Abstract.–Leopard shark tag recovery data, obtained from a 1979–88 study in San Francisco Bay, were analyzed to determine temporal and geographic distribution of the tagged population. Virtual population analysis of the tag recovery data was used to derive fishing mortality rates, which in turn were used to obtain yield-per-recruit and stock replacement values, and to estimate the effect of management by size limit on stock replenishment and yield per recruit.

Of the tagged population, 11% was recovered by sport anglers and commercial fishermen, and the distribution of recoveries indicates that leopard sharks are mostly resident in San Francisco Bay, although a portion of the population moves out of the Bay during fall and winter. An unusually high number of recaptures was made in 1983, a year of El Niño conditions and high river run-off. After obtaining mortality, yield, and stock replacement values, it was proposed that a viable management strategy for the San Francisco Bay leopard shark would be a size limit of 100 cm or 40 inches to ensure maintenance of the stock and provide a yield per recruit not too far below a maximum.

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Leopard Shark *Triakis semifasciata* Distribution, Mortality Rate, Yield, and Stock Replenishment Estimates Based on a Tagging Study in San Francisco Bay

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Shark has now become a familiar item at seafood counters and on restaurant menus in the United States (Slosser 1987), while in the past these fish were often discarded as trash fish, or at best valued for fish meal or their vitamin A-rich livers (Frey 1971). California has seen the rise of four new commercial elasmobranch fisheries since the mid-1970s (Holts 1988), and recreational shark fishing has grown in popularity in California and in other coastal states (Ristori 1987). The relatively rapid increase in shark harvesting has created a pressing need for more biological information to support management of targeted species, particularly information relating to population structure, mortality and replenishment rates, and degree of exchange between stocks. Elasmobranchs may be particularly vulnerable to exploitation, because they are generally slow growing and produce relatively few young, with recruitment appearing to be largely determined by parental stock size (Holden 1977).

The leopard shark *Triakis semifasciata* is harvested both commercially and recreationally in California. It occurs along the coast from Baja California, Mexico, to Oregon, and is very common in northern California bays (Squire and Smith 1977, Eschmeyer et al. 1983). Its fairly large size (maximum recorded is 180 cm; Kato et al. 1967) and accessibility in nearshore areas and bays probably contribute to its appeal with anglers and small-scale commercial boat operators. Reported commercial landings in California since 1980 have ranged from 18,199 kg (40,085 lbs) in 1980 to 45,994 kg (101,309 lbs) landed in 1983 (Table 1), with the San Francisco area contributing a large portion of the catch. Recreational landings are comparatively larger, judging from estimates of landings compiled by the U.S. Department of Commerce Pacific Coast Marine Recreational Fishery Statistics Survey (Table 2). Recorded commercial landings of leopard sharks may be misleading, as leopard sharks are often lumped with other species under the general category "shark, unspecified." Because of this reporting bias, it is difficult to determine the full extent of the commercial harvest. Further, it should be noted that reliable data for stratifica-

Table 1
Reported commercial leopard shark landings (in kilos) by California port area. Source: Joyce Underhill, Calif. Dep. Fish Game, Long Beach, CA 90801, pers. commun., 17 May 1989.

Year	Eureka	San Francisco	Monterey	Santa Barbara	Los Angeles	San Diego	California total
1980	—	11 006	54	3 103	3 672	363	18 199
1981	94	12 334	55	5 505	3 482	1 913	23 384
1982	—	13 308	128	11 262	5 894	1 464	32 057
1983	—	33 764	202	7 218	2 632	2 177	45 994
1984	—	14 664	1 322	7 482	5 185	2 153	30 806
1985	24	8 054	7 620	8 135	8 725	1 871	34 430
1986	400	11 435	3 553	7 805	7 499	3 239	33 932
1987	741	6 684	3 523	6 357	6 113	1 720	25 138
1988*	1 263	2 367	2 038	5 161	3 728	4 357	18 914

*Preliminary.

Table 2
Reported commercial landings and estimates of the total marine recreational landings of leopard sharks in northern California, 1980–87. Recreational landings are Type A catches (observed landings) for north of San Luis Obispo County to the Oregon border, based on the Pacific Coast Marine Recreational Fishery Statistics Survey (provided by John F. Witzig, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv., Silver Spring, MD 20910, 14 June 1989). Commercial landings are summed for northern California ports.

	Northern California landings	
	Commercial	Recreational
Year	(kilos)	
1980	11 060	68 682
1981	12 484	62 664
1982	13 436	7 578
1983	33 966	116 517
1984	15 986	33 610
1985	15 698	131 787
1986	15 388	158 778
1987	10 948	289 097

tion of catch and effort by moderately small time or area segments are unavailable for either the recreational or commercial fisheries. The smallest divisions for the recreational fishery are northern and southern California. For the commercial fishery, only the place of landing and not the place of catch is recorded, and effort data are nonexistent.

