abundant in the spring and summer, with fewer leopard sharks and young bat rays found in the winter. Leopard sharks and bat rays were categorized as being partial residents of Elkhorn Slough, meaning that they primarily live in the slough, seasonally or ontogenetically move to the ocean, and return to reproduce in the slough. They also categorized the round stingray and gray smoothhound as being marine, meaning that they are a coastal species rarely found in Elkhorn Slough.

San Filippo (1995) found slightly different patterns than those found in previous studies. Gray smoothhounds were the most abundant elasmobranch caught, comprising 71% of the catch. Bat rays made up 15% of the catch, leopard sharks 6%, shovelnose guitarfish 5%, thornbacks 2.5%, and round stingrays 0.5%. The abundance of gray smoothhounds was lowest in the late fall and winter months. Differences between San Filippo (1995) and the other studies is likely a result of different methods and sampling areas, habitat alteration, plus the extended period of time that passed between studies. San Filippo (1995) sampled in ESNERR in the early

1990's using only a beach seine. Barry (1983), Talent (1985), and Yoklavich et al. (1991) all sampled between 1971 and 1980 primarily using a mix of gill nets and otter trawls, and they all sampled in the main channel and major tidal creeks.

These patterns of abundance may be related to prey availability, reproduction, or the physical environment (Ackerman, 1971; Talent, 1976; Talent, 1982; Barry, 1983; Talent, 1985; Martin and Cailliet, 1988a; San Filippo, 1995; Hopkins and Cech Jr., 2003). Reproduction is likely a major factor in these patterns of seasonal abundance. Elkhorn Slough is believed to function as a nursery area for several elasmobranchs, such as the leopard shark (Ackerman, 1971; Barry, 1983; Talent, 1985), bat ray (Barry, 1983; Talent, 1985; Martin and Cailliet, 1988a), gray smoothhound (San Filippo, 1995), and possibly the shovelnose guitarfish (Herald et al., 1960). There is also some evidence that thornbacks also may currently use Elkhorn Slough as a nursery area, but this has not been confirmed (Carlisle¹).

These studies provide periodic information on the structure and seasonality of the elasmobranch assemblage in Elkhorn Slough. They function primarily as independent snapshots of species composition and biological characteristics based on various sampling methods in different parts of the slough. Assessing long-term changes in the elasmobranch assemblage requires more consistent sampling over an extended period of time. Short-term, independent studies that use various types of sampling gear, different objectives, and sample different habitats within Elkhorn Slough are of value, but they are not the best way to characterize long-term trends, either independently or collectively.

This study was done to assess long-term trends in elasmobranch catch composition and catch per unit effort (CPUE) from data collected during Elkhorn Slough shark derbies from 1951 to 1995. In addition, size and weight

relationships, size class distributions, stage of maturity, and sex ratios were determined for bat rays, shovelnose guitarfish, and leopard sharks. The use of such a long-term and unique data set provides a rare opportunity to track changes in the composition and population structure of elasmobranchs in a coastal estuary.

Methods and Materials

Field Collection

Elasmobranch catch data from 55 shark derbies in Elkhorn Slough were collected by various researchers, as well as the derby organizers themselves, from 1951 through 1995 (Table 1). Usually there was only one derby per year, but in some years, there were two derbies or none at all. Prior to 1988, data were collected at a single weigh-in station at the mouth of the slough in Moss Landing Harbor. Starting in 1988 and continuing until the end of the derbies, elasmobranchs were also sampled at roving weigh-in stations on boats staffed primarily by MLML graduate students. The purpose of the on-the-water stations was to reduce fishing mortality and conduct tagging/mark-recapture studies. Over the years, besides being weighed, total length (leopard sharks, brown/gray smoothhounds, shovelnose guitarfish, and thornbacks) or disk width (bat rays) for many individuals was also measured.

We assume that the elasmobranch catch was fully and accurately reported and that this is representative of the elasmobranch assemblage in the slough during a given derby. Because different species, sexes, and size classes may have different feeding ecologies (feeding habits, feeding chronology, frequency of feeding, susceptibility to capture, etc.), these data may not necessarily represent the relative abundance of each species or the exact nature of the population structure of a given species in the slough during the derbies. In addition, it is possible that there were gear biases or problems with the reporting of the catch by fishermen, such as under reporting small individuals or species.

¹Carlisle, A. 2004. Hopkins Marine Station, Stanford Univ., Pacific Grove, Calif. Personal observ.

However, we believe that there is no evidence that there were systematic problems with the reporting of the catch, or that the different feeding ecologies of the different species influenced the accuracy of the data. Our confidence in the data is due to the fact that the species composition did not vary significantly from derby to derby and that the

catch of each species was composed of individuals of all size ranges and both sexes. Despite potential issues with the data, this 44-year data set is extremely valuable, especially due to its unique ability to assess elasmobranch populations in Elkhorn Slough during the late spring and early summer over a long period of time.

Data Analysis

Catch composition, size class distributions, stage of maturity of the catch, sex ratios, and CPUE were analyzed graphically. Bat rays, shovelnose guitarfish, and leopard sharks were the only species caught in numbers large enough to analyze for shifts in size class distributions, stage of maturity, sex ratios, and to generate length (TL or DW) weight regressions. Length-weight regressions were calculated using specimens that were measured for both length and weight. When only weight or length was known for an individual sample, the other parameter was estimated from the calculated length-weight relationship. Size class distributions, stage of maturity, and sex ratios include both the specimens that were measured and weighed, plus the specimens whose weight or length/disc width were estimated using the calculated length weight regressions.

Catch records for brown and gray smoothhounds were lumped together as *Mustelus* spp. due to the lack of certainty in many of the species identifications. Weight data from the 24 June 1956 derby were not used in our analysis due to suspected poor quality data (i.e. high weight values probably due to an uncalibrated scale). Bat ray disc width and weight data from six derbies during the late 1950's were lost from the original paper files and therefore were not included in our analyses. In addition, data considered to be suspect (e.g. abnormal weights or lengths) were not included in these analyses due to the likelihood of a measurement or transcription error.

The size at 100% maturity (where all animals above that size were believed to be mature) was used to estimate the proportion of the catch that was mature. We chose this estimate because we felt that this was the more conservative and biologically relevant estimate and because it is the only estimate available for all species. However, this estimate of size at maturity will artificially increase the number of immature animals. This is especially true for bat rays, where females reach first maturity and 100% maturity at 45 cm DW and 100 cm DW

Table 1.—Elkhorn Slough elasmobranch derbies sampled for catch statistics from 1951 to 1995 with derby sponsors, researcher affiliation, and estimated number of fishermen.

Derbies	Sponsors ¹	Researcher affiliation ²	No. of fishermen
20 May 1951	PVRGC	CAS	237
08 Jun 1952	PVRGC	CAS	308
27 Jul 1952	CRGC	CAS	322
14 Jun 1953	Unknown	CAS	270
28 Jun 1953	Unknown	CAS	351
06 Jun 1954	Unknown	CAS	Unknown
20 Jun 1954 ³	Unknown	CAS	Unknown
05 Jun 1955	Unknown	CAS	Unknown
19 Jun 1955 ³	Unknown	CAS	Unknown
10 Jun 1956 ³	Unknown	CAS	Unknown
24 Jun 1956 ³	CRGC	CAS	60
16 Jun 1957 ³	PVRGC	CAS	600
14 Jul 1957 ³	Unknown	CAS	Unknown
01 Jun 1958	Unknown	CAS	Unknown
15 Jun 1958	Unknown	CAS	Unknown
07 Jun 1959	Unknown	CAS	Unknown
21 Jun 1959	Unknown	CAS	Unknown
12 Jun 1960	Unknown	CAS	Unknown
04 Jun 1961	CRGC	CAS	Unknown
18 Jun 1961	PVRGC	CAS	72
03 Jun 1962	PVRGC	CAS	275
17 Jun 1962	CRGC	CAS	400
23 Jun 1963	PVRGC	PVRGC	Unknown
21 Jun 1964	CRGC	CRGC	Unknown
23 May 1971	Unknown	MLML	Unknown
06 Jun 1971	Unknown	MLML	Unknown
11 Jun 1972	Unknown	MLML	Unknown
25 Jun 1972	Unknown	MLML	Unknown
03 Jun 1973	PVRGC	MLML	Unknown
01 Jul 1973	Unknown	MLML	Unknown
25 May 1975	Unknown	CAS	Unknown
08 Jun 1975	PVRGC	CAS	Unknown
16 May 1976	IWL	CDFG	552
13 Jun 1976	PVRGC	CDFG	515
11 Jun 1978	PVRGC	CDFG	Unknown
25 Jun 1978	IWL	CDFG	Unknown
01 Jun 1980	IWL	MLML	450
15 Jun 1980	PVRGC	MLML	459
14 Jun 1981	PVRGC	MLML	444
05 Jul 1981	IWL	MLML	501
26 Jun 1983	PVRGC	MLML	510
03 Jun 1984	PVRGC	MLML	492
16 Jun 1985	PVRGC	MLML	609
22 Jun 1986	PVRGC	MLML	489
28 Jun 1987	PVRGC	MLML	483
26 Jun 1988	PVRGC	MLML	390
25 Jun 1989	PVRGC	MLML	330
24 Jun 1990	PVRGC	MLML	336
23 Jun 1991	PVRGC	MLML	360
07 Jun 1992	PVRGC	MLML	Unknown
25 Jul 1993	PVRGC	MLML	400
10 Jul 1994	PVRGC	MLML	360
16 Jul 1995	PVRGC	MLML	Unknown

¹ PVRGC = Pajaro Valley Rod and Gun Club; CRGC = Castroville Rod and Gun Club; IWL = Izaak Walton League.

² CAS = California Academy of Sciences; CDFG = California Department of Fish & Game; MLML = Moss Landing Marine Labs.

³ Records on bat ray sizes and weights were lost.

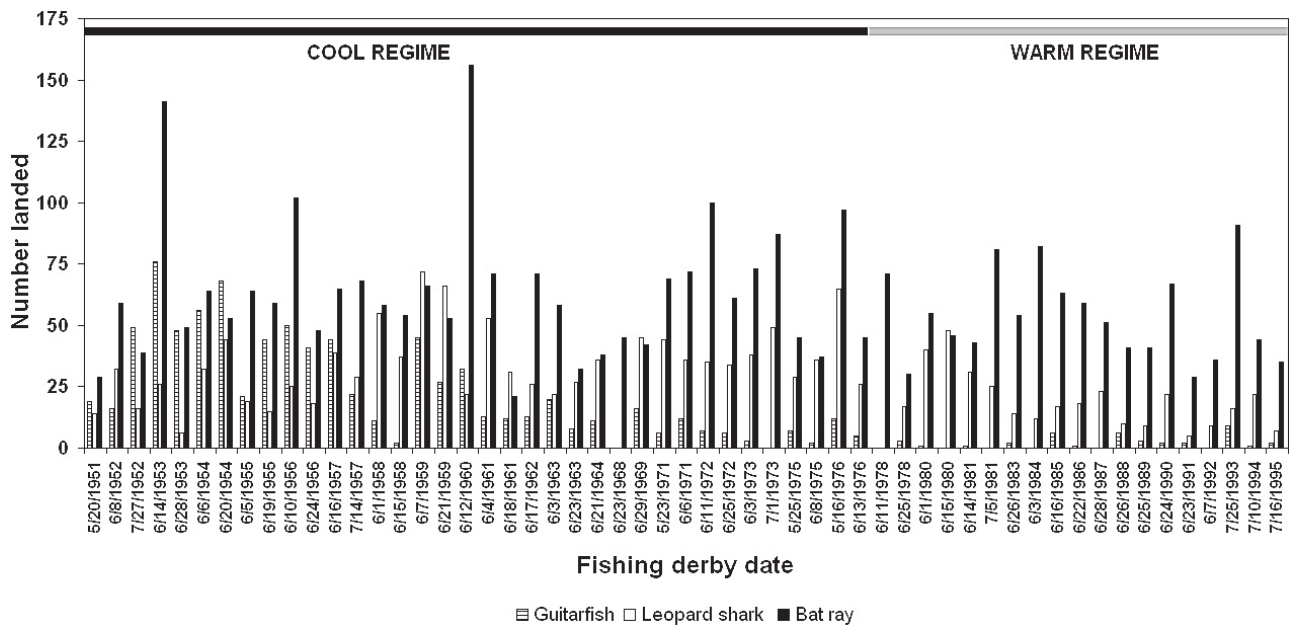


Figure 2.—Species composition of derby landings for the three major species: bat ray, leopard shark, and shovelnose guitarfish. The derbies are listed in chronological order and there are gaps for the years where derbies did not occur. The bar at the top of the graph shows the cool (black) or warm (gray) phases of the Pacific Decadal Oscillation during the time of the derbies based on Mantua and Hare (2002).

respectively, while for males it was 45 cm and 62 cm DW (Martin and Cailliet, 1988a), so there is a large discrepancy between the different estimates, especially for females.

For leopard sharks and shovelnose guitarfish the differences between sizes at first maturity and 100% maturity are not as great. Size at maturity for leopard sharks was based on Kusher et al. (1992), with a size of maturity for males of 105 cm TL and 110 cm TL for females. The size at maturity of shovelnose guitarfish was based on Timmons and Bray (1997), with males maturing at 100 cm TL and females at 99 cm TL. The studies that were used to estimate the size at maturity for leopard sharks and bat rays were conducted in Elkhorn Slough, but the study of shovelnose guitarfish was conducted in southern California.

