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The Physiological Ecology of Bat Rays, Myliobatis californica, in Tomales Bay, California

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The physiological ecology of bat rays, *Myliobatis californica*, in Tomales Bay, California

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University of California, Davis, 1993

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The Physiological Ecology of Bat Rays, *Myliobatis californica*, in Tomales Bay, California.

By

TODD EVAN HOPKINS
B.S. (University of California, Berkeley) 1985
M.A. (California State University, San Francisco) 1988

DISSERTATION

Submitted in partial satisfaction of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

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of the

UNIVERSITY OF CALIFORNIA

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Approved:

Mark R. Pattison

Committee in Charge

1993

DEDICATION

This dissertation is dedicated to my wife Lori,
who gives my life the balance it so often needs
and who gave me the time, encouragement, criticism,
and enthusiasm that I needed to finish my degree.
My deepest thanks to Dr. Joseph J. Cech, Jr.,
for his infinite encouragement and support,
and for allowing me to do it my way,
even when it wasn't always
the right way.

To Barbara Nichols,
who convinced me not to jump ship
in my darkest hour.

TABLE OF CONTENTS

Todd Evan Hopkins
March 1993
Ecology

The Physiological Ecology of Bat Rays, *Myliobatis californica*, in Tomales Bay, California.

ABSTRACT

I tested the hypothesis that temperature, salinity, and dissolved oxygen influence the distribution and abundance of elasmobranchs (sharks, skates, and rays) in Tomales Bay, California. I captured elasmobranchs monthly (September 1990-April 1992) on longlines set in the bay. A Poisson regression under generalized least squares was used to determine that temperature and salinity were the most important factors determining the distribution and abundance of the three most commonly captured species; bat ray, *Myliobatis californica*, leopard shark, *Triakis semifasciata*, and brown smoothhound shark, *Mustelis henlei*. Females of all three species were more abundant than males throughout the bay, and were most abundant in the warmer more saline inner bay. All three species left Tomales Bay in late fall as water temperatures in the bay dropped below 10-12°C, and returned in early spring after temperatures rose above 10°C.

The oxygen consumption of bat rays, *Myliobatis californica*, was determined at 8, 14, 20, and 26°C. Mean, standard, mass-independent metabolic rates (MO_2 in mg $O_2 \bullet kg^{-0.67} \bullet h^{-1}$) of unacclimated rays at each temperature were significantly different from one another. MO_2 was extremely temperature sensitive from 20-26°C ($Q_{10} = 6.62$), and moderately

sensitive at the upper (20-26°C: Q_{10} = 1.85) and lower (8-14°C: Q_{10} = 2.23) temperature ranges.

The effects of four temperatures (8, 14, 20, 26°C) on blood oxygen equilibrium curves of the bat ray, Myliobatis californica, was investigated. Blood oxygen equilibrium curves at all temperatures were hyperbolic ($n_{50} < 2$), with high affinity (low P_{50}), large Bohr factors (Ø = -0.45 to -0.52), high blood oxygen carrying capacity (CBO_2 = 6.8 to 9.06), and very large non-bicarbonate buffering capacity (ß = -14.25 to -16.43). CBO_2, Ø, and ß are among the largest measured in a poikilothermic elasmobranch. Affinity decreased with increasing temperature except at 26°C. The affinity shift at 26°C and a concomitant 25% drop in CBO_2 at this temperature suggests a hemoglobin heterogeneity. Blood oxygen equilibrium curves were temperature insensitive between 8-14°C and 20-26°C and most sensitive between 14-20°C, the temperature range in which bat rays are most commonly found in Tomales Bay. Bat rays appear capable of tolerating anoxia and hypercapnia (low P_{50}, n_{50}, and high ß), and sustaining high activity levels (high CBO_2, Ø, and ß) by virtue of their unique hematological characteristics.

Introduction.