Information on reproduction, stock replacement rates, and stock interaction is scanty and mostly undocumented. Estimates of length at maturity for males have ranged from 70 to 119 cm and for females from 100 to 129 cm; size at birth is about 20 cm (Ackerman 1971, Compagno 1984, Kusher 1987). The gestation period is estimated at 10–12 months and parturition takes place in spring, according to Ackerman (1971) who worked with Elkhorn Slough fish in Monterey County, California. Certain other observations corroborate this. Moser and Sakanari* examined an aggregate of pooled embryos from fish taken in the fall in San Francisco Bay and the measurements formed a unimodal distribution with little variation in embryo sizes among litters, which is the expected pattern for an annual reproductive cycle. More than one mode among litters would be observed for a gestation period of 2 or more years. In addition, R. Russo (East Bay Park Dist., Alameda, CA 94169, pers. commun., 27 March 1984), sampling in South San Francisco Bay, has noted a predominance of pregnant females with near-term pups mainly from March through June (April–May peak), indicating a once-a-year parturition in spring. Pupping could be annual and occur in alternate years, with a 'recuperative' year between, but then about half of the mature female population would be in a nonreproductive condition at any given time. Of the 90 females over 120 cm that Ackerman (1971) examined from Elkhorn Slough, 94% had embryos or fertilized eggs in at least one ovisac; and all females >110 cm total length (TL) collected by Kusher (1987) in Elkhorn Slough and Monterey Bay and San Francisco Bay showed signs of either pregnancy, recent birth, or embryo abortion. Therefore, we use the assumption of an annual reproductive cycle in later sections dealing with stock replacement by reproduction. The leopard shark is primarily a benthic feeder (Russo 1975, Talent

*Drs. M. Moser and J. Sakanari (Long Marine Lab., Univ. Calif., Santa Cruz, pers. commun., Sept. 1984) report that in a sample of nine pregnant females taken on 10 September 1984, presumably in midterm, the mean embryo length was 11.26 cm (1.51 SD), ($n = 51$ embryos).

1976). Prior to the work described here, nothing was known of its movements or the degree of exchange with other leopard shark populations along the California coast.

In 1979, a tagging study was initiated in San Francisco Bay to obtain information on age validation, growth, and movements of this species. Tag recaptures were monitored over a 9-year period. This report gives results of movements that were deduced from the temporal and geographic distribution of tag recoveries. In addition, although beyond the planned design of this study, we decided to utilize the tag recovery data together with published information to estimate the effect of management by size limit on stock replenishment and on yield per recruit. The lack of suitable statistical information on catches, as mentioned previously, prevented us from performing analyses that involve weighting tag recoveries by catch or effort. Results of the age validation segment of the study have been published elsewhere (Smith 1984), and results on age and growth are also being published separately (Kusher et al. In prep.).

Methods

All sharks were tagged off Hunters Point in south San Francisco Bay in 1979. Collections were made with a 183-m longline rigged with an average of 150 baited hooks fished on the bottom at depths of 15–20 m. Prior to release, total and precaudal lengths were recorded to the nearest centimeter, and each fish was given an intraperitoneal injection of oxytetracycline hydrochloride to mark vertebral centra for age verification purposes (Smith 1984). A record was made of the sex and general physical condition of each fish; seriously injured animals were not tagged. Those with minor hook injuries or with partially everted stomachs were classified as "injured"; the rest were classified as "healthy." A plastic rototag of the type recommended by Kato and Carvallo (1967) was applied to the first dorsal fin and the fish released at the capture point. The fin tags were imprinted with a legend informing the recoverer that a reward (amount unspecified) was offered for return of the tag and the fish or a section of its vertebral column for age verification purposes. The legend also provided an address and phone number to contact to arrange delivery.

Mortality estimation

Fishing mortality rates were estimated from the tagging data using the concept described by Murphy (1965), Gulland (1965), and Tomlinson (1970), which is now commonly referred to as virtual population analysis (VPA), though it differs from the original VPA procedure of Fry (1949). The computer program COHORT, written by John Geibel and Phil Law (Calif. Dep. Fish Game, 411 Burgess Drive, Menlo Park, CA 94025) was used to calculate the estimates. The natural mortality estimate was based on Hoenig's (1983) regression equation $\log(Z) = 1.46 - 1.01 \log(t_{max})$ where Z is the instantaneous annual total mortality coefficient and t_{max} is maximum age attained by the species. If the maximum age was determined from a period when there was virtually no fishing directed at the species, then one could assume the estimated Z approximates the instantaneous annual natural mortality coefficient, M.

The basic procedure involved assuming values of M over each 1-year time interval, taking a trial value of F_n, the instantaneous annual fishing mortality coefficient, for the ultimate interval, and executing the backward VPA computation on the tag recoveries to obtain an estimate of N_0, the number of tagged fish at the beginning of the first interval. Trial values were then iterated until the series converged on N_0.

Before conducting the VPA, it was necessary to consider two additional factors which would cause adjustments to the actual observations used in the analysis: (1) the likely rate of tag loss and (2) the level of tag recovery nonreporting. Since the tagging experiment was not designed for this type of analysis, there were no built-in procedures to estimate these factors. We therefore used what we judged to be the best available information from outside sources.