Results

Catch Composition

A total of 5,954 elasmobranchs were sampled from the 55 derbies that oc-

curred between 1951 and 1995. Four derbies occurred in May, 44 in June, and 7 in July. As a result, these data are primarily representative of elasmobranch populations in Elkhorn Slough in June. Of the total catch, 3,310 (55.6%) were bat rays, 1,544 (25.9%) were leopard sharks, 863 (14.5%) were shovelnose guitarfish, 113 (1.9%) were smoothhounds, 94 (1.6%) were thornbacks, 25 (0.4%) were round stingrays, 4 (0.1%) were spiny dogfish, and 1 was a big skate. These are the first records of spiny dogfish and big skates in Elkhorn Slough. One spiny dogfish was caught in both the 13 June 1976 and 28 June 1987 derbies, and two were caught in the 23 June 1991 derby; the big skate was caught in the 23 June 1991 derby. The three most common species (bat ray, leopard shark, and shovelnose guitarfish) comprised more than 90% of the catch in most individual derbies and 96% of the cumulative derby catch, with bat rays being the most abundant species in nearly every derby.

Over the period of this study, several shifts occurred in the elasmobranch

species composition (Fig. 2, 3). The most obvious change has been the relative disappearance of shovelnose guitarfish from the catch. During the 1950's, shovelnose guitarfish were the second most abundant species, averaging about 28% of the catch. In those years, the shovelnose guitarfish even surpassed the number of bat rays caught in some derbies. However the relative abundance of shovelnose guitarfish declined steadily, and by the early 1970's their numbers had dropped considerably to about 5% of the catch. By the 1990's they composed about 3% of the catch. The average number landed per derby declined from around 38 fish per derby in the 1950's to around 3 per derby by the 1990's (Table 2).

The relative abundance of bat rays has steadily increased from 47% in the 1950's to 68% in the 1990's. While the relative abundance has increased, the number landed has decreased from an average of 63 fish per derby in the 1950's to around 50 fish per derby in the 1990's. The relative abundance of

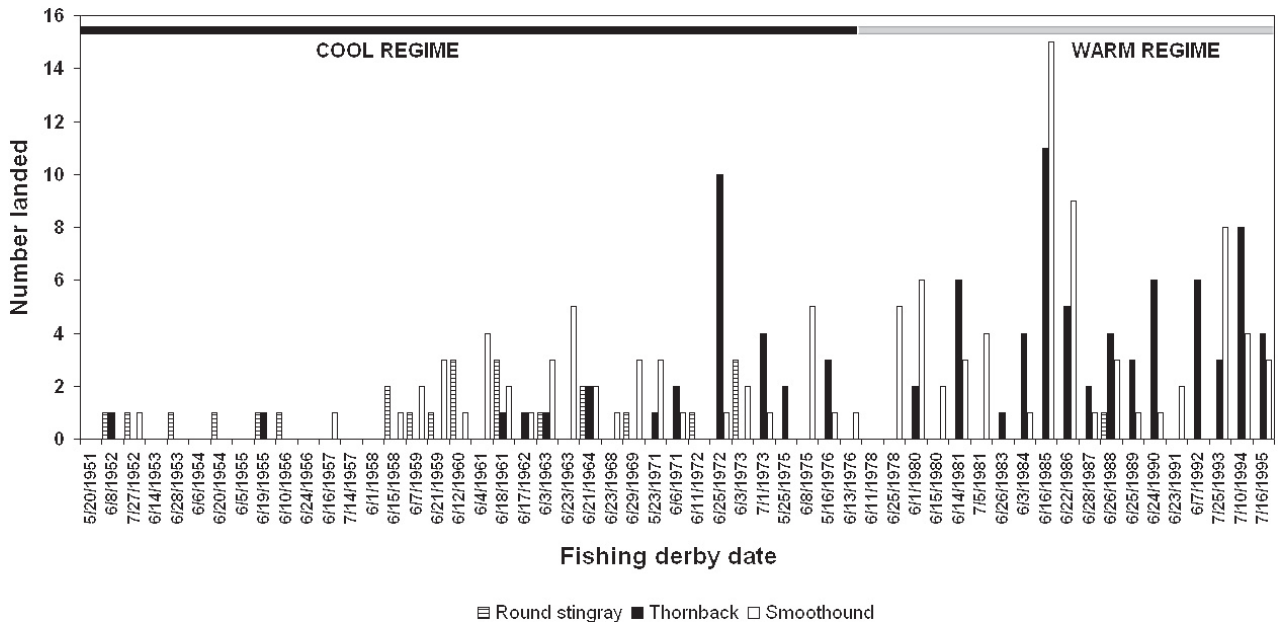


Figure 3.— Species composition of derby landings for the three minor species: round stingray, thornback, and smoothound. The derbies are listed in chronological order and there are gaps for the years where derbies did not occur. The bar at the top of the graph shows the cool (black) or warm (gray) phases of the Pacific Decadal Oscillation during the time of the derbies based on Mantua and Hare (2002).

Table 2.—Average proportion of total catch, stage of maturity, and sex ratios grouped by decade. Values are the mean and standard error (SE) for all of the derbies occurring in that decade. In the total landed column, the number in brackets (No. with data) refers to the number of animals that were used in estimating the stage of maturity and sex ratios. Fewer animals were used to estimate maturity and sex ratios than were caught due to data being lost or incomplete. All data from a particular species were pooled together to calculate values shown in "overall" rows. For shovelnose guitarfish the entire catch of the 1980's and 1990's were grouped due to the low numbers that were caught.

	Decade	Total landed (No. with data)	Avg. landed per derby (SE)	Avg. proportion of total catch (SE)	Avg. proportion mature (SE)	Avg. immature ♀/♂ sex ratio (SE)	Avg. mature ♀/♂ sex ratio (SE)	Avg. overall ♀/♂ sex ratio (SE)
Bat rays	1950's	1,071 (580)	63.00 (±6.10)	0.47 (±0.02)	0.33 (±0.02)	2.97 (±0.37)	0.84 (±0.17)	1.77 (±0.20)
	1960's	534 (522)	59.30 (±13.30)	0.55 (±0.07)	0.33 (±0.02)	4.61 (±1.18)	0.98 (±0.19)	2.09 (±0.22)
	1970's	787 (765)	65.60 (±6.60)	0.61 (±0.04)	0.32 (±0.04)	4.05 (±1.01)	1.01 (±0.20)	1.93 (±0.21)
	1980's	616 (565)	56.00 (±4.40)	0.64 (±0.03)	0.38 (±0.05)	7.98 (±3.77)	2.03 (±0.51)	4.05 (±1.06)
	1990's	302 (291)	50.30 (±9.80)	0.68 (±0.02)	0.35 (±0.04)	10.10 (±3.96)	1.86 (±1.04)	4.84 (±2.02)
	Overall	3,310 (2723)	60.20 (±3.40)	0.57 (±0.02)	0.35 (±0.02)	5.64 (±1.09)	1.30 (±0.19)	2.65 (±0.34)
Leopard shark	1950's	545 (526)	32.10 (±4.50)	0.24 (±0.03)	0.39 (±0.04)	1.05 (±0.16)	0.82 (±0.14)	0.96 (±0.14)
	1960's	262 (217)	29.10 (±5.00)	0.28 (±0.05)	0.26 (±0.05)	1.45 (±0.39)	1.17 (±0.43)	1.15 (±0.14)
	1970's	409 (390)	34.10 (±4.60)	0.31 (±0.03)	0.31 (±0.05)	0.96 (±0.20)	1.90 (±0.78)	0.84 (±0.10)
	1980's	247 (216)	22.40 (±3.80)	0.25 (±0.04)	0.29 (±0.05)	1.68 (±0.39)	1.35 (±0.31)	1.32 (±0.16)
	1990's	81 (77)	13.50 (±3.10)	0.18 (±0.02)	0.34 (±0.08)	1.08 (±0.22)	6.08 (±2.08)	1.87 (±0.48)
	Overall	1,544 (1426)	28.10 (±2.20)	0.26 (±0.02)	0.33 (±0.02)	1.23 (±0.12)	1.66 (±0.32)	1.13 (±0.09)
Shovelnose guitarfish	1950's	639 (577)	37.60 (±4.90)	0.28 (±0.03)	0.84 (±0.02)	1.03 (±0.16)	3.09 (±0.58)	2.19 (±0.26)
	1960's	125 (109)	13.90 (±2.90)	0.12 (±0.02)	0.64 (±0.06)	2.36 (±0.54)	2.95 (±0.94)	2.83 (±1.04)
	1970's	63 (48)	5.30 (±1.10)	0.05 (±0.01)	0.81 (±0.12)	0.17 (±0.17)	0.95 (±0.27)	0.68 (±0.17)
	1980's	20 (14)	1.80 (±0.70)	0.02 (±0.01)	0.64	0.67	8.00	2.50
	1990's	16 (17)	2.70 (±1.30)	0.03 (±0.01)	0.71	0.67	1.40	1.13
	Overall	863 (765)	15.70 (±2.60)	0.12 (±0.02)	0.76 (±0.04)	1.12 (±0.21)	2.57 (±0.39)	1.84 (±0.28)

leopard sharks fluctuated over the years but remained the second most abundant species caught in the derbies, comprising about 25% of the total catch.

Leopard sharks exhibited a gradual increase in relative abundance from 24% of the catch in the 1950's to 31% of

the catch in the 1970's. However, during the 1980's and 1990's, the relative abundance of leopard sharks declined and by the 1990's it was approximately 18% of the catch. The average number of leopard sharks landed per derby showed the same pattern, ranging from

29 to 34 fish from the 1950's to the 1970's, but the average number of leopard sharks declined to about 22 and 13 fish per derby in the 1980's and 1990's, respectively.

The frequency of occurrence and relative abundance of thornback and

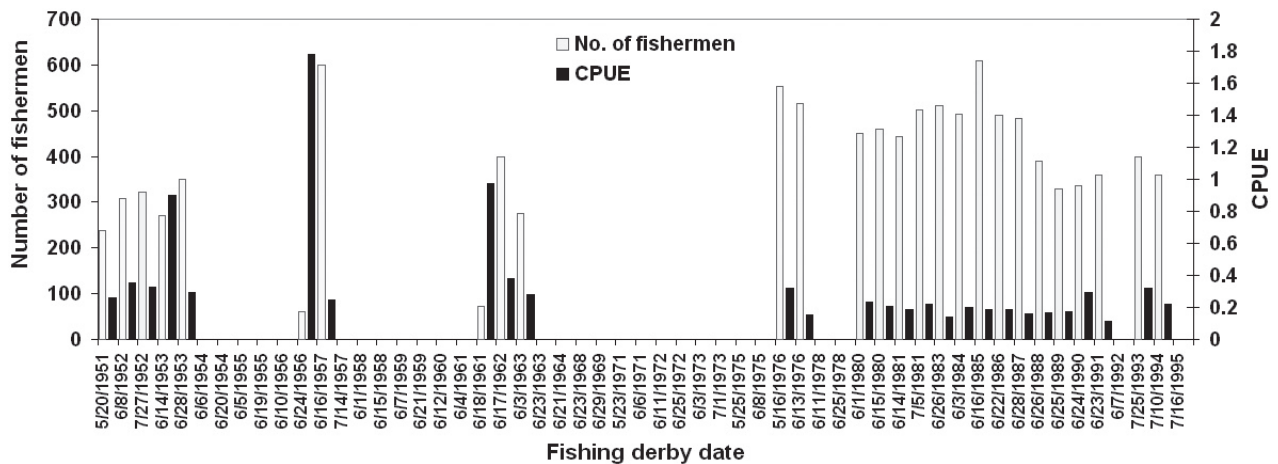


Figure 4.—Number of derby fishermen by derby date and their CPUE.

smoothhounds increased in later derbies compared to the derbies in the 1950's and 1960's, but they continued to comprise only a small percentage of the catch. Round stingray were never caught in significant numbers, but nearly all of them were caught between 1951 and 1973.

Catch Per Unit of Effort

Fisherman numbers at individual derbies are only available for 27 out of the 55 derbies. These data were collected intermittently during the early years but were collected relatively consistently from the 1980's to the end of the derbies (Table 1). The number of fishermen generally increased as the derbies progressed, averaging 277.5 ± 60.29 (SE) for the first decade (1951–61) to 417.4 ± 30.74 (SE) in the last decade (1985–95), up 50.4%. Fewer fishermen participated during the first half of the derbies (1951–73, mean = 290 ± 49.1 (SE)) than during the last half of the derbies (1974–95, mean = 452 ± 19.2 (SE)), and the overall average was 392 ± 26.2 (SE) fishermen/derby.

The fewest fishermen recorded (attributed to bad weather) was 60 at the 24 June 1956 derby, and the greatest number was 609 at the 16 June 1985 derby. Also, elasmobranch landings per decade decreased steadily, with average

landings of 133.8, 106.4, 108.8, 88, and 74.5 from the 1950's to 1990's, respectively. The average landings declined from 135 ± 10.255 (SE) during the first decade (1951–61) to 77.4 ± 8.305 (SE) for the last decade (1985–95), down 42.7%.

CPUE was higher and more variable during the first two decades (Fig. 4) after which it declined, and it was relatively low and stable during the 1980's and 1990's. There were three peaks in the CPUE during the 14 June 1953, 24 June 1956, and 18 June 1961 derbies. Two of those peaks (24 June 1956 and 18 June 1961) were the two derbies with the lowest number of fishermen (60 and 72, respectively), and the other peak was during the 14 June 1953 derby with 270 fishermen. During the first 22 years of derbies, the average CPUE was 0.581 ± 0.16 (SE) fish/fisherman (0.31 ± 0.02 (SE) when the peaks are not included), while for the second half it was 0.205 ± 0.014 (SE).