Elasmobranchs are fundamentally different from teleosts in their life history, behavior, and physiology (Hoenig and Gruber 1990, Pratt and Casey 1990, Nelson 1990). They are slow growing, late maturing, have long gestation periods, produce few young, and attain a large body size (Hoenig and Gruber 1990). While less abundant in most systems than teleosts, they forage near the top of the food chain (Compagno 1990) and may account for a significant portion of the total biomass in a system (e.g Horn 1980, Recksiek and McCleave 1973). In addition, they may segregate by sex and by size on both local and regional scales (Pratt 1979, Castro 1983). Many species use bays and estuaries for part of the year and depart during the winter months (Steven 1932, Bearden 1959, Jensen 1965, Struhsaker 1969, Sage et al. 1972, Snelson and Williams 1981, van der Elst 1981, Smith and Merriner 1987, Rousset 1990). Previous studies on elasmobranchs have shown that temperature and salinity play a role in their distribution (Smith and Merriner 1987, Struhsaker 1969, Funicelli 1975, Sage 1972, Bearden 1959, Snelson et al. 1988, Snelson et al. 1989, Rousset 1990) but the effects of these environmental factors has not been quantified.

From a physiological standpoint, temperature, salinity, and dissolved oxygen should, alone or in concert, influence the distribution of elasmobranchs. The majority of nearshore elasmobranchs are ectothermic and changes in the environmental temperature are rapidly transferred to the body of the animal where nearly every physiological process is affected (Prosser and Heath 1991). Furthermore, elasmobranchs use various end products of nitrogen metabolism as osmotically active solutes to maintain themselves hyperosmotic to their environment (reviewed by Perlman and

Goldstein 1988), but they are unable to maintain this balance in the face of decreased salinities (reviewed by Pang et al. 1977). Thus, their physiological niche (Spotila et al. 1989) is constrained along these axes. Finally, seasonal or diel dissolved oxygen depressions (hypoxia) are common in shallow bays and estuaries (Loesch 1960, Taft et al. 1980, Day et al. 1989) and constitute an important physical disturbance to aquatic communities (Coutant 1985, Kennedy 1990, Breitburg 1992). Unfortunately, hypoxia adaptations in elasmobranchs are complex and can be altered over several time scales (e.g. hours, days, months; Jensen 1991) so that no clear patterns exist (Johansen and Weber 1976, Butler and Metcalf 1988).

The bat ray, *Myliobatis californica*, is a large, common, benthic predator which forages in shallow mudflats and seagrass beds in bays and estuaries from southern Oregon to the Gulf of California (MacGintie 1935, Talent 1985, Ferguson and Cailliet 1990, Love 1991). Rays are active swimmers (Dubsky 1974, McEachran 1990) and are found in large numbers from April through November in Tomales Bay, California (Ridge 1963, Love 1991) when the temperatures in the bay range from 10°C at the mouth to 26°C in the slightly hypersaline mudflats of the inner bay (Smith et al. 1991)

Tomales Bay is a 20 km long straight basin which averages 1.4 km in width and 3 m in depth formed by the intersection of the San Andreas fault with the northern California coastline (Hollibaugh et al. 1988). The bay watershed covers about 570 km^2 and is almost entirely rural, with a population of about 10,000 persons and 20,000 cows (Smith et al. 1991). The bay is hydrographically simple and has been divided into two parts based on chemical and physical characteristics (Hollibaugh et al. 1988, Smith et al 1991). The outer bay (12 km^2) is mostly fine sand and has 6 km^2 of dense seagrass beds. The inner bay (16 km^2) has extensive intertidal and shallow subtidal mudflats covered with macroaglae and 1 km^2 of seagrass beds (Ridge 1963, Spratt 1989)(Figure 1). Longitudinal gradients of hydrographic variables are large relative to lateral and vertical gradients, and vertical stratification is weak and episodic (Smith et al. 1991). Exchange of water between the inner and outer bay during summer is near zero, and the inner bay tends to be 2-6^{o}C warmer and 1-3 ppt more saline than the outer bay at this time of year (Ridge 1963, Smith et al. 1991). Mixing is greatest in winter due to increased runoff and the inner/outer bay temperature gradient disappears. Inner bay salinity is largely a function of runoff from Lagunitas Creek, while Walker Creek has little impact on the salinity of the outer bay.

The simple hydrography of Tomales Bay, and the abundance of bat rays found in this bay allowed me to combine field and laboratory work to examine hypotheses about effects of temperature on bat ray metabolism (chapter 1) and blood-oxygen binding (chapter 2) and to study the importance of temperature, salinity, and dissolved oxygen on their distribution and abundance in the bay (chapter 3).