Yield per recruit

Yield per recruit was calculated by piecewise integration of the yield curve. The yield in weight at each age was taken to be the product of the annual rate of exploitation, the midpoint between an individual's weights at the beginning and end of the age interval, and the population size at the beginning of the interval.

$$Y = \exp[-M(t_{r'} + 1)]\,[1 - \exp(-Z)]\,(F/Z) \times \sum_{t \geq t_{r'}}^{t_{max}} \{\exp[-Z(t - t_{r'})]\}\bar{w}_t \tag{1}$$

where Y is yield per recruit in weight (kg), t is age, $t_{r'}$ is age at first capture, and $\bar{w}_t$ is the midpoint between the weights at t and $t+1$.

Weight at age was computed by using predicted values from the von Bertalanffy length equation from Kusher (1987) and the weight-length formula in Smith (1984). Note that equation (1) assumes constant M and Z except that natural mortality is doubled during

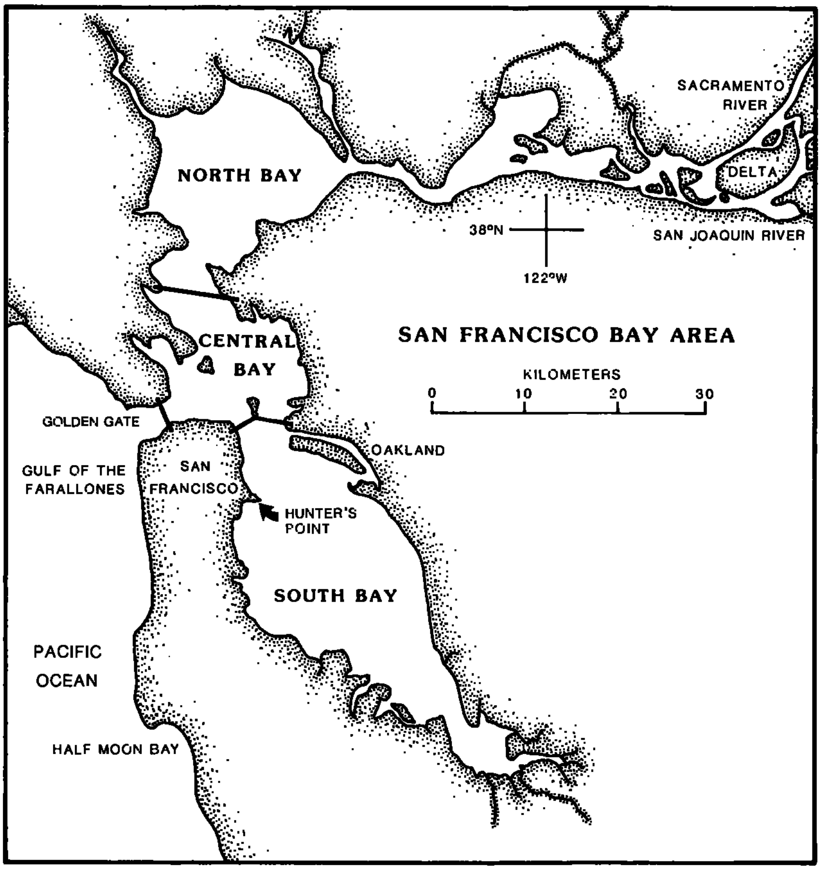

Figure 1
Map of San Francisco Bay showing location of release area (arrow) and major Bay Area divisions and names referred to in the text.

year 1. This gives some weight to a higher mortality these young fish must suffer relative to the adult sharks. The phenomenon of the young being preyed on by larger sharks has been cited by Springer (1960, 1967) and by Holden (1974).

Stock replacement

Also calculated for various levels of age at first capture (knife-edge selection) and fishing mortality were the percentages of stock which would be replaced due to reproduction. Assuming an even division among the sexes, this was done by summing over ages, from age at first maturity to maximum age, the products of the number of female survivors per recruit and the number of pups produced by females at each age above the age of maturity and multiplying this sum by 100. For given $t_{r'}$ and F

$$R = \sum_{t \geq t_m} 50 \exp[-M(t+1) - F(t - t_{r'})\,\delta]\,P_t \qquad (2)$$

where t_m is female age at maturity, R is stock replacement per recruit in percent, P_t is estimated number of progeny produced annually by an age t female, and

$$\delta = \begin{cases} 1 & t > t_{r'} \\ 0 & t \leq t_{r'} \end{cases} \qquad (3)$$

Fecundity as a function of maternal body weight was estimated by fitting a monomolecular curve of the form $P_t = \beta - \theta\rho^{w(t)}$, with P the number of progeny, $w(t)$ the weight of the female at age t, and β, θ, and ρ constants. For computation, age at maturity was taken as the age corresponding to the weight which produced a value of zero for P_t in the above equation.