Size-Weight Relationships

Male bat rays had a disc width-weight relationship of $y = 2.02671e-08x^{2.97357}$ ($r^2 = 0.95$) and female bat rays had a disc width-weight relationship of $y = 1.03747e-08x^{3.08729}$ ($r^2 = 0.96$) (Fig. 5). Male leopard sharks had a length-weight relationship of $y = 5.13e-09x^{2.95917}$ ($r^2 = 0.96$) and female leopard sharks

had a length-weight relationship of $y = 2.67e-009x^{3.06261}$ ($r^2 = 0.96$) (Fig. 6).

Male and female shovelnose guitarfish exhibited more variability in their growth regressions than the other species. Male shovelnose guitarfish had a length-weight relationship of $y = 1.83739e-08x^{2.76348}$ ($r^2 = 0.81$) and female shovelnose guitarfish $y = 5.37655e-09x^{2.96729}$ ($r^2 = 0.89$) (Fig. 7). Smaller size classes of shovelnose guitarfish were underrepresented in the data, so their regression calculations were not as robust as the bat rays or leopard sharks.

Size Class Distributions

Bat rays (Fig. 8), leopard sharks (Fig. 9), and shovelnose guitarfish (Fig. 10) showed no dramatic size frequency shifts over the course of the derbies. The size of female bat rays may have increased slightly since the average disc width of females was slightly larger during the 1980's and 1990's. There were always very few of the smaller shovelnose guitarfish, but they had disappeared almost completely by 1970. The average size of male and female leopard sharks was slightly larger in the 1950's than in following decades. Female bat rays and shovelnose guitarfish in Elkhorn Slough attained a larger size than their male counterparts, while male

and female leopard sharks were of a similar size.

Stage of Maturity

Bat ray catches were dominated by immature individuals, specifically immature females (Table 2). Based on

Martin and Cailliet's (1988a) estimate of size at 100% maturity for females and males, between 60 and 70% of the catch was immature. Even with the potential bias due to the size at maturity estimate used, the average size of the female bat catch (78.9 cm DW, which is 100 mm

smaller than size at 50% maturity (88.1 cm DW)), indicates that the majority of females were immature. The proportion of mature bat rays ranged from an average of 32% in the 1970's to 38% in the 1980's, and averaged 35% overall. The proportion of mature leopard sharks caught varied more than in bat rays, ranging from an average of 26% in the 1960's to 39% in the 1950's, with an overall average of 33%. Unlike bat rays and leopard sharks, the majority of shovelnose guitarfish caught were mature (average of 63% in the 1960's to 84% in the 1950's, with an overall average of 76%).

Sex Ratios

The sex ratios of the total catch showed that both bat rays (Fig. 11) and shovelnose guitarfish (Fig. 12) exhibited a similar trend in which females generally outnumbered males by a ratio of two to one. The sex ratio for all the bat rays caught during the derbies was 1.9:1 (♀:♂), while for shovelnose guitarfish it was 1.8:1 (♀:♂). However, for bat rays, this sex ratio was primarily due to the large number of immature females since the sex ratio of mature rays was closer to 1:1 (♀:♂). The numbers of female and male leopard sharks were more evenly balanced (Fig. 13), with an overall sex ratio of 0.96:1 (♀:♂).

The sex ratios, grouped by decade and stage of maturity, showed that bat ray, leopard shark, and shovelnose guitarfish catches were generally dominated by females. The sex ratio of immature bat rays was heavily skewed towards females (ranging from a sex ratio of 2.97:1 (♀:♂) in the 1950's to 10.1:1 (♀:♂) in the 1990's), while for adults it was closer to 1:1 (♀:♂), except for the 1980's and 1990's when it was closer to 2:1 (♀:♂) (Table 2). Both immature and mature leopard sharks had a sex ratio closer to 1:1 (♀:♂) than bat rays, but females usually were more abundant than males. Overall, the catches of mature leopard sharks were more dominated by females than were immature animals, and while most of the ratios were slightly greater than 1:1 (♀:♂), they were as high as 6.08:1 (♀:♂) in the 1990's. Adult shovelnose guitarfish catches were

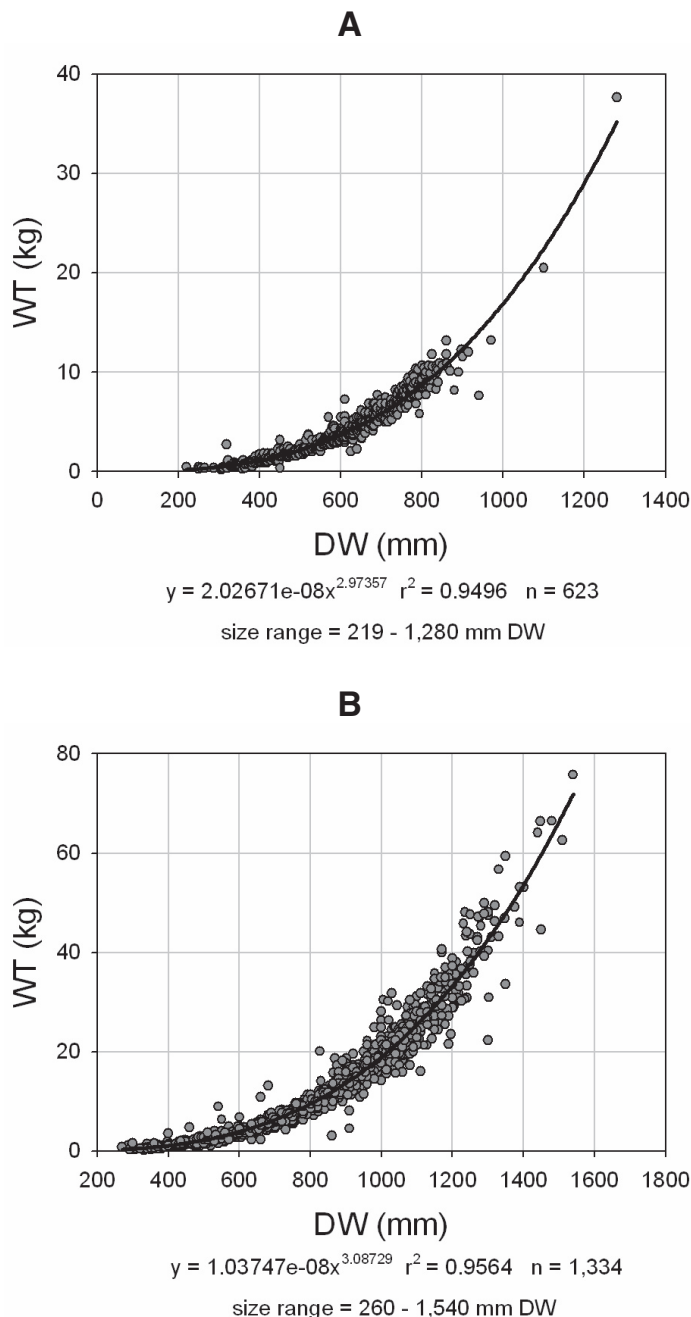


Figure 5.—Disc width-weight regression for A) male bat rays and B) female bat rays.

consistently dominated by females until the 1970's and 1990's, when the ratio was closer to 1:1 (♀:♂). Sex ratios of immature shovelnose guitarfish were less dominated by females than were adults, and during the 1970's–90's males dominated.

Minor species (thornback, round stingray, and smoothhounds) numbers were insufficient to examine sex ratio by individual derby, decade, or stage of maturity, but the sex ratio for these species was calculated for the overall catch. The overall sex ratio of the thornback was strongly dominated by females at 6.75:1 (♀:♂). The overall sex ratio of the round stingray was strongly dominated by males at 0.31:1 (♀:♂), and the overall smoothhound sex ratio was 1.5:1 (♀:♂).

Discussion

Elkhorn Slough has undergone substantial changes over the last 150 yr due to human activity, mainly through diking of marshland for agricultural purposes, channel construction for habitat restoration, and destruction of levees (Van Dyke and Wasson, 2005). The most dramatic period of change started in 1946–47 when the U.S. Army Corps of Engineers dredged a channel to make Moss Landing Harbor. This opened Elkhorn Slough, once a sluggish wetland system with muted tides, to direct tidal flow, greatly increasing erosion and changing it from a depositional to an erosional area (Caffrey and Broenkow, 2002). In addition, several diked areas were reopened to tidal flow during the following decades. This included the creation of the ESNERR marsh restoration site in 1983, which increased the wetted area of the slough by 20% and increased the total volume of the slough by 30% (Malzone and Kvitek²). These habitat changes have likely influenced the composition of elasmobranch populations in Elkhorn Slough.

In total, the tidal volume of Elkhorn Slough increased by over 200% since

²Malzone, C., and R. Kvitek. 1994. Tidal scour, erosion, and habitat loss in Elkhorn Slough, California. A report of the Elkhorn Slough Foundation pursuant to NOAA Award #NA37OM0523.

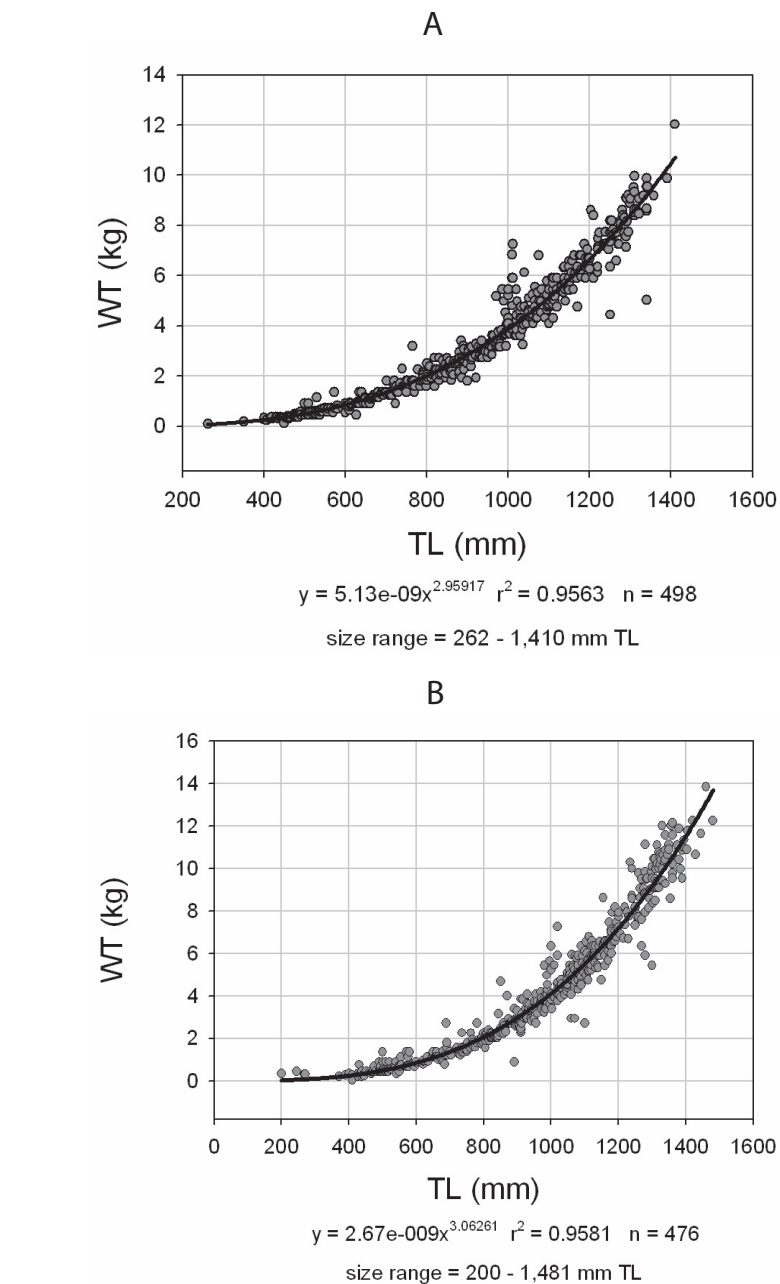


Figure 6.—Length-weight regression for A) male leopard sharks and B) female leopard sharks.

1947 (Crampton, 1994; Malzone, 1999). As a result, Elkhorn Slough has been transformed into a highly tidal embayment with a significant amount of tidal scour causing erosion in the main channel, tidal creeks, mudflats, and bordering salt marsh (Malzone, 1999; Caffrey and Broenkow, 2002; Van Dyke and Wasson,

2005). Channels and tidal creeks have become wider and deeper (the average cross sectional width of tidal creeks has increased from 2.5 m in 1931 to 12.4 m in 2003), salt marsh has converted to mudflats, existing mudflats have been eroded to lower tidal levels, and degraded marshland and mudflats are now

the primary habitats in Elkhorn Slough (Van Dyke and Wasson, 2005). Since the 1970's the substrate has shifted from a more unconsolidated soft bottom towards a more consolidated clay bottom (Lindquist, 1998). The onset of these changes and disruption of ecological

processes (e.g. hydrology, habitat type) in 1947 corresponded closely with the onset of the derbies in 1946.

These alterations have changed the type and amount of habitat available for elasmobranchs and almost certainly the diversity and availability of prey.