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The Effect of Temperature on Oxygen Consumption of the Bat Ray, Myliobatis californica.

Abstract.

The oxygen consumption of bat rays, Myliobatis californica, from Tomales Bay, California was determined at 8, 14, 20, and 26°C. Mean, standard, mass-independent metabolic rates (MO_2 in mg $O_2 \bullet kg^{-0.67} \bullet h^{-1}$) of unacclimated rays at each temperature were significantly different ($p < 0.05$) from one another. MO_2 was extremely temperature sensitive from 20-26°C ($Q_{10} = 6.62$), and moderately sensitive at the upper (20-26°C: $Q_{10} = 1.85$) and lower (8-14°C: $Q_{10} = 2.23$) temperature ranges.

Tomales Bay is a long shallow bay divided into a warm, slightly hypersaline inner bay with extensive intertidal and subtidal mudflats, and a colder more oceanically influenced outer bay which contains mostly fine sand substrate and dense seagrass beds. Our MO_2 data, coupled with preliminary data from an ultrasonic tracking study, suggests that bat rays may behaviorally thermoregulate; foraging in the warm prey-rich inner bay, and using the cooler outer bay as a thermal refuge.

The bat ray, Myliobatis californica, is a common inhabitant of bays and estuaries from Oregon to the Gulf of California (Love 1991). Rays are active swimmers (Dubsky 1974, McEachran 1990) and are found in large numbers from April through November in Tomales Bay, California (Ridge 1963, Love 1991) when the temperatures in the bay range from 10°C at the mouth to 26°C in the slightly hypersaline mudflats of the inner bay (Smith et al. 1991, Hopkins personal observation). Telemetered bat rays have been tracked moving between the inner and outer bay, traversing temperature differences of 4.5°C over a period of several hours (Hopkins unpubl.).

Behavioral thermoregulation in fishes is widespread (reviewed by Reynolds and Casterlin 1979, Noakes and Baylis 1990) and the seasonal onshore and offshore movements of many skates and rays are well documented (Gunter 1945, Bearden 1959, Struhsaker 1969, Sage et al. 1972, Talent 1985, Smith and Merriner 1987, Snelson et al. 1988, Yoklavich et al 1991). Virtually all nearshore elasmobranchs, like the bat ray, are ectothermic. For most aquatic ectotherms, metabolic rate, and therefore oxygen demand varies directly with environmental temperature (Schmidt-Nielsen 1983). Respiratory metabolism (oxygen consumption) is a sensitive, non-invasive indicator of overall physiological status which can be used to quantify how rapidly oxygen and energy are used (Cech 1990). Increased oxygen consumption is equated with an elevated cost of homeostasis (Fry 1974, Schreck 1990). Because our field data indicated that bat rays may be responding to environmental temperatures we wished to quantify the respiratory metabolism sensitivity of unacclimated bat rays to a range of temperatures (e.g. 8, 14, 20, and 26°C) characteristic of their habitats in Tomales Bay in order to better understand the potential energetic cost to the rays of inhabiting various thermal environments.

Materials and Methods.

Fish Collection and Holding. - Rays were captured by beach seine in Tomales Bay (15°C and 33 ppt) and transported to the University of California, Bodega Marine Laboratory. They were kept without food in an outdoor, shaded, circular 8,000 L tank, with flowing seawater (14 ±1°C and 33 ±1 ppt) for 5 days. Experimental animals ranged in disc width from 65-75 cm (mean 72.2), and mean live body mass was 5.042 kg (range 4.326-6.814).

Respirometry. - The oxygen consumption of rays was determined by flow-through respirometry (Cech 1990) using a system of solenoids controlled by a sprinkler timer (Toro EL-12+) which sequentially shunted part of the outflowing water from a single respirometer or from an inflow line, for 17 min every 2 hr, past a Nester oxygen electrode (model 617034), which was connected to a Nester oxygen meter (model 8500). The oxygen meter output was plotted on a Soltec 310 chart recorder. Flow rates were measured by timed collection of water from the total outflow of a respirometer. Oxygen content of the outflowing water was never allowed to drop below 70% of saturation.