Ackerman (1971, his table 6) gives the numbers of embryos observed in 66 female leopard sharks ranging in size from 9.3 to 16.3 kg. Although his data are in a form which allows only the computation of mean number of embryos per female for five weight classes, he does give the number of females observed in each weight category. Using the numbers of females as weighting factors, the curve was fitted to these means with the Levenberg-Marquardt algorithm as implemented in the NCSS nonlinear regression program*.

*Number Cruncher Statistical System, Version 5.3–Power Pack, 1988. NCSS, Kaysville, UT 84037. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Progeny as a function of maternal age was then estimated by applying the weight-length-age relationships cited above. We assume all nondeformed embryos survive to time of birth. Data were not available for applying the preferable procedure of directly regressing fecundity on age.

Geographical names and location of the tagged-fish release area are given in Figure 1.

Results

Tagging

A total of 948 sharks were tagged off Hunters Point, San Francisco, in south San Francisco Bay between 26 July and 13 September 1979. Most were tagged in August (68%) and September (26%). The hook rate was very high: 22 *Triakis* per 100 hooks, and a 44% hook rate for all elasmobranchs. Other sharks and rays taken in order of abundance were brown smoothhound *Mustelus henlei* ($n = 872$), bat ray *Myliobatis californica* ($n = 159$), soupfin shark *Galeorhinus galeus* ($n = 6$), sevengill shark *Notorhynchus cepedianus* ($n = 5$), and spiny dogfish *Squalus acanthias* ($n = 2$).

The lengths of tagged leopard sharks ranged from 51 to 144 cm TL (mean 81 cm, Fig. 2). The male:female ratio was 53:47. Large individuals may have been underrepresented in the tagging, since only 9% of females and 11% of males were over 100 cm. Commercial fishermen have reported a higher proportion of large fish in their catches, fishing at the same time with similar gear but in different areas of the south bay (B. Van Gorp and B. Fraser, commercial shark fishermen, pers. commun., June 1980). On the other hand, leopard sharks were probably recruited to our gear at a larger size than would be true for typical sportfishing tackle. Anglers fishing from shore and piers using small hooks would surely take a higher percentage of fish under 70 cm than that shown in Figure 2.

Of the 948 fish tagged, 82 individuals were classified as "injured" and the remaining 866 fish as "healthy." Return rates would presumably be higher for healthy, uninjured fish than for injured fish if the tagging operation caused mortalities; the absence of such a difference could be taken as suggestive of little or no tagging-induced mortality (Gulland 1983).

Recoveries

As of 30 September 1988, 108 fish had been recaptured of which 101 had known recapture date and location. A breakdown of all methods of recapture is given in Table 3, and provides an interesting glimpse of the various users of the leopard shark resource. The proportions reported by each group should approximate the proportions of the natural population harvested or caught by each group.

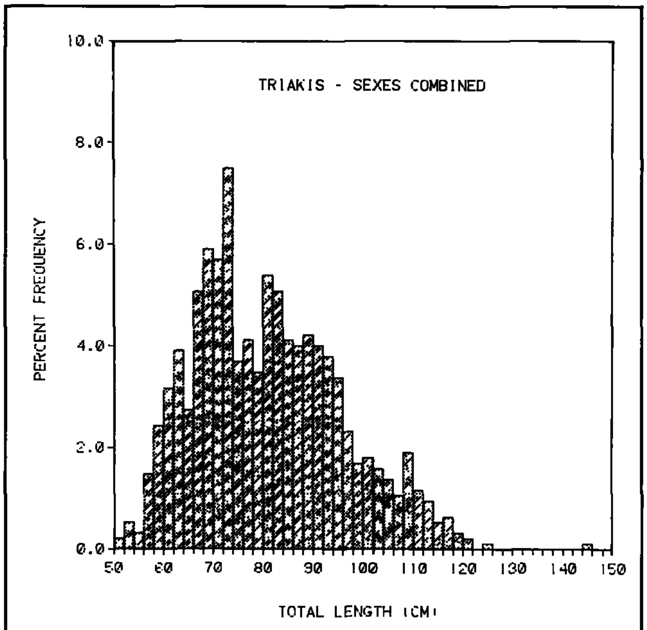

Figure 2
Length frequency of tagged leopard sharks (sexes combined) released off Hunter's Point in south San Francisco Bay, California, 1979.

Table 3
Distribution of leopard shark tag recaptures by recovery method and area in and around San Francisco Bay, California, 1979–88.