Yoklavich et al. (2002) reported that the changes to Elkhorn Slough have impacted the species composition, abundance, and trophic patterns of the ichthyofaunal assemblage of the slough through such processes as changing prey availability and habitat alteration. Teleosts have been directly affected by these changes, with their diets being less diverse in the 1990's than in the 1970's, due to the lower diversity and density of the invertebrate assemblage in the slough which resulted from erosion (Lindquist, 1998; Yoklavich et al., 2002). The diet of leopard sharks has similarly shifted as a result of habitat alteration. In the 1970's leopard sharks had a more diverse diet than they do currently and they exhibited an ontogenetic shift in diet (Talent, 1976). Kao (2000) found that the diets of leopard sharks are less diverse than they were in the 1970's and that the ontogenetic shift was no longer apparent as the diets of both small and large sharks converged on a smaller number of prey. Because they likely compete directly with elasmobranchs for certain prey items (Kao, 2000), the reestablishment of sea otters may also have impacted the elasmobranchs of Elkhorn Slough.

In addition to diet changes, the alteration has likely had a direct effect on the function of the slough as a nursery area for elasmobranchs. Barry (1983) found that leopard sharks likely used the shallow tidal creeks and mudflats of the slough as nursery areas. Those tidal creeks and mudflats have since experienced significant amounts of erosion, becoming wider and deeper so it is likely that their function as a nursery area has changed. The fact that the spiny dogfish and big skate were all caught during the later years demonstrates how the slough has changed from a sluggish backwater wetland to an open tidally influenced embayment that is more accessible to coastal marine species.

Changes in the prevailing oceanographic conditions could also affect the elasmobranch assemblage of Elkhorn Slough. There is strong interannual to interdecadal variability in the climate in the Pacific Basin, which leads to warm or cool climatic regimes (Mantua and

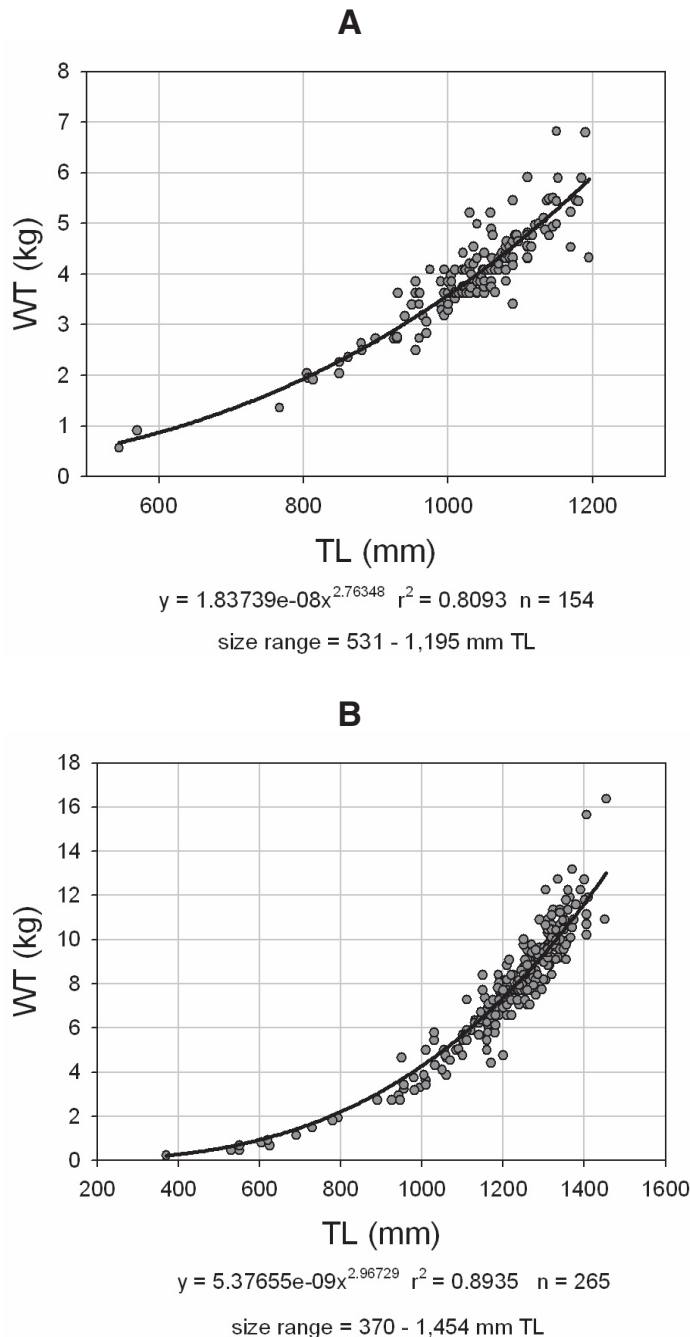


Figure 7.—Length-weight regression for A) male shovelnose guitarfish and B) female shovelnose guitarfish.

Hare, 2002). This is often called the Pacific Decadal Oscillation (PDO). It has been described as a long-lived El Niño-like pattern of Pacific climate variability because they have very similar climatic effects but are very different in duration.

These regimes are longer in duration than El Niño, usually lasting for several decades. In addition to several other climatic characteristics, warm PDO phases (warm regimes) are characterized by anomalously cool sea surface temperatures and increased productivity in the central North Pacific and anomalously warm temperatures and decreased productivity along the west coast of the Americas. The inverse is true during cool PDO phases (cool regimes).

There have been two full PDO cycles over the last century. Cool regimes existed from 1890–24 and 1947–76 and warm regimes occurred from 1925–46 and from 1977 to the late 1990's (Mantua and Hare, 2002). These regime shifts are reported to have a dramatic effect on Pacific marine ecosystems. The abundance of plankton, fishes, marine mammals, and birds have all been shown to track these shifts, with certain suites of species or assemblages being abundant during warm regimes and others more abundant during cool regimes (Francis et al., 1998; Beamish et al., 1999; Mantua and Hare, 2002).

Bat Rays

The average number of bat rays landed per derby decreased in the 1980's and 1990's, and this could indicate a decrease in the abundance of bat rays in Elkhorn Slough. This decline could be due to habitat alteration, fishing pressure, or regime shifts, although it is unlikely that regime shifts would impact the abundance of bat rays since Monterey Bay is in the middle of their range. It is more likely that habitat alteration and fishing pressure are responsible for any possible decline in bat ray abundance.

Habitat alteration, which has been well documented in Elkhorn Slough (Crampton, 1994; Malzone, 1999; Cafrey and Broenkow, 2002; Van Dyke and Wasson, 2005), could impact the

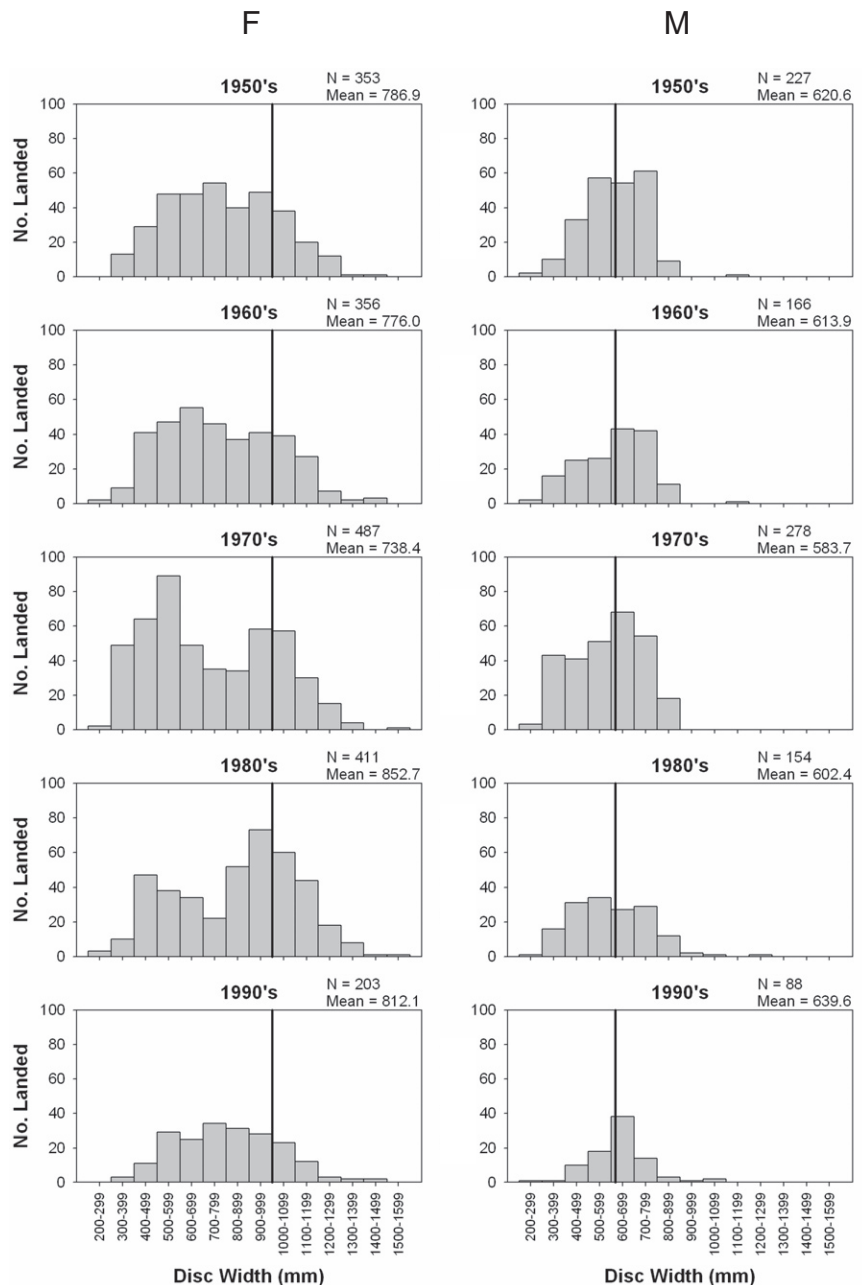


Figure 8.— Size class distribution of male and female bat rays by decade. The vertical line indicates size at 100% maturity.

abundance of bat rays through a number of mechanisms. It could alter prey availability (as documented by Kao (2000) for leopard sharks and Lindquist (1998) for teleosts) or impact the type and availability of habitats used by juveniles and adults. In addition it could alter the function of the slough as a nursery area.

Fishing pressure also could impact their abundance. The decrease in abundance appears to correspond with the increase in fishing pressure which appears to have started in the second half of the derbies, although due to gaps in the fishing effort data this is speculative. Herald (1953) suggested that bat rays

were more residential than other species of elasmobranchs in the slough, and as a result they might be more susceptible to overfishing.

However, based on our current understanding of the dynamics of elasmobranchs in the slough, bat rays do not

appear to be any more residential than the other common elasmobranchs. In fact, the relative abundance of bat rays in the catch has increased steadily over the decades, which indicates that while their numbers may have declined, they may be less susceptible to habitat alteration

or fishing pressure than leopard sharks or shovelnose guitarfish.

Elkhorn Slough is believed to function as a nursery area for a number of elasmobranchs. For coastal species, nursery habitats are usually located in productive shallow waters, such as bays or estuaries. These habitats are thought to be utilized as nursery areas due to abundance of prey, increased water temperatures, and lack of predators (Springer, 1967; Castro, 1993; Holland et al., 1993; Morrissey and Gruber, 1993; Simpfendorfer and Milward, 1993). Nursery areas can be further broken down into primary and secondary nursery areas (Bass, 1978). Primary nursery areas are where pupping occurs, while secondary nursery areas are utilized by neonates or juveniles for a period of time ranging from weeks to years.

Elkhorn Slough serves as a primary nursery area for bat rays (Barry, 1983; Talent, 1985; Martin and Cailliet, 1988a). This conclusion is supported by the fact that female bat rays were observed aborting pups during derby weigh-ins (Herald, 1953; King³) and near term fetuses were found during female dissections at derby weigh-ins (Herald et al., 1960). In addition, young-of-the-year bat rays were caught during the derbies.