Six rays were placed into 65 L ray-shaped plexiglass respirometers which were 90% submerged on a large water table (2.4 m wide x 4.6 m long x 38cm high). The tops of the respirometers were covered with black plastic and the room lights were kept off so that only indirect light (natural photoperiod) entered the room. We used a sequential temperature design wherein rays were placed into the respirometers and allowed to acclimate for 12 h. Then the temperature was altered by 0.5°C/h for 6 h until it reached the new experimental temperature, the fish were again allowed to adjust for 12 h, and their oxygen consumption recorded for 12 h. Then the cycle of temperature change, adjustment, and oxygen consumption recording was repeated. Thus, once rays were put into the respirometers their oxygen consumption was measured in the following temperature sequence: 14, 8, 14, 20, and 26°C. Experimental temperatures were maintained within ±0.3°C.

An electronic temperature relay controlled the addition of warm (28°C) or cold (6°C) aerated seawater (33 ppt) to a continuous flow (60-80 L/h) of ambient 14°C seawater in a central 250 L mixing tank. Water from the mixing tank was pumped into a second 250 L tank and then up to an insulated 40 L cooler, with an overflow standpipe, suspended 1.5 m above the water table to provide a constant pressure head for flow to the respirometers. Water quality was maintained by the continuous seawater flow and by two filters in the second mixing tank with cartridges which removed particles > 25 µm and were changed twice daily. During the temperature changes the water table was siphoned of any particulate matter which had accumulated.

Standard metabolism (Fry 1974) was determined from the mean of the two lowest MO_2 values recorded over the 12 h measurement period (2000 to 0800 hr). Standard mass-independent metabolism (Heusner 1984, 1985) or MO_2 in mg $O_2 \bullet kg^{-0.67} \bullet h^{-1}$ was calculated from:

$$MO_2 = (O_2in - O_2out) \bullet (VW \bullet 60) \bullet (M_{-0.67}), \text{ where:}$$

O_2in = inflowing water $[O_2]$ in mg/L

O_2out = outflowing water $[O_2]$ in mg/L

VW = water flow in L/min

Mb = live body mass of fish in kg.

Standard MO_2 at the experimental temperatures were compared using a repeated measures analysis with Bonferroni post-hoc tests. Standard MO_2 at the 14°C(initial) was compared to that at 14°C(experimental) using a paired t-test. All statistics were performed using PC-SAS version 6.04. Q_{10}, a measure of temperature sensitivity, was calculated as specified in Schmidt-Nielsen (1983).

Results.

Standard, mass-independent MO_2 of bat rays increased with increasing temperature (Figure 1), and all means were significantly different from one another (all $p < 0.05$) with the exception of the 14°C(initial) and 14°C(experimental) values (t-test, $p > 0.88$). Thus, the experimental protocol (14°C to 8°C to 14°C) had no significant effect on standard MO_2 within this temperature range. Q_{10} analysis showed that MO_2 sensitivity was greatest between 14°C and 20°C ($Q_{10} = 6.52$) and moderate at the upper (20-26°C:$Q_{10} = 1.85$) and lower temperatures (8-14°C:$Q_{10} = 2.23$). The overall Q_{10}(8-26°C) was 3.00.

Discussion.

Bat ray oxygen consumption increased with increasing temperature (Figure 1), although the magnitude of the increase between 14°C and 20°C ($Q_{10} = 6.81$) was surprising because bat rays are most abundant in Tomales Bay from April to October when the temperatures in the bay are in this range (Ridge 1963, Love 1991, Smith et al. 1991). Temperature sensitivity for 8-14°C (Q_{10} = 2.23) and 20-26°C (Q_{10} = 1.85) ranges were similar to that seen in other fishes, that is, near 2.0 (Cameron 1989).

Few studies have measured skate or ray oxygen consumption at more than one temperature, and we found none which had used unacclimated fish. Du Preez et al. (1988) studied the effects of temperature on the oxygen consumption of bullrays, Myliobatis aquila, acclimated to 10, 15, 20, and 25°C, using a similar semi-automated respirometry system (Marais et al. 1976). They found a less temperature dependent response (Figure 1); increasing temperature increased MO_2 with the overall Q_{10} (10-25°C) = 1.87

(Du Preez et al. 1988). Bullray MO2 at 10 and 15°C was close to that of bat rays at 8 and 14°C, however, bullray MO_2 increased slowly with a continued increase in temperature (15-20°C:Q_{10} = 1.36, 20-25°C:Q_{10} = 2.54).