Method of recapture	Area of recapture: South bay	Central & north bays	Outside bay/ ocean	Totals
Recreational				
Private boat/skiff	32	15	1	48
Sportfishing boat (commercially operated)	0	4	0	4
Bank	13	3	2	18
Pier	10	6	0	16
Jetty	0	1	0	1
Bridge	1	0	0	1
Total	56	29	3	88
Commercial				
Bottom trawl	0	0	5	5
Gillnet	0	0	4	4
Longline	4	0	0	4
Total	4	0	9	13
Total all methods	60	29	12	101

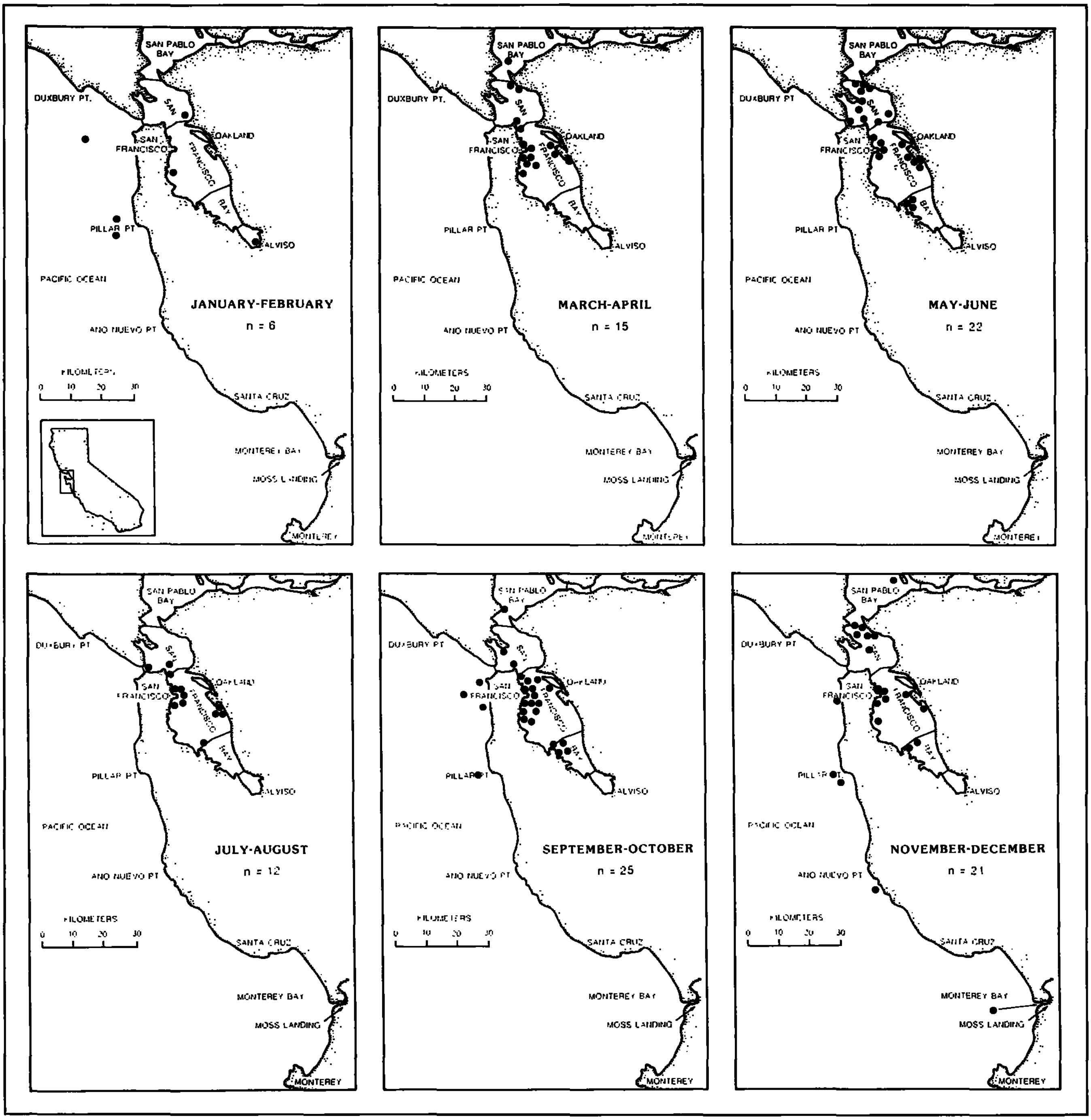

Figure 3
Bimonthly distribution of leopard shark recoveries in and around San Francisco Bay, California, 1979–88, for which recapture location and date were known.

Of the recoveries, 81.5% were reported by sport anglers, 12.0% by commercial fishermen, and 6.5% of the fish were found on shore or had an unknown recapture method. Those recovered by recreational anglers were rather evenly divided between shore and boat anglers, with skiff fishermen dominating the latter category. The important role of recreational anglers in the recovery of tagged fish appears to reemphasize the predominance of recreational users of the leopard shark resource.

Over the 9-year period, most fish were recaptured during the months of September (20%) and June (13%);

the fewest were returned in February (2%), January (4%), and July (5%). The return rate for 'healthy' fish was 9.9% and that of 'injured' fish, 15.8%. Clearly, there is no indication that handling during the tagging process induced excess tagging mortality. The sex ratio of recaptured fish was exactly the same as at tagging (53% males) indicating little if any selective mortality with regard to sex.