The large number of immature animals caught during the derbies could also indicate that Elkhorn Slough serves as a secondary nursery area for this species. Elkhorn Slough is a highly productive environment with no significant predators which would make it an ideal place for small bat rays to utilize until they reach a large enough size to safely enter coastal waters. Talent (1985) found that small bat rays (<60 cm DW) were more common than larger rays during all seasons, though their abundance was lowest in the winter. This indicates that they use the slough as a secondary nursery area on a seasonal basis. It is likely that bat rays leave the slough in the winter when temperature and salinity decline, and return the following year once temperature and salinity increase

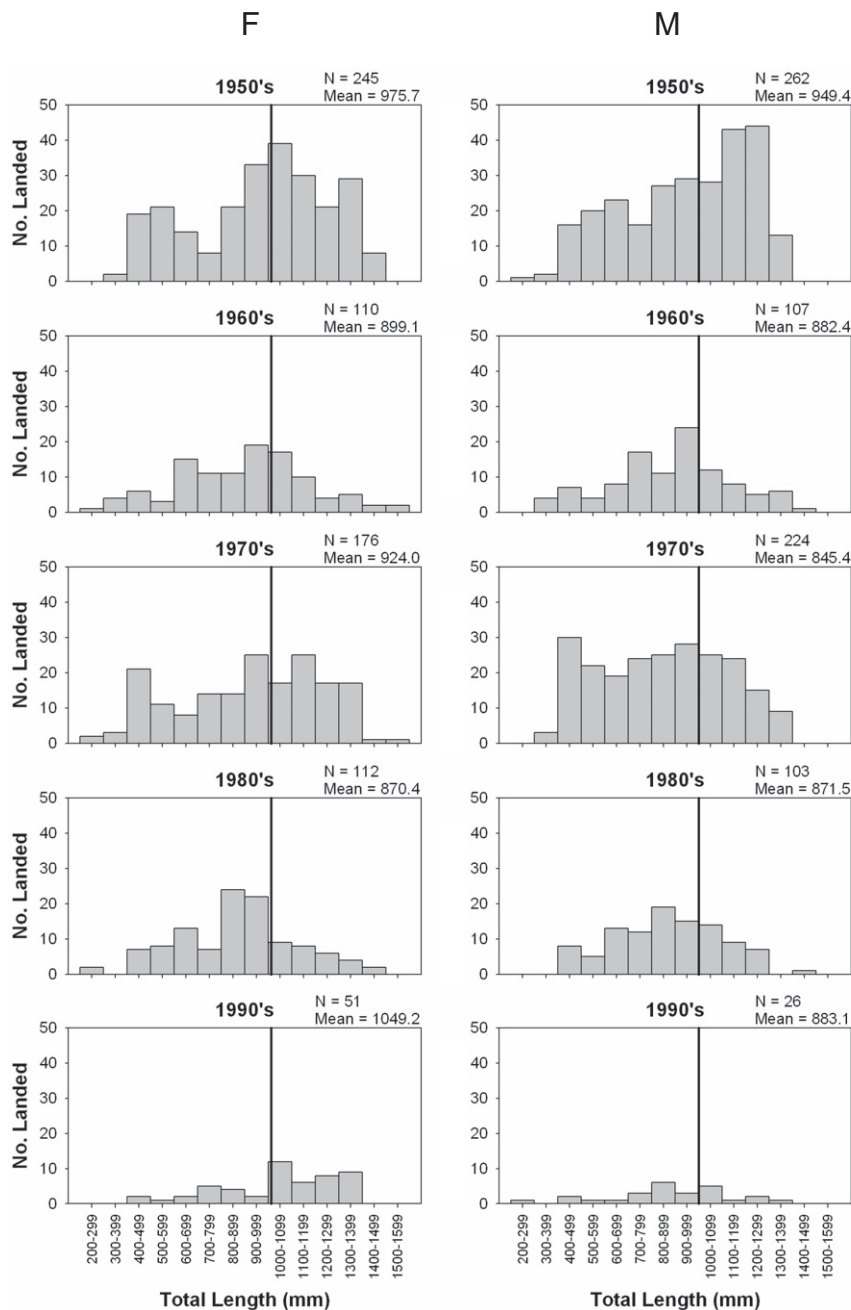


Figure 9.—Size class distribution of male and female leopard sharks by decade. The vertical line indicates size at 100% maturity.

³King, A. 1988. Peace Corps., Oakland, Calif. Personal observ.

as was found by Hopkins and Cech Jr. (2003) in Tomales Bay.

The role of Elkhorn Slough as a nursery area could also explain the difference between mature and immature sex ratios of bat rays. The nearly even sex ratio of mature bat rays is likely attributable to the reproductive seasonality of mature bat rays. Bat rays give birth in the late spring and summer and mate soon after giving birth (Talent, 1985; Martin and Cailliet, 1988a). The majority of derbies occurred in June, which would be near the end of their pupping period. If fertilization occurs shortly after pupping, as is suspected, one would expect there to be a sex ratio close to 1:1 at this time. In several bays along the coast of California and Baja California, Mexico, adult females greatly outnumber males during the spring and early summer, but the sex ratio evens out during the summer when males enter these areas to mate, at which point the sex ratio is around 1:1 (Ebert, 2003). It is likely that same pattern is occurring in Elkhorn Slough.

The sex ratio of immature animals heavily favored females and could be due to sexual segregation, which is well documented in elasmobranchs (Ripley, 1946; Springer, 1967; Myrberg and Gruber, 1974; Pratt, 1979; McKibben and Nelson, 1986; Klimley, 1987). Sexual segregation has been well documented in mature elasmobranchs. However, instances of immature elasmobranchs sexually segregating are not as common or as well known.

Ebert (2002) found that although male and female neonate and small juvenile broadnose sevengill sharks, *Notorynchus cepedianus*, utilize nursery areas in a similar fashion, juvenile females remain in nursery areas while adolescent males of a similar size leave. It appears as if this is related to size at maturity. Male broadnose sevengills reach maturity at a smaller size than females, and when they get close to maturity they leave nursery areas, while similarly sized females are still maturing and remain in nursery areas.

Klimley (1987) found that immature female scalloped hammerheads, *Sphyrna lewini*, moved into deeper waters at smaller sizes than males, and this move

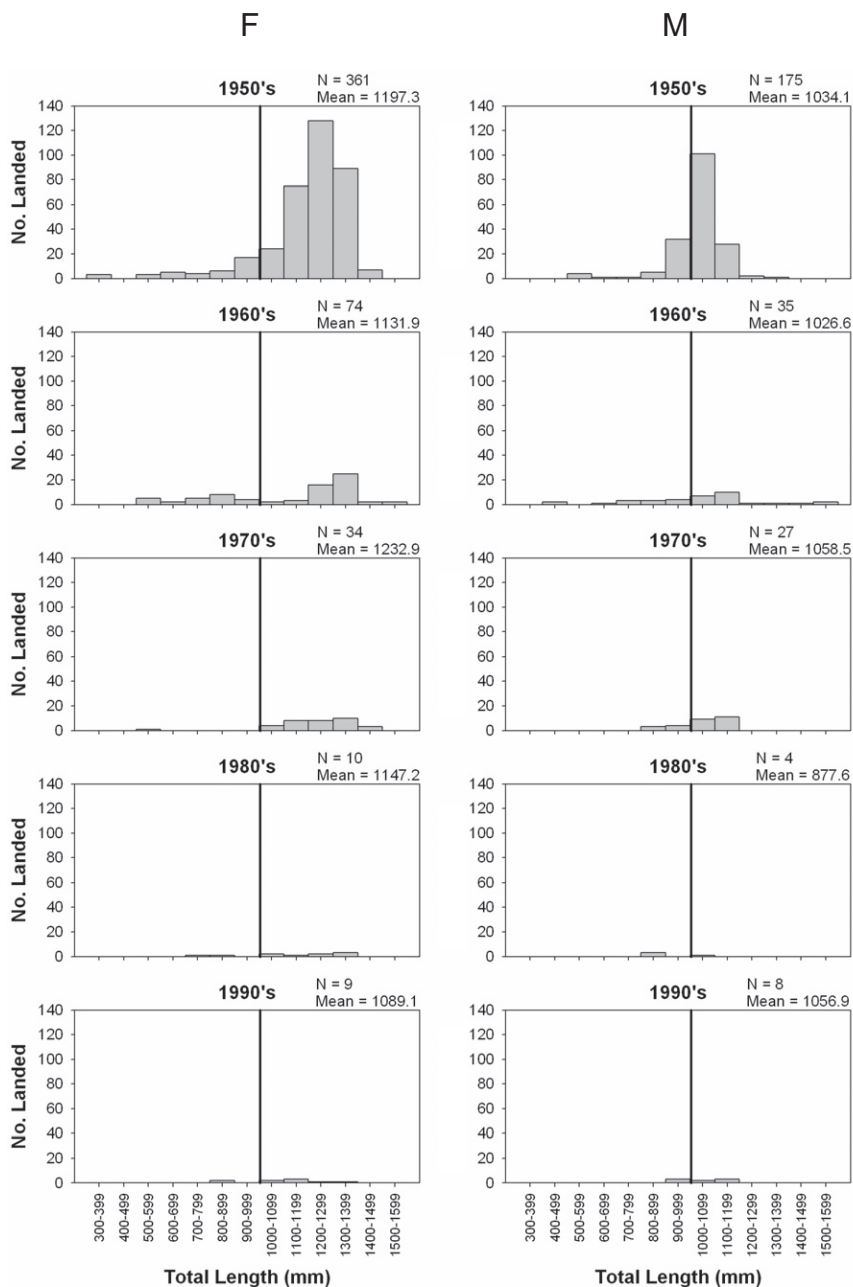


Figure 10.—Size class distribution of male and female shovelnose guitarfish by decade. The vertical line indicates size at 100% maturity.

resulted in an increased feeding rate. He theorized that by utilizing this different habitat, females were able to increase their growth rate and thereby reach maturity and attain a larger size more rapidly, which would allow them to increase their reproductive success. It is possible that bat rays are segregating by

sex for a similar reason. Females mature at a larger size and attain larger sizes than males, so by utilizing the warm, prey rich and predator free waters of Elkhorn Slough as a secondary nursery area, immature female bat rays could increase their growth rates and reproductive success.

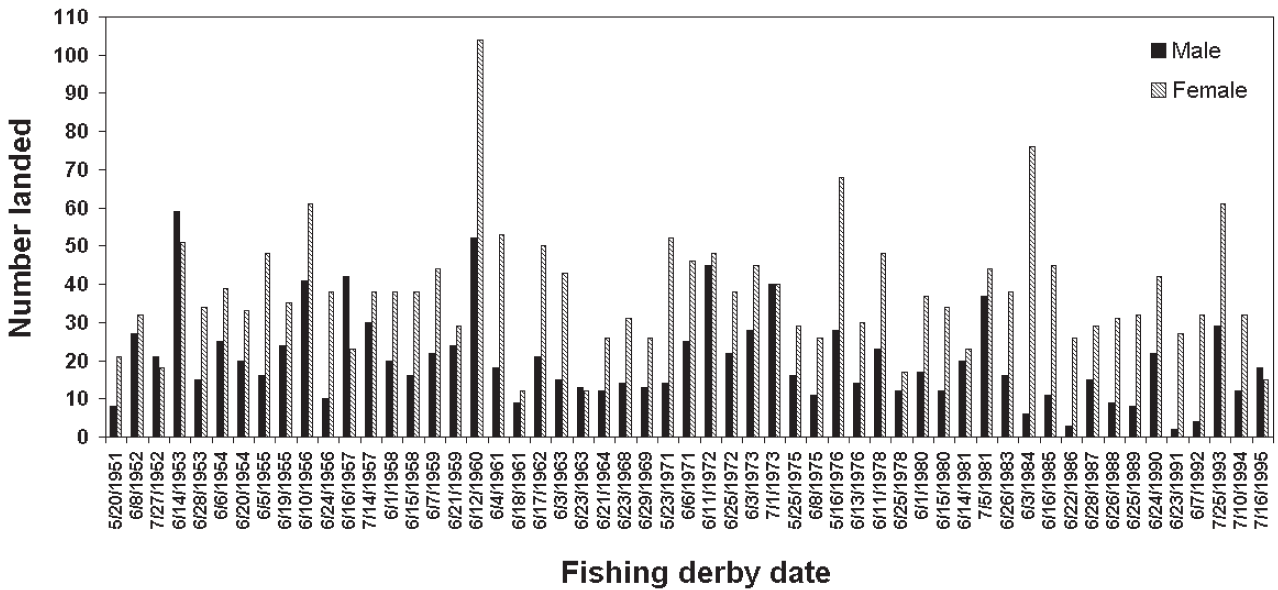


Figure 11.—Sex ratio of bat rays for each derby.

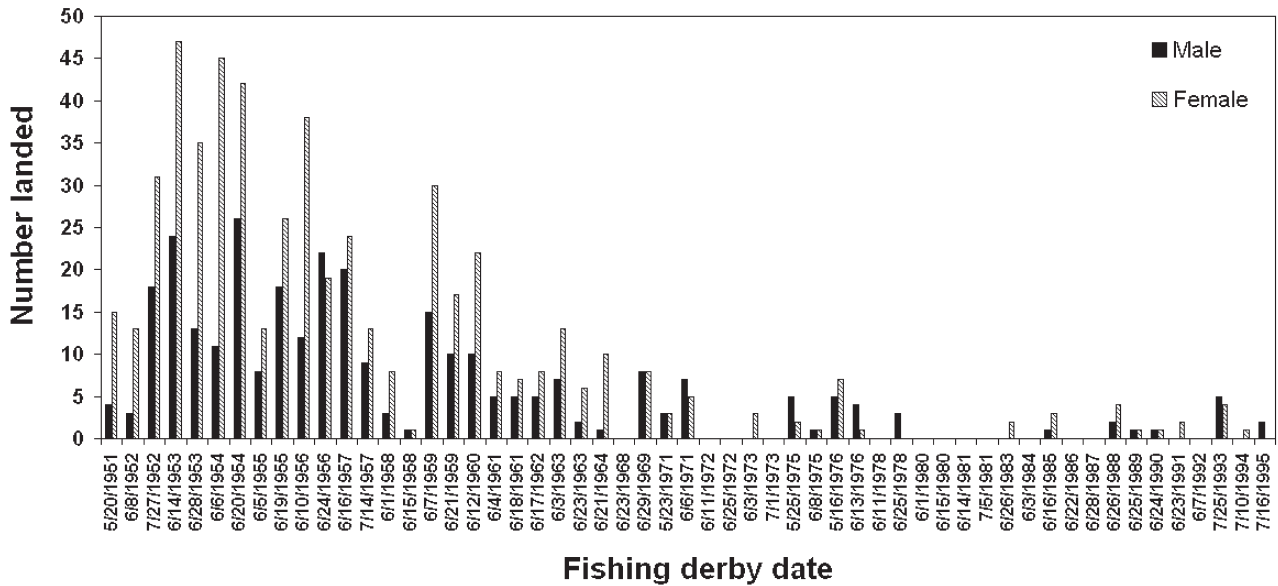


Figure 12.—Sex ratio of shovelnose guitarfish for each derby.