Several studies have shown that acclimation results in a metabolic compensation which yields smaller MO_2 differences between temperatures and thus lower Q_{10} values (see reviews by Fry 1974, Hochachka and Somero 1974, Johnston and Dunn 1987, Burggren and Roberts 1991). We used unacclimated rays to determine the effects of the relatively abrupt temperature changes observed in the field on the bat rays' standard MO_2. In contrast, Du Preez et al. (1988) acclimated bullrays by altering temperature 1°C/24 h and holding the fish at the desired temperature for 8 days prior to oxygen consumption measurements. Both bat rays and bullrays are specialized for active swimming (McEachran 1990), seasonally common nearshore, and forage for benthic invertebrates in shallow bays and estuaries (Ridge 1963, van der Elst 1981, Love 1991) where they are likely to experience large temperature fluctuations. Because the autecology of these rays is very similar the differences in their MO_2 response to temperature are likely the result of the bullray's acclimation to experimental temperatures.

Tomales Bay is a thermally heterogenous environment, 20 km long by 1.4 km wide, which averages 3 m in water depth, and has a channel with a maximum depth of about 20 m. It is divided into two parts based on chemical and physical characteristics, a 12 km^2 outer bay which is mostly fine sand and 6 km^2 of dense seagrass beds, and a 16 km^2 inner bay which has extensive intertidal and shallow subtidal mudflats but only 1 km^2 of seagrass beds (Ridge 1963, Spratt 1989, Smith et al 1991). Exchange of water between the inner and outer bay during summer is near zero, and the inner bay tends to be warmer by 2-6°C and more saline, by 2 ppt, than the outer bay at this time of year (Ridge 1963, Smith et al 1991). Rays in this study were captured in August 1991 when the temperature difference between the inner (19.4°C) and outer bay (14.9°C) was 4.5°C, and shallow mudflat areas were occasionally as warm as 26°C (Hopkins personal observation). During this same time period we tracked several telemetered rays moving from the inner to the outer bay late in the day and returning to the inner bay early the next morning, a round trip distance of about 16 km (Hopkins unpubl.). If rays are preferentially foraging in the warmer (i.e. 20°C) inner bay, as Ridge's (1963) data suggest, then they may reduce their respiratory metabolic cost 216% by retreating to the cooler outer bay after foraging where temperatures were about 14°C (Figure 1).

Our data indicate that the standard, mass-independent MO_2 of bat rays is extremely sensitive to temperature between 14°C and 20°C, and only moderately sensitive between 8°C and 14°C, or between 20 and 26°C. This finding, coupled with preliminary data from an ultrasonic tracking study suggests that bat rays may behaviorally thermoregulate; foraging in the warm prey-rich inner bay, and using the cooler outer bay as a thermal refuge. We plan a more detailed ultrasonic tracking study to test our hypothesis.