Movements

Bimonthly distribution patterns were plotted using recapture information from 101 recoveries made during 1979–88, for which recapture location and date were known (Fig. 3). From about March through August recoveries were restricted to the bay, while from September through February a marked pattern of dispersal occurred within and outside of the bay. One shark traveled as far as Elkhorn Slough near Monterey, about 140 km south of the entrance to San Francisco Bay.

To discern year-to-year differences in the temporal and general geographic pattern, Table 4 shows recoveries by year and recapture area (south San Francisco Bay, central and north bays, ocean/outside bay). The year 1983 was unique in that the greatest number of recoveries in any one year was made that year (22 fish, plus 2 fish recovered dead). It was also the only year that ocean recoveries were made as early as September, and the only year when an unusual number of recoveries (6 fish) was made in the central bay in June. (During the 9-year study period, there was only one other instance, in 1981, of a fish being taken in the central bay in June.)

No distribution pattern appeared to be correlated with fish size or sex, but due to the small sample size, the results do not preclude the possibility that the pattern may vary with sexual maturity or age. The sex ratio of fish taken in the ocean was normal (1:1); however, one commercial fisherman, who caught 3 of the 12 tagged fish taken in the ocean, reported that all 3 were gillnetted from the same depression on the sea floor in Half Moon Bay (one taken 13 Nov. 82, the other two taken in 1986 on 20 Oct. and 17 Nov.), and all 3 were large females with developing embryos.

Mortality rates and virtual population analysis

The oldest ages reported for this species are 24 years for a male of approximately 135 cm in length and 20 years for a 130-cm female (Kusher 1987, fig. 8). However, we arbitrarily decided to use a maximum age of 30 years in Hoenig's (1983) regression equation since there are records of fish larger (180 cm; Kato et al. 1967) than those that were aged; we also noted that

Table 4

Distribution of leopard shark tag recaptures in and around San Francisco Bay, California, by year and area of recapture for which date and recovery area are known.

Calendar year of recapture	Area of recapture: South bay	Central & north bays	Outside bay/ ocean	Totals
1979	10	2	1	13
1980	8	9	0	17
1981	11	1	1	13
1982	5	4	3	12
1983	9	9	4	22
1984	9	2	0	11
1985	2	2	0	4
1986	1	0	3	4
1987	2	0	0	2
1988	3	0	0	3
Total	60	29	12	101

the largest female aged by Kusher (140 cm) was, at 18 years, not the oldest. Because the largest fish cited above was taken prior to the time when there was more than nominal fishing directed at this species, we feel that M may be assumed approximately equal to the Z from Hoenig's regression equation. The result of taking $t_{max} = 30$ in the equation was an estimated M of 0.14.

While we have no explicit estimate of a tag-shedding rate from this experiment, the results of Kato and Carvallo (1967) from multiple tagging of sharks at the Revillagigedo Islands, Mexico, indicated a minimal annual shedding rate of 0.095. We have taken this value, converted it to an annual instantaneous loss rate of 0.10, and added it to the previously estimated 0.14 to obtain $X = M + 0.1 = 0.24$ for use in lieu of natural mortality in the VPA. We assume, and believe it reasonable given the apparent hardiness of the animals and toughness of their skin, that there was no instantaneous (type I) tag shedding.

With regard to the percent of tag recoveries reported to us, we again have no "built-in" estimate, but the California Department of Fish and Game has conducted extensive studies on the return rates for various reward levels associated with tagged striped bass in the same general area that the leopard shark tagging occurred (Stevens et al. 1985). Based on their experience (D. Kohlhorst, Calif. Dep. Fish Game, Stockton, CA 95205, pers. commun., Nov. 1988), it seemed that a 50% reporting rate would be the best value to use as an adjustment for tag recoveries in this case. To utilize this adjustment in the VPA, we use half the actual number of tag releases as the target for convergence.

Table 5
Leopard shark tag recoveries in and around San Francisco Bay, California, including natural mortality (M), estimated fishing mortality (F), and rate of exploitation (E), by post-tagging annual time intervals.

Time interval	Recovery period	Tags recovered	Assumed $M+0.1$	F	E
1	10/1/79–9/30/80	25	0.24	0.061	0.055
2	10/1/80–9/30/81	18	0.24	0.059	0.054
3	10/1/81–9/30/82	12	0.24	0.053	0.048
4	10/1/82–9/30/83	26	0.24	0.163	0.141
5	10/1/83–9/30/84	13	0.24	0.119	0.105
6	10/1/84–9/30/85	3	0.24	0.038	0.035
7	10/1/85–9/30/86	3	0.24	0.050	0.046
8	10/1/86–9/30/87	5	0.24	0.116	0.103
9	10/1/87–9/30/88	3	0.24	0.099	0.088
	Total	108		$\bar{F}=0.084$	