Leopard Sharks

Leopard sharks showed a similar pattern to bat rays in that the average number of leopard sharks landed per

derby decreased in the 1980's and 1990's, and their relative abundance declined during that same period. It is unlikely that shifts in the oceanographic conditions would cause this,

since Monterey Bay is in the middle of their range. It is more likely that any decline would be a result of other factors, such as habitat alteration or fishing pressure.

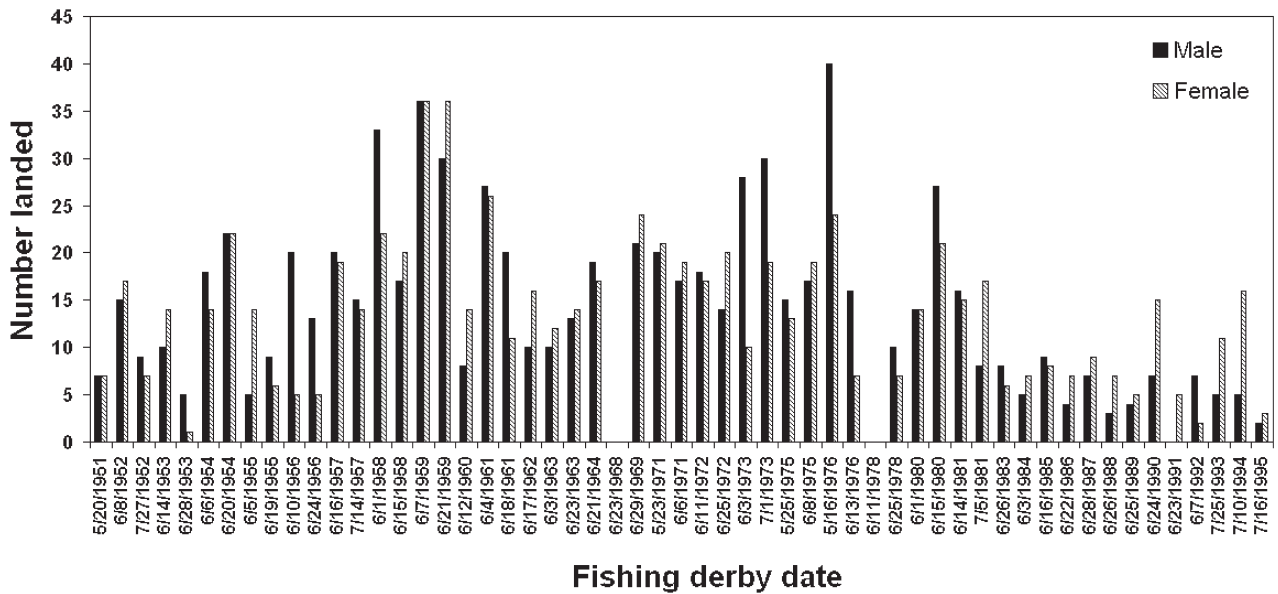


Figure 13.—Sex ratio of leopard sharks for each derby.

Habitat alteration likely played a role in any changes in leopard shark abundance. The diet of leopard sharks has been altered due to erosion, and possibly also to competition with sea otters (Kao, 2000). In addition, the type and amount of available habitat has changed, which likely has influenced patterns of habitat use. Habitat alteration has also likely impacted the nursery function of the slough as well as the tidal creeks that were used as nursery areas in the 1970's have been greatly altered (Barry, 1983).

In addition, the accumulation of agricultural pesticides and chemicals in the sediments of Elkhorn Slough (Phillips et al., 2002) could potentially impact leopard sharks directly through toxic effects or indirectly through impacting prey items (especially invertebrate infauna). This also may have played a role in the decrease in leopard shark abundance. Leopard sharks in Elkhorn Slough have been shown to contain significant concentrations of polychlorinated biphenyl (PCB) and organochlorine pesticide (OCP) contaminants (Vega, 1999), although how this affects their fitness is not known.

Another factor that could have impacted the catches of leopard sharks could be changes in regulations. A bag

limit of three sharks and size limit of 36 inches was instituted in 1992. This could help explain a decline in the catch after that time, but the decline appears to have started in the early 1980's, so it cannot be attributed to new regulations alone.

The decline in the early 1980's could be due to the creation of Elkhorn Slough National Estuarine Research Reserve (ESNERR) in 1983. This created a large area that was off limits to fishermen, and ESNERR is heavily utilized by leopard sharks, especially during the spring and summer (Carlisle, 2006). This would not be surprising since leopard sharks use mudflats extensively and mudflats make up a large area of ESNERR (Carlisle, 2006). This could have effectively removed part of Elkhorn Slough's leopard shark population from fishing pressure from the derbies after 1983. This may also help explain the decline in bat rays in the 1980's and 1990's, as bat rays heavily utilize intertidal mudflats as well. The apparent decline in the abundance or catchability of leopard sharks in the 1980's and 1990's is likely a combination of these factors.

The proportion of the leopard shark catch that was mature varied from decade to decade, but the catch was

always strongly dominated by immature sharks. Leopard sharks use the slough as a primary nursery area (Ackerman, 1971; Barry, 1983; Talent, 1985), and near-term females and young-of-the-year leopard sharks were caught during the derbies. However, the abundance of immature sharks indicates that like bat rays, leopard sharks also utilize the slough as a secondary nursery area.

Talent (1985) found that leopard sharks exhibited pronounced seasonal differences in their size class distribution, with the relative abundance of larger sharks (100+ cm) being greatest in the winter and spring and small and large sharks both being well represented in the summer and fall. While he was unable to sample very small leopard sharks due to the large mesh gill nets he used, the size class distribution of leopard sharks during the summer reported by Talent (1985) closely mirrors what was seen in this study. The lack of smaller sharks during the winter and spring indicates that the slough likely functions as a secondary, seasonal nursery area, much like in bat rays, with smaller sharks likely coming into the slough during the warmer months and leaving once the temperature and salinity drops (Hopkins and Cech Jr., 2003).

Similar to bat rays, the sex ratio of leopard sharks was likely due to reproductive seasonality. Both immature and mature leopard sharks had sex ratios that were relatively close to 1:1. However, the sex ratio of mature leopard sharks was often slightly more skewed towards females, especially in the 1990's when it was heavily dominated by females.

Leopard sharks give birth in the late spring-early summer, in particular during April and May, and they are likely fertilized shortly after giving birth (Ackerman, 1971; Talent, 1985; Ebert and Ebert, 2005). June is likely around the end of the pupping period and the beginning of the mating period, so one might expect that the sex ratio should be close to 1:1 at that time. The sexual segregation in immature leopard sharks is not nearly as dramatic as is seen in immature bat rays, indicating that both immature male and female leopard sharks are using Elkhorn Slough as a nursery area.

Shovelnose Guitarfish

The abundance of shovelnose guitarfish was very high in the early 1950's, but it declined steadily until they were only a very small component of the catch by the early 1970's. Shovelnose guitarfish are still caught in Monterey Bay and Elkhorn Slough but in low numbers. It is possible that the decline could be due to overfishing or habitat alteration. However, these options do not seem likely to be the principle causes of the decline. Their life history characteristics, which would be an indication of their susceptibility to overfishing, are similar to those of leopard sharks and bat rays (Ebert, 2003) which were abundant throughout the derbies, so it seems unlikely that they would be so strongly impacted by fishing pressure while the other species were not.

Habitat alteration should have increased the amount of habitat available to shovelnose guitarfish since they are commonly found in shallow soft bottom habitats such as mudflats (Ebert, 2003). A more likely explanation for the decline is that shovelnose guitarfish simply became less abundant in the Monterey Bay area due to a southern shift in their

distribution. The range of shovelnose guitarfish is typically reported as being from San Francisco Bay to the Gulf of California and possibly to Mazatlan, Mexico (Ebert, 2003), but they are most abundant in southern California. Herald and Dempster (1952) state that although the northern extent of the range of the shovelnose guitarfish is San Francisco, there are no authentic records of specimens north of Monterey Bay, so Monterey Bay is likely the northern limit of their range.

The relatively high abundance of shovelnose guitarfish in Elkhorn Slough in the 1950's could have been due to large-scale shifts in their distribution brought about by the Pacific Decadal Oscillation. Based on the records from the early derbies, it seems likely that there were more of them in the northern part of their range during the warm regime that occurred from 1925–46. As water temperatures cooled after the regime shift in 1947 it is possible that the thermal regime became less favorable to this warmer-water species and their numbers declined as their range shifted south. If this is the case, then the fishing pressure from the derbies may have hastened the decline of the species, since Elkhorn Slough was at the northernmost extent of their range, and their numbers may have been already declining. Their numbers declined north of Point Conception in general, not just in Elkhorn Slough. Data from the Recreational Fisheries Information Network (RecFIN⁴) shows that from 1980 (the earliest year on record in the database) to 2003 shovelnose guitarfish were almost completely absent from recreational fisheries north of Point Conception, but they were very abundant south of Point Conception.

In the southern extent of their range it also appears as if there was a shift in shovelnose guitarfish. In May 1974 in the Gulf of California off Guaymas, Mexico, the speckled guitarfish, *Rhinobatos glaucostigma*, and whitenose guitarfish, *R. leucorhynchus*, were abundant, but the shovelnose guitarfish was completely absent from the artisanal

fishery landings or shrimp trawl bycatch (Compagno⁵). However, shovelnose guitarfish are now the most abundant species of *Rhinobatos* off Guaymas (Márquez-Farias, 2002). This information from the southern end of their range combined with their decline north of Point Conception at the northern part of their range could possibly indicate that the range of shovelnose guitarfish may have shifted south, although this is speculative. If the range of the shovelnose guitarfish has indeed shifted south, why they have not shifted back north again during the warm regime from 1977 to the late 1990's remains an open question.

There is some evidence that shovelnose guitarfish used Elkhorn Slough as a nursery area. The majority of shovelnose guitarfish were mature, and females outnumbered males nearly 2 to 1, which could be indicative of the females using the slough as a nursery area. Bays and estuaries are known to be used as nursery areas by shovelnose guitarfish, and during their reproductive period their sex ratios can be highly skewed towards females in those areas (Ebert, 2003).

However, based on the very small number of immature animals caught, it is unlikely that Elkhorn Slough was an important primary or secondary nursery area for shovelnose guitarfish during the derbies. Small and young-of-the-year shovelnose guitarfish were caught on occasion, although not nearly as frequently as was observed in leopard sharks or bat rays. Based on what is known about the prey and foraging behavior of these species, it does not seem likely that small guitarfish would be more difficult to catch than small leopard sharks or bat rays, so it seems unlikely that the lack of small shovelnose guitarfish is due to gear selectivity.

Another possibility is that due to timing of parturition young of the year were not present during the time of year that the derbies occurred. In southern California they pup in the summer (Ebert, 2003), so if they were pupping

⁵Compagno, L. J. V. 2003. Checklist of Guaymas chondrichthyans. Shark Research Center, South Africa Museum. SRC report 2003-05-14, 4 p.

⁴RecFIN <http://www.recfin.org/>

in Elkhorn Slough at the same time as in southern California young-of-the-year would likely be present in June. Talent (1985) only found eggs with little embryonic development in mature females and stated that there was no evidence that they use the slough as a nursery area. However, he sampled from 1971 to 1972 after their abundance had declined greatly, plus he primarily caught shovelnose guitarfish in the fall and winter when embryonic development would be less advanced if they pupped and mated in the summer.

Herald et al. (1960) observed that most of the adult females were carrying "eggs and embryos in their ovaries at the time of the derbies," which may suggest that shovelnose guitarfish may have used Elkhorn Slough as a primary nursery area during the early years of the derbies. However, Herald et al. (1960) argued that since so few very small shovelnose guitarfish were caught, it was unlikely that shovelnose guitarfish were giving birth in the slough. While it is possible that it was at one time a primary nursery area for the shovelnose guitarfish, there is no direct evidence from these data or the literature that Elkhorn Slough served as a nursery area from May to July during the time frame that the derbies occurred.

It is also possible that the age and sex structure of the shovelnose guitarfish catch is due to sexual segregation. Herald et al. (1960) suggested that they may segregate like the soupfin (or tope) shark, *Galeorhinus galeus*, which segregate by sex along the coast of California, with mature males being more common in northern California and mature females more common in southern California (Ripley, 1946). This type of segregation also occurs in the salmon shark (*Lamna ditropis*), where females are more common in the eastern Pacific and males in the western Pacific (Goldman and Musick, 2006). However, there is no evidence of this type of large-scale segregation occurring in shovelnose guitarfish.

Thornback

Thornbacks were very rarely caught during the earlier derby years, but

during the late 1960's and 1970's their frequency of occurrence and abundance started to increase. This could be due to a northward expansion of their range. Currently, thornbacks range from Tomales Bay, Calif., to Thurloe Head, Baja California (Miller and Lea, 1972; Plant, 1989). As of the 1950's, thornbacks were reported as abundant south of Point Conception, and had only been found north of there on a few occasions (Starks, 1918; Walford, 1935; Herald, 1953; Herald et al., 1960), indicating that the few caught in the early years of the derby reflected the extreme northern extent of their range. While their numbers increased slightly until the end of the derbies in 1995, it is likely that this reflected their slow shift north and if data had continued to be collected it likely would have shown a sharp increase in the late 1990's.