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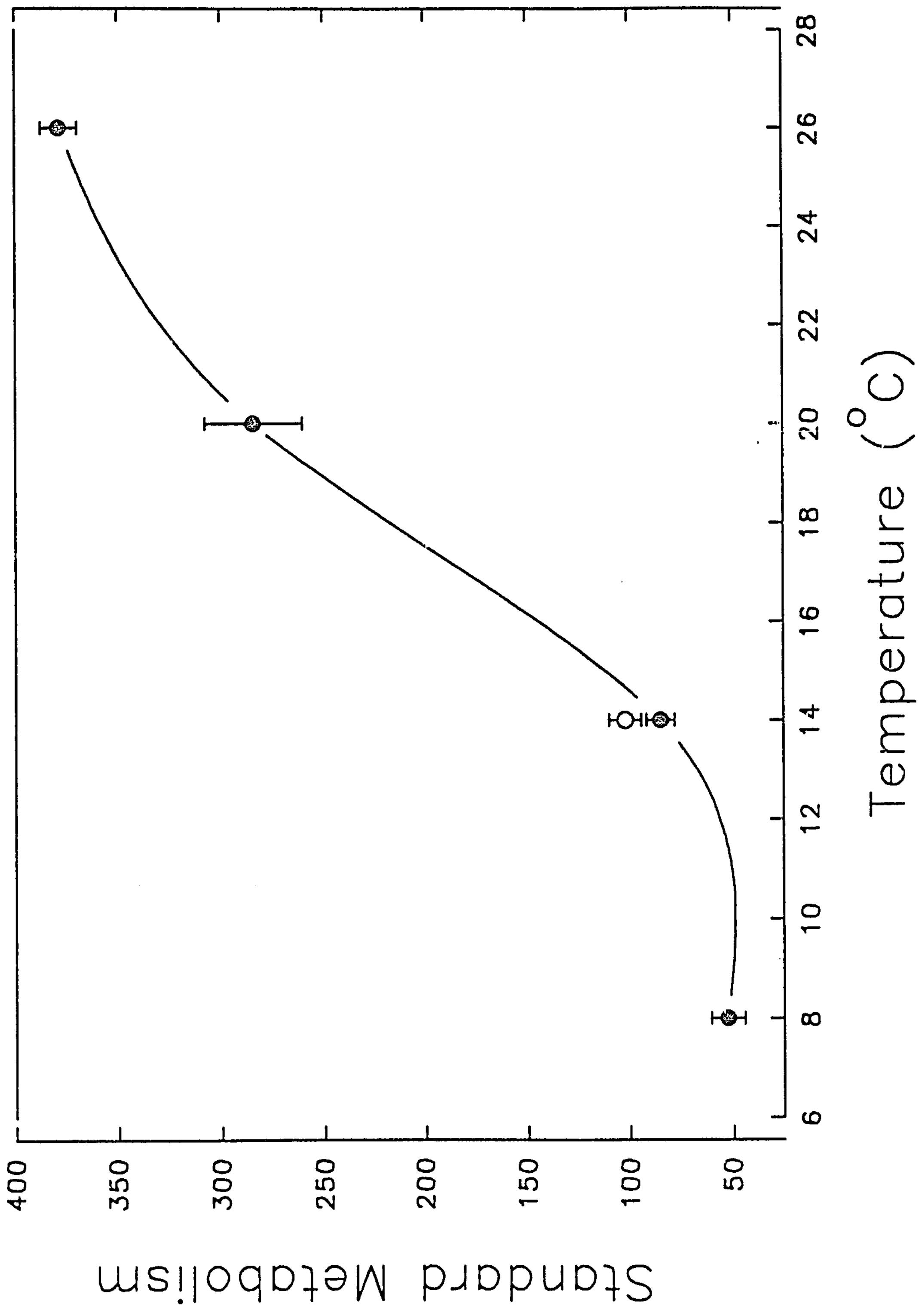
Figure 1. Mean (± 1 SE) standard, mass-independent oxygen consumption rates (mg $O2 \bullet kg^{-0.67} \bullet h^{-1}$) of six bat rays determined in the following sequence: open circle, 14(initial), solid circles, 8, 14, 20, 26°C. All means are significantly different ($p < 0.05$) except the two 14°C values ($p > 0.89$). Open squares are values for a 5 kg bullray calculated from Du Preez et al. (1988).


Standard Metabolism
400
350
300
250
200
150
100
50
Temperature (°C)
6
8
10
12
14
16
18
20
22
24
26
28

Temperature Effects on Blood-Oxygen Equilibria in the Bat Ray, *Myliobatis californica*.

Abstract.