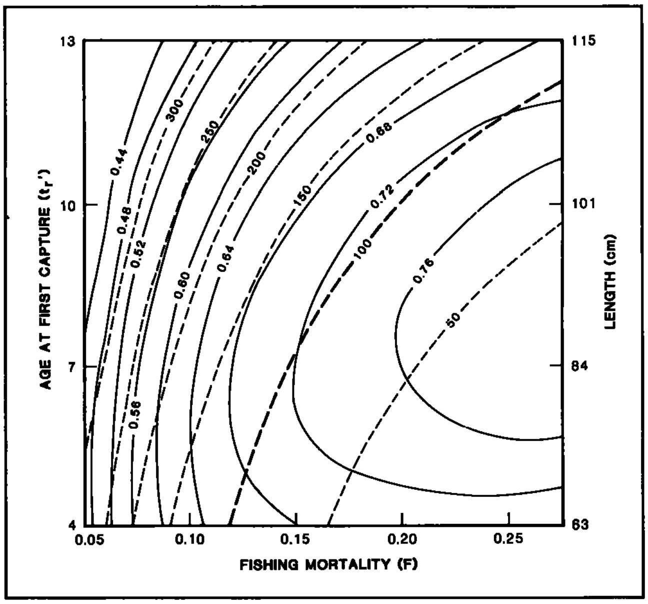

Figure 4
Isopleths showing percent population replacement of leopard sharks tagged in San Francisco Bay, California, in numbers (dashed lines) and yield per recruit in kilograms (solid lines), for $M=0.28$ during the first year of life and 0.14 thereafter.

Tag recoveries by yearly intervals after the release period, estimated annual instantaneous fishing and natural mortality coefficients, and rates of exploitation are shown in Table 5. Note that these are all of the tag recoveries which could be assigned to the time intervals; other tabulations of recoveries in this paper may differ because of various missing information components.

Yield and stock replacement per recruit

Shown in Figure 4 is the yield-per-recruit isopleth diagram for $M=0.28$ during the first year of life and 0.14 thereafter. Age at first capture ranges from 4 to 13 years, and F runs from 0.05 to 0.28. The graph indicates a fairly flat yield contour between $F=0.15$ and $F=0.28$, with age at first capture between 5 and 10 years.

Also in Figure 4 are isopleths showing percent population replacement per recruit over the same parameters used for the yield computations. For use in calculating population replacement, the fitted curve (Fig. 5) relating Ackerman's data on number of embryos to parental weight was

$$P_t = 22.64 - (7592)\,(0.4208)^{w(t)},$$

where P_t is number of embryos, $w(t)$ is maternal weight (kg) at age t, and the standard error of estimate equals 0.38313. The value for $w(t)$ was obtained from

$$w(t) = 0.00000305 \times \{172.4[1-\exp(-0.0717[t+2.302])]\}^{3.05}.$$

Replacement increases steadily as F tends toward 0 and age at first capture increases (equation 2). The shape of this surface is not unexpected, but clearly some type of density-related compensation would be needed to increase mortality or reduce fecundity as the population increases; otherwise in the absence of fishing the sea would be filled with leopard sharks. This mechanism might be in the form of higher juvenile mortality, less frequent litter bearing, or reduced average litter size. Holden (1973, 1977) discusses some possible mechanisms of this type and cites examples from the literature of marine mammals and elasmobranchs. We do not have information to examine any of these possibilities in the present case.

Discussion

If it is assumed that the tagged population approximates the real population, these results suggest that San Francisco Bay leopard sharks are mostly resident, with some moving out of the bay during fall and winter. Judging from the single Moss Landing recovery, limited population exchange evidently occurs between Elkhorn Slough and San Francisco Bay leopard sharks. Also, previously undocumented evidence was received during the course of this study from L. Talent (Oklahoma State Univ., Stillwater, OK 74078, pers. commun., July

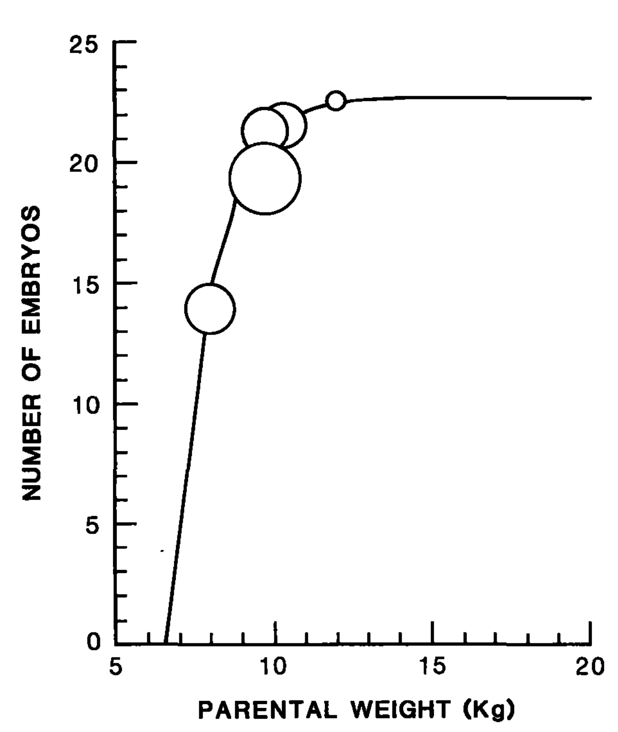

Figure 5
Fitted monomolecular curve relating mean number of leopard shark embryos in litters to parental weight. Areas of symbols are proportional to weighting factors of points used in the fitting process.