Currently, thornbacks are one of the most abundant elasmobranchs in Elkhorn Slough (Carlisle⁶). Plant (1989) extended the northern range of thornbacks from San Francisco Bay to Tomales Bay based on thornbacks being caught in Tomales Bay in 1988, which was during a warm-water period of the Pacific Decadal Oscillation. He also reported an increase in the abundance of thornbacks caught around and north of San Francisco Bay and suggested that they may not be as uncommon as they were previously. RecFIN⁴ data shows that thornbacks started appearing in the recreational catch north of Point Conception around 1994 and dramatically increased after 2000. All of this information indicates that the range of thornbacks has expanded northward, and this would account for their increase in abundance in the derbies during the later years.

Whether or not the concurrent decline in shovelnose guitarfish and increase in thornbacks in Elkhorn Slough are related is debatable. It is possible that the northward expansion of the thornback was facilitated by the decline of shovelnose guitarfish north of Point Conception. While shovelnose guitarfish were

abundant in Elkhorn Slough, there were very few thornbacks caught, but once their numbers decreased to a very low level, thornbacks started being caught regularly and in increasing abundances. This is interesting since thornbacks and shovelnose guitarfish are of a generally similar ecomorphotype, so if shovelnose guitarfish were to be replaced by another species it makes sense that it would be by a species that fills a similar niche in the system.

Shovelnose guitarfish and thornbacks generally feed on similar prey items. Shovelnose guitarfish feed on crustaceans, bivalves, polychaetes, and teleosts (Roedel and Ripley, 1950; Talent, 1982; Eschmeyer et al., 1983; Love, 1996; Ebert, 2003) while thornbacks feed on crustaceans, molluscs, polychaetes, cephalopods, and teleosts (Feder et al., 1974; VanBlaricom, 1982; Ebert, 2003; Limbaugh⁷). Their overall ranges are similar and they also utilize similar habitats. Shovelnose guitarfish and thornbacks both occur primarily in shallow soft bottom habitats such as the mud and sandy bottoms of bays, sloughs, and coastal beaches (Roedel and Ripley, 1950; Dubsky, 1974; Feder et al., 1974; Eschmeyer et al., 1983; Larson and DeMartini, 1984; Ebert, 2003; Limbaugh⁷). However, these two distributional shifts could be purely coincidental and the lack of information on movements, patterns of habitat utilization, and competition between these species makes it difficult to draw any concrete conclusions.

The thornback catch was highly skewed towards females, which may indicate that the slough served as a nursery area or that sexual segregation was occurring. While data on their life history is lacking, Ebert (2003) states that they pup in the late summer and, if this is true, it could explain the dominance of females in the catch. They could follow a pattern similar to bat rays, where females enter bays and estuaries earlier than males to pup and males enter after pupping to mate with females.

⁶Carlisle, A. Unpubl. data. Hopkins Marine Station, Stanford Univ., Pacific Grove, Calif.

⁷Limbaugh, C. 1955. Fish life in the kelp beds and the effects of kelp harvesting. Inst. Mar. Resour., Univ. Calif. La Jolla, IMR Ref. 55-9, 158 p.

Based on this model, May to July would be when females should be more abundant than males. However, although it is possible that thornbacks used the slough as a nursery area later in the year than the derbies occurred, there is no evidence that this actually occurred. It is more likely that the sex ratio observed during the derbies is due to sexual segregation. It is possible, however, that thornbacks currently use the slough as a nursery area. There is anecdotal information that gravid thornbacks have been caught in Elkhorn Slough in the last several years, but this has not been confirmed.

Round Stingray

Round stingrays were rarely caught during the shark derbies in Elkhorn Slough. Interestingly, most of the round stingrays were caught during the first half of the derbies. Although they are known to move north of Point Conception during periods of warm water, such as El Niño events (Babel, 1967), it is a more southerly species that is uncommon north of Point Conception.

Because they are more common in southern California, it is counterintuitive that they were caught primarily during the cool regime that lasted from 1947 to 1976. One possible explanation is that they used Elkhorn Slough as a thermal refuge, due to its warmer temperatures. This is a likely explanation since their distribution is strongly influenced by water temperature. They are more abundant in waters that are above 10°C, and are believed to aggregate in areas that experience increased temperatures (Babel, 1967; Ebert, 2003). Elkhorn Slough is significantly warmer than coastal waters during the summer, so it would not be surprising that round stingrays may be more abundant in the area. In addition, most of the round stingrays that were landed were caught near the thermal discharge from the Moss Landing power plant in the lower part of the slough, where water temperatures could be quite warm (Lea⁸). This is similar to what has been found in southern

California, where round stingrays have been reported to prefer warmer waters where thermal effluent from power plants is discharged (Hoisington and Lowe, 2005).

Another explanation for this pattern of abundance is that habitat alteration has decreased the amount of suitable habitat for this species. Round stingrays utilize soft bottomed habitat (Babel, 1967; Ebert, 2003), so the shift away from an unconsolidated soft bottom to a more consolidated clay bottom that has occurred since the 1970's may have reduced the value of Elkhorn Slough to the species. This change also could have impacted the availability of prey items, as has been demonstrated for teleosts (Lindquist, 1998) and leopard sharks (Kao, 2000).

The low numbers of round stingrays caught and the male dominated sex ratio indicate that round stingrays did not use Elkhorn Slough as a nursery area during the derbies and that they may segregate based on sex. Females move inshore to mate and give birth during the spring and summer in southern California (Babel, 1967). If they were pupping or mating in the slough, one would expect a sex ratio closer to 1:1. Talent (1985) did not catch any gravid females or juveniles, and believed that they did not breed in Elkhorn Slough. In this study, only 25% of the round stingray catch was measured, but they were all mature based on the maturity estimates from Babel (1967). They are known to segregate by age and sex with females living offshore in water deeper than 14 m, while adult males and juveniles occupy shallower habitats (Babel, 1967), which could explain the preponderance of males in the shallow slough.

Smoothhounds

The frequency of occurrence and relative abundance of smoothhounds increased starting in the 1960's. It is difficult to relate the increase in abundance in smoothhounds to temperature regime shifts because we have lumped together both brown smoothhounds, which have a more northern distribution, and gray smoothhounds, which have a more southern distribution (Ebert,

2003). Since the majority of smoothhounds caught in previous studies were gray smoothhounds (100% reported by Yoklavich et al. (1991); 77% reported by Talent, (1985); and 100% reported by San Filippo (1995)), it is likely that the smoothhounds caught during the derbies were mainly gray smoothhounds.

That the gray smoothhound has historically been the most abundant smoothhound species in Elkhorn Slough is curious since they are a more southerly species, and brown smoothhounds are one of the most abundant elasmobranchs in San Francisco Bay (De Wit, 1975; Ebert, 1986), which is geographically much closer. There was an increase in the frequency of occurrence of smoothhounds between the late 1950's and mid 1970's, which was during a cool regime, but it appears as if there is an even greater increase in smoothhound catch after the regime shift in 1977 to a warm regime. Sixty percent of the smoothhounds caught in the derbies were caught during this period of time. Assuming that most of the smoothhounds were gray smoothhounds, it is possible that the warmer water temperatures following the 1977 regime shift could have led to an increase in the abundance of this more southerly, warmer water species in Elkhorn Slough, although this is speculative.

San Filippo (1995) caught 312 gray smoothhound (71% of the catch) in 2 years of sampling between 1990 and 1992 in ESNERR. Only four smoothhounds were caught during that same time period in the derbies. This indicates that smoothhounds were more abundant in Elkhorn Slough during that period of time than the data from the derbies reveals, and suggests that the creation of ESNERR possibly led to shifts in the distribution and habitat use of smoothhounds and other elasmobranchs in Elkhorn Slough.

While sampling between early 2003 through late 2004 in ESNERR and the rest of the slough, only nine smoothhounds were caught (6 gray and 3 brown smoothhounds) (Carlisle⁹). Although

⁸Lea, R. 2006. Calif. Dept. Fish Game (retired), Monterey, Calif. Personal commun.

⁹Carlisle, A. Unpubl. data. Hopkins Marine Station, Stanford Univ., Pacific Grove, Calif.

different methods were used (Carlisle used gill nets, San Filippo used beach seines), this seems to indicate that their numbers have declined since the early 1990's. If the number of grey smoothhounds has indeed declined, this suggests that their presence in the northern part of their range (i.e. Monterey Bay) is influenced by water temperatures. The period of highest smoothhound abundance appears to have been during the warm regime from 1977 to the mid 1990's, and their numbers appear to have declined after the PDO started to shift to a cold regime in the mid to late 1990's. The influence of temperature on gray smoothhound abundance is logical given that the northern extent of their range is Elkhorn Slough (Ebert, 2003).

Effects of the Derbies

It is hard to say whether or not the fishing derbies directly impacted the elasmobranch assemblage of Elkhorn Slough. Herald et al. (1960) theorized that the elasmobranch yield at an Elkhorn Slough derby was more an accurate reflection of the elasmobranch content of the slough on a particular day, rather than the number of fishermen participating in the derby, so smaller catch would indicate fewer elasmobranchs in the slough. The fact that the average catch decreased steadily over the decades and declined by 42% from the first decade to the last decade of the derbies despite a 50% increase in effort (number of fishermen) over the same period of time indicates that the size of the elasmobranch assemblage has declined.

CPUE data would be one way to examine the effect of the derbies, since CPUE calculated from a small area can be considered to be proportional to the local abundance (Maury and Gascuel, 2001). However due to the large gaps in the CPUE data it is difficult to directly address this question, although it still does provide valuable insight into the elasmobranch assemblage. Because the highest CPUE's (including the three large spikes in CPUE) all occurred during the early years of the derbies while the later years all had the lowest CPUE's, local overexploitation may have occurred since significant fishing

effort in a small area may tend to reduce local biomass and local CPUE (Fonteneau and Richard, 2003).

Whereas it appears as if the abundance or catchability of elasmobranchs in the slough has decreased over the years, it is impossible to directly attribute this to the derbies since other factors (e.g. regime shifts, habitat alteration, the creation of ESNERR) also contribute to the abundance and distribution of elasmobranchs. However, the derbies certainly had management and conservation implications. Given the limited size and semi-enclosed nature of the slough, the decline in CPUE with increasing numbers of fishermen indicates that the slough was likely getting "fished out" during large derbies. Herald (1953) suggested that the drop in bat ray catch from 59 in the 8 June 1952 derby to 39 in the 27 July 1952 derby might have been partially due to mortality from the earlier derby.

Despite significant fishing pressure, the number of elasmobranchs appeared to often rebound after the derbies, likely due to immigration of more elasmobranchs from coastal areas. This is demonstrated by the fact that in years when there were two derbies, at most a month apart, large numbers of elasmobranchs were usually caught in both derbies. If their numbers were not being replenished, one would expect the catch to always be less during the following derby, which was not always the case. At times the second derby actually had larger catches.

While the derbies at least temporarily depleted the number of elasmobranchs in the slough, the stability of the size class distributions in bat rays, leopard sharks, and shovelnose guitarfish (when present in significant numbers) indicates that neither fishing pressure from the derbies nor habitat alteration dramatically impacted the size or age structure of these three most abundant species. This also suggests that the populations of elasmobranchs in Elkhorn Slough are open populations with potentially high rates of immigration and emigration.

However, effectively managing elasmobranch populations is of great consequence given the important role that

they play in maintaining the overall health and stability of marine ecosystems (Bascompte et al., 2005). Because these species have late ages at maturity and low fecundity, they are vulnerable to overexploitation, and our knowledge of elasmobranch fisheries suggests a precautionary approach is warranted. Elkhorn Slough is the nursery area for a number of these species, and the derbies were occurring during the peak of their reproductive seasons, resulting in the killing of many gravid females. In addition to pregnant females, many immature animals were killed, and this can also have a large impact on the health of a population (Heppel et al., 1999). The cessation of the derbies was a positive event that will aid in the protection and management of local populations of elasmobranchs, which are an important component in local marine and estuarine ecosystems.

Summary

This study documents several shifts in the elasmobranch assemblage of Elkhorn Slough between 1951 and 1995, indicating that the elasmobranch assemblage of the slough is dynamic and responds to several factors. Possible reasons for these changes are the direct or indirect effects of habitat alteration, fishing pressure, and large-scale shifts in the oceanographic conditions, such as the Pacific Decadal Oscillation. Habitat alteration could influence the abundance of species by changing the amount and type of available habitat and the abundance and diversity of prey items. Whether it was habitat alteration, changes in the oceanographic conditions, or fishing pressure from the derbies that influenced the abundance of different species is difficult to say. It is most likely that the different factors worked in concert, but for different species, one factor may have been more important than the others.

The most notable change was the shovelnose guitarfish decline, which was possibly due to their range having shifted south, potentially as a result of the regime shift that occurred in 1947. This decline in shovelnose guitarfish coincided with an increase in the frequency

of occurrence and a slight increase in the relative abundance of thornbacks and smoothhounds. Thornbacks have since become one of the most abundant elasmobranchs in the slough, most likely due to their range having expanded northwards over the last several decades, possibly during the increased temperatures that occurred during the warm regime. The increase in smoothhounds was possibly a result of the increased water temperature that occurred during the warm regime.

Round stingrays were most common during the early years of the derby, possibly as a result of thermal refuging. They were very infrequently caught during the later years, possibly as a result of a decrease in the amount of suitable habitat. Bat rays steadily increased in relative abundance throughout the derbies, possibly due to habitat alteration increasing the amount of habitat suitable for bat rays, while the relative abundance of leopard sharks was fairly stable throughout the derbies, except for a slight decline during the 1980's and 1990's.