1982), who reported that a leopard shark tagged by him in December 1971 in Elkhorn Slough, Moss Landing, California, was recaptured February 1973 in south San Francisco Bay.

It is not known to what extent fishing effort influenced the recapture pattern, because effort information on the commercial and recreational catch is not available to the degree of geographic precision needed for such an analysis. We do know that leopard sharks are susceptible to bottom fishing gear, whether it be baited hook, gillnet, or, to a lesser extent, bottom trawl. Judging from the available data on recreational and commercial landings, and the much greater proportion of recreational versus commercial tag recaptures, recreational anglers are the primary users of the leopard shark resource in northern California. Angling for bottom fishes takes place in most areas inside the bay system year-round (Squire and Smith 1977), although in winter, inclement weather may lower fishing effort within the bay as well as along the open coast. Bottom-fishing effort in the ocean is thought to be comparatively less than in the Bay at least in waters shallower than 91 meters, the reported depth range of this species.

The 1983 peak in the tagged fish recovery rate and the associated rise in fishing mortality that we calculated (Tables 4 and 5) was unexpected. We have no evidence that fishing effort increased that year to cause this jump in the tag return rate, but there was a substantial rise in the California commercial catch of leopard shark that year, primarily driven by an increase in San Francisco landings (Table 1). There was also a similar rise in the estimated recreational catch (Table 2). The year 1983 was also one of unusual oceanographic conditions, when warm, nutrient-poor El Niño water intruded along the central California coast (McClain 1983, Norton et al. 1985). These El Niño conditions may have caused an influx of sharks from more southerly populations, but the increased rate of recovery for San Francisco Bay tagged fish should be independent of immigration of fish from other areas.

The California Department of Fish and Game (1987) and Pearson (1989), conducting trawl surveys of San Francisco Bay fishes, have observed higher trawl catches of leopard sharks during wet as opposed to dry years, and 1983 was indeed a wet year. That year the bay system experienced the highest delta outflows from the Sacramento-San Joaquin River systems in over 10 years, and June freshwater outflows were twice that of the previous wet year of 1982 and six times the previous decade's average outflow for that month (Calif. Dep. Water Resour., DAYFLOW Prog. Summ., Sacramento, CA 95816, Sept. 1987). Perhaps the anomalous conditions affected the local distribution and availability of central California leopard sharks and possibly their benthic prey, making the sharks more vulnerable to centers of fishing pressure.

In estimating the mortality, yield, and stock-replacement values, it was neccessary to make many assumptions and adjustments. Clearly we must assume that the tagged fish rapidly mix with the balance of a relatively closed San Francisco Bay population, and that tagged and untagged animals are equally likely to be caught. But because of the paucity of this type of information on these animals, an apparent high susceptibility of elasmobranch stocks to fishing pressure, and the noticeable increase in fisheries targeting on sharks, we felt it appropriate to present our best estimates based on the available data and current knowledge of elasmobranch biology.

In the case of the leopard shark, high stock maintenance is surely more important than a large yield per recruit. And while there is obviously something wrong with the stock replacement values which exceed 100% on an equilibrium basis, we would like to accept the 100% isopleth as reasonably valid. Noting in Table 5 that estimated F's ranged from 0.038 to 0.163 with a mean of 0.084, and observing in Figure 4 that the 100% replacement isopleth runs well to the right of the

0.68-kg isopleth over the higher observed levels of fishing mortality, it appears that management for full stock replacement would not involve a very great loss of yield per recruit. In fact, assuming an F of 0.2 and an age of first capture of 10 years, which equates to a 100-cm (40-inch) size limit, yield per recruit is less than 10% below the maximum shown in Figure 4. And given any F between the mean estimated value of 0.084 and the maximum estimate of F, the yield with the 100-cm size limit is within 10% of the maximum for that F.

However, in terms of numbers caught per recruit there is a substantial decline as the size limit increases. At $F = 0.2$, numbers per recruit values are 0.126, 0.192, and 0.292 for size limits of 100, 84, and 63 cm respectively; corresponding mean weights of fish comprising the retained catch are 5.8, 4.0, and 2.4 kg. All of these estimates assume that mortalities due to hooking and releasing undersized fish are negligible.

Based on the above information, a viable management strategy for the leopard shark would appear to be a size limit of 40 inches (100 cm). Although this size limit results in a 34% decline in numbers caught compared with a 33-inch (84 cm) limit, the fish which can be kept are almost 50% larger. Further, stock replacement is at the 100% level as compared with only 55% at the smaller size limit.

We stress, however, that our mortality and fecundity estimates were based on data from studies in only one area within the animal's geographic range, and the extent to which these can be extrapolated to the entire coastal population is not known.

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