This study provides further evidence that Elkhorn Slough functions as both a primary and secondary nursery area for bat rays and leopard sharks. The sex ratios of bat ray, shovelnose guitarfish, thornback, and round stingray catch indicates that sexual segregation is occurring in these species in Elkhorn Slough. In immature animals this could be due to habitat or prey partitioning, and in mature animals it likely reflects reproductive seasonality.

It appears that the abundance of elasmobranchs in the slough declined during the course of the derbies, although it is difficult to attribute the decline directly to the derbies since other factors likely influenced elasmobranch abundance and distribution such as regime shifts, habitat alteration, etc. However, the derbies did appear to temporarily deplete the numbers of elasmobranchs in the slough, although they usually appeared to recover afterward. The cessation of the derbies has been beneficial to the health of the local populations of elasmobranchs, especially because Elkhorn Slough

plays such an important role in the life history of most of the elasmobranchs that utilize the slough.

Acknowledgments

We would like to thank everyone who helped with this project, most notably Wade Smith, Joe Bizarro, Christopher Rinewalt, Guillermo Moreno, Lucy Wold, Teresa Farrar, William Hayden, Sandra Zeiner, and Rich San Filippo. We also would like to thank Robert Lea, Mary Yoklavich, Todd Hopkins, and three anonymous reviewers for critically reviewing manuscript drafts. Finally, we would like to acknowledge the late Earl S. Herald, whose early insight into the benefit of a long-term study of shark assemblages in Elkhorn Slough made this study possible.

Literature Cited

- Ackerman, L. T. 1971. Contributions to the biology of the leopard shark, *Triakis semifasciata* (Girard) in Elkhorn Slough, Monterey Bay, California. M.A. thesis, Sacramento State College, Sacramento, 54 p.
- Babel, J. S. 1967. Reproduction, life history and ecology of the round stingray *Urolophus halleri* Cooper. Calif. Dep. Fish Game, Fish Bull. 137, 104 p.
- Barry, J. P. 1983. The utilization of shallow marsh habitats by fishes in Elkhorn Slough, California. M.A. thesis, San Jose State Univ., San Jose, 95 p.
- _____, M. M. Yoklavich, G. M. Cailliet, D. A. Ambrose, and B. S. Antrim. 1996. Trophic ecology of the dominant fishes in Elkhorn Slough, California, 1974-1980. *Estuaries* 19(1):115-138.
- Bascompte, J., C. J. Melian, and E. Sala. 2005. Interaction strength combinations and the overfishing of a marine food web. *Proc. Natl. Acad. Sci.* 102(15):5,443-5,447.
- Bass, A. J. 1978. Problems in studies of sharks in the southwest Indian Ocean. *In* E. S. Hodgson and R. F. Mathewson (Editors), *Sensory biology of sharks, skates, and rays*, p. 545-594. Off. Nav. Res., Dep. Navy, Arlington, Va.
- Beamish, R. J., D. J. Noakes, G. A. McFarlane, L. Klyashtorin, V. V. Ivanov, and V. Kurashov. 1999. The regime concept of natural trends in the production of Pacific salmon. *Can. J. Fish. Aquat. Sci.* 56(3):516-526.
- Caffrey, J., and W. Broenkow. 2002. Hydrography. *In* J. Caffrey, M. Brown, W. B. Tyler, and M. Silberstein (Editors), *Changes in a California estuary: a profile of Elkhorn Slough*, p. 29-42. Elkhorn Slough Found., Moss Landing, Calif.
- Carlisle, A. 2006. Movements and habitat use of female leopard sharks in Elkhorn Slough, CA. M.S. thesis, San Jose State Univ., 195 p.
- Castro, J. I. 1993. The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. *Environ. Biol. Fishes* 38:37-48.
- Crampton, T. A. 1994. Long term effects of Moss Landing Harbor on the wetlands of Elkhorn Slough. M.S. thesis, Univ. Calif., Santa Cruz, 65 p.
- De Wit, L. A. 1975. Changes in the species composition of sharks in south San Francisco Bay. *Calif. Fish Game* 61(2):106-111.
- Dubsky, P. A. 1974. Movement patterns and activity levels of fishes in Morro Bay, California as determined by ultrasonic tagging. M.S. thesis, Calif. Polytechnic State Univ., San Luis Obispo, 86 p.
- Ebert, D. A. 1986. Observations on the elasmobranch assemblage of San Francisco Bay. *Calif. Fish Game* 72(4):244-249.
- _____. 2002. Ontogenetic changes in the diet of the sevengill shark (*Notorynchus cepedianus*). *Mar. Freshwater Res.* 53:517-523.
- _____. 2003. Sharks, rays and chimaeras of California. Univ. Calif. Press, Berkeley, 284 p.
- _____, and T. B. Ebert. 2005. Reproduction, diet, and habitat use of leopard sharks, *Triakis semifasciata* (Girard) in Humboldt Bay, California, U.S.A. *Mar. Freshwater Res.* 56:1,089-1,098.
- Eschmeyer, W. N., E. S. Herald, and H. Hammann. 1983. A field guide to Pacific coast fishes North America. Houghton Mifflin Co., Boston, 336 p.
- Feder, H. M., C. H. Turner, and C. Limbaugh. 1974. Observations on fishes associated with kelp beds in southern California. *Calif. Dep. Fish Game, Fish Bull.* 160, 44 p.
- Fonteneau, A., and N. Richard. 2003. Relationship between catch, effort, CPUE and local abundance for non-target species, such as billfishes, caught by Indian Ocean longline fisheries. *Mar. Freshwater Res.* 54:383-392.
- Francis, R. C., S. R. Hare, A. B. Hollowed, and W. S. Wooster. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fish. Oceanogr.* 7(1):1-21.
- Goldman, K. J., and J. A. Musick. 2006. Growth and maturity of salmon sharks in the eastern and western North Pacific, and comments on back-calculation methods. *Fish. Bull.* 104:278-292.
- Heppel, S. S., L. B. Crowder, and T. R. Menzel. 1999. Life table analysis of long-lived marine species with implications for conservation and management. *Am. Fish. Soc. Symp.* 23:137-148.
- Herald, E. S. 1953. The 1952 shark derbies at Elkhorn Slough and Coyote Point, San Francisco Bay. *Calif. Fish Game* 39(2):237-243.
- _____, and R. P. Dempster. 1952. The 1951 shark derby at Elkhorn Slough, California. *Calif. Fish Game* 38(1):133-134.
- _____, W. Schneebeli, N. Green, and K. Innes. 1960. Catch records for 17 shark derbies held at Elkhorn Slough, Monterey Bay, California. *Calif. Fish Game* 46(1):59-67.
- Hoisington, G., and C. G. Lowe. 2005. Abundance and distribution of round stingray, *Urobatis halleri*, near a thermal outfall. *Mar. Environ. Res.* 60:437-453.
- Holland, K. N., B. M. Wetherbee, J. D. Peterson, and C. G. Lowe. 1993. Movements and distribution of hammerhead shark pups on their natal grounds. *Copeia* 1993(2):495-502.
- Hopkins, T. E., and J. J. Cech Jr. 2003. The influence of environmental variables on the distribution and abundance of three elasmobranchs in Tomales Bay, California. *Environ. Biol. Fishes* 66:279-291.

- Kao, J. S. 2000. Diet, daily ration and gastric evacuation of the leopard shark (*Triakis semifasciata*). M.S. thesis, Calif. State Univ., Hayward, 96 p.
- Klimley, A. P. 1987. The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. Environ. Biol. Fishes 18:27–40.
- Kusher, D. L., S. E. Smith, and G. M. Cailliet. 1992. Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction. Environ. Biol. Fishes 35:187–203.
- Larson, R. J., and E. E. DeMartini. 1984. Abundance and vertical distribution of fishes in a cobble-bottom kelp forest off San Onofre, California. Calif. Dep. Fish Game, Fish Bull. 82(1):37–53.
- Lindquist, D. C. 1998. The effects of erosion on the trophic ecology of fishes in Elkhorn Slough, CA. M.S. thesis, Calif. State Univ., Hayward, 65 p.
- Love, M. 1996. Probably more than you want to know about the fishes of the Pacific coast. Really Big Press, Santa Barbara, Calif., 381 p.
- Malzone, C. M. 1999. Tidal scour and its relation to erosion and sediment transport in Elkhorn Slough. M.S. thesis, San Jose State Univ., San Jose, 73 p.
- Mantua, N. J., and S. R. Hare. 2002. The Pacific Decadal Oscillation. J. Oceanogr. 58:35–44.
- Márquez-Farías, F. J. 2002. The artisanal ray fishery in the Gulf of California: development, fisheries research, and management issues. IUCN Shark Specialist Group, Shark News 14:1–5.
- Martin, L. K., and G. M. Cailliet. 1988a. Aspects of reproduction of the bat ray, *Myliobatis californica*, in central California, USA. Copeia 1988(3):754–762.
- _____, and _____. 1988b. Age and growth determination of the bat ray, *Myliobatis californica* Gill. Copeia 1988(3):762–773.
- Maury, O., and D. Gascuel. 2001. 'Local over-fishing' and fishing tactics: theoretical considerations and applied consequences in stock assessment studied with a numerical simulator of fisheries. Aquat. Living Resour. 14(4):203–210.
- McKibben, J. N., and D. R. Nelson. 1986. Patterns of movement and grouping of gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. Bull. Mar. Sci. 38:89–110.
- Miller, D. J., and R. N. Lea. 1972. Guide to coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 249 p.
- Morrissey, J. F., and S. H. Gruber. 1993. Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. Environmental Biol. Fishes 38:311–319.
- Myrberg, A. A., and S. H. Gruber. 1974. The behavior of the bonnethead, *Sphyrna tiburo*. Copeia 1974(2):358–374.
- Phillips, B., M. Stephenson, M. Jacobi, G. Ichi-kawa, M. Silberstein, and M. Brown. 2002. Land use and contaminants. In J. Caffrey, M. Brown, W. B. Tyler, and M. Silberstein (Editors), Changes in a California estuary: a profile of Elkhorn Slough, p. 237–256. Elkhorn Slough Found., Moss Landing, Calif.
- Plant, R. 1989. A northern range extension for the thornback ray, *Platyrrhinoidis triseriata*. Calif. Fish Game 75(1):54.
- Pratt, H. L. 1979. Reproduction in the blue shark, *Prionace glauca*. Fish. Bull. 77(3):445–470.
- Ripley, W. E. 1946. The biology of the soupfin *Galeorhinus zyopterus* and biochemical studies of the liver. Calif. Dep. Fish Game, Fish Bull. 64:4–37.
- Roedel, P. M., and W. E. Ripley. 1950. California sharks and rays. Calif. Dep. Fish Game, Fish Bull. 75, 88 p.
- San Filippo, R. A. 1995. Diet, gastric evacuation and estimates of daily ration of the gray smoothhound, *Mustelus californicus*. M.S. thesis, San Jose State Univ., San Jose, 71 p.
- Simpfendorfer, C. A., and N. E. Milward. 1993. Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environ. Biol. Fishes 37:337–345.
- Springer, S. 1967. Social organization of shark populations. In P. W. Gilbert, R. F. Mathewson, and D. P. Rall (Editors), Sharks, skates and rays, p. 149–174. Johns Hopkins Press, Baltimore.
- Starks, E. C. 1918. The skates and rays of California, with an account of the ratfish. Calif. Fish Game 4(1):1–15.
- Talent, L. G. 1976. Food habits of the leopard shark, *Triakis semifasciata*, in Elkhorn Slough, Monterey Bay, California. Calif. Fish Game 62(4):286–298.
- _____. 1982. Food habits of the gray smoothhound (*Mustelus californicus*), the brown smoothhound (*Mustelus henlei*), the shovelnose guitarfish (*Rhinobatos productus*), and the bat ray (*Myliobatis californica*), in Elkhorn Slough, California. Calif. Fish Game 68(4):224–234.
- _____. 1985. The occurrence, seasonal distribution, and reproductive condition of elasmobranch fishes in Elkhorn Slough, CA, USA. Calif. Fish Game 71(4):210–219.
- Timmons, M., and R. N. Bray. 1997. Age, growth, and sexual maturity of shovelnoseguitarfish, *Rhinobatos productus* (Ayres). Fish. Bull. 95:349–359.
- VanBlaricom, G. R. 1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. Ecol. Monogr. 52(3):283–305.
- Van Dyke, E., and K. Wasson. 2005. Historical ecology of a central California estuary: 150 years of habitat change. Estuaries 28(2):173–189.
- Vega, R. L. 1999. Organochlorine pesticides and polychlorinated biphenyls in leopard shark (*Triakis semifasciata*) serum: a comparison of contaminant profiles in leopard shark serum from urban and agricultural estuaries. B.A. thesis, Univ. Calif., Santa Cruz, 25 p.
- Walford, L. A. 1935. The sharks and rays of California. Calif. Dep. Fish Game, Fish Bull. 45, 66 p.
- Yoklavich, M. M., G. M. Cailliet, J. P. Barry, D. A. Ambrose, and B. S. Antrim. 1991. Temporal and spatial patterns in abundance and diversity of fish assemblages in Elkhorn Slough, California. Estuaries 14(4):465–480.
- _____, _____, D. S. Oxman, J. P. Barry, and D. C. Lindquist. 2002. Fishes. In J. Caffrey, M. Brown, W. B. Tyler, and M. Silberstein (Editors), Changes in a California estuary: a profile of Elkhorn Slough, p. 163–182. Elkhorn Slough Found., Moss Landing, Calif.
- Yudin, K. G., and G. M. Cailliet. 1990. Age and growth of the gray smoothhound, *Mustelus californica*, and the brown smoothhound, *M. henlei*, sharks from central California. Copeia 1990(1):191–204.