We studied the effects of four temperatures (8, 14, 20, 26°C) on blood oxygen equilibrium curves of the bat ray, *Myliobatis californica*, a vagile, seasonally abundant, benthic elasmobranch common to bays and estuaries along the eastern Pacific coast. Blood oxygen equilibrium curves at all temperatures were hyperbolic ($n_{50} < 2$), with high affinity (low P_{50}), large Bohr factors (Ø = -0.45 to -0.52), high blood oxygen carrying capacity (CBO_2 = 6.8 to 9.06), and very large non-bicarbonate buffering capacity (ß = -14.25 to -16.43). CBO_2, Ø, and ß are among the largest measured in a poikilothermic elasmobranch. Affinity decreased with increasing temperature except at 26°C. The affinity shift at 26°C and a concomitant 25% drop in CBO_2 at this temperature suggests a hemoglobin heterogeneity. Blood oxygen equilibrium curves were temperature insensitive between 8-14°C and 20-26°C and most sensitive between 14-20°C, the temperature range in which bat rays are most commonly found in Tomales Bay, California. Bat rays appear capable of tolerating hypoxia and hypercapnia (low P_{50}, n_{50}, and high ß), and sustaining high activity levels (high CBO_2, Ø, and ß) by virtue of their unique hematological characteristics.

Introduction.

The bat ray, Myliobatis californica, is a large benthic predator which commonly forages in shallow mudflats and seagrass beds in bays and estuaries from southern Oregon to the Gulf of California (MacGintie 1935; Talent 1985; Ferguson and Cailliet 1990; Love 1991). Bat rays are abundant in Tomales Bay, California, during most of the year when bay temperature ranges between 14 and 24°C, but leave the bay during the winter months (November-February) when water temperatures drop below 10°C (Ridge 1963; Smith et al. 1991).

During a telemetry study of bat ray movements in Tomales Bay, we tracked several rays moving from the shallow inner bay to the deeper outer bay late in the afternoon, and returning to the inner bay early the next morning (Hopkins unpublished). The temperature difference between these areas of the bay was often greater than 5°C. Because the resting metabolism of bat rays is highly temperature sensitive between 14 and 20°C (Hopkins and Cech 1993), we hypothesized that the rays might be thermoregulating; foraging in the inner bay, and using the outer bay as a temperature refuge (Hopkins and Cech 1993). However, diel movements of fishes in shallow bays has also been shown to be due to recurring (often nightly) oxygen depressions (Hubbs Baird and Gerald 1967, Saint-Paul and Soares 1987, Breitburg 1992).

Tomales Bay is 20 km long by 1.4 km wide and averages 3 m in depth (Smith et al. 1991). The inner reaches of Tomales Bay, an area of 16 km^2, has a 1 km^2 seagrass bed and extensive intertidal and subtidal mudflats covered with benthic macro and microalgae (Spratt 1989; Smith et al. 1991). In aquatic habitats respiration by plants, bacterial decomposition, and invertebrate respiration can remove a significant amount of oxygen from the overlaying water (Goldman and Horne 1983). Seasonal or diel dissolved oxygen depressions (hypoxia), while undocumented in Tomales Bay, are common in shallow bays and estuaries (Loesch 1960; Taft et al. 1980; Day et al. 1990) and constitute an important physical disturbance to aquatic communities (Coutant 1985; Kennedy 1990; Breitburg 1992). Thus, the movements of bat rays in Tomales bay may have been the result of an avoidance of areas of nightly oxygen depression.

The purpose of this study was to examine the blood-oxygen binding characteristics of bat rays to determine if inherent physiological limitations, such as a heightened sensitivity to hypoxia or temperature changes, might account for their diel movements in Tomales Bay.

Material and Methods.

Collection and holding.

Seven bat rays (mean disc width 60.3 cm, range 50-80 cm, mean weight 5.30 kg, range 4.66-9.09 kg) were captured by hook and line in Tomales Bay at temperatures of 11.8 to 13.8°C and 33 ppt salinity. Only rays with superficial hook wounds were transported to the University of California, Bodega Marine Laboratory and held in a circular, shaded, 8,000 L outdoor tank, with flowing aerated seawater (11 ±1°C and 33 ±1 ppt) for 2 weeks.

Cannulation.

Fish were anesthetized in 300 mg/L 3-aminobenzoic acid ethyl ester (MS-222) until spiracular ventilation ceased and then placed on an operating table (Reinecker and Ruddell 1974) with recirculating, aerated seawater with 50 mg/L MS-222 over their gills. The lighter anesthetic dose during surgery decreased recovery time. A 17 gauge needle was inserted through the skin on the ventral side of the tail, about 3 cm anterior to the origin of the dorsal fin, and a PE-50 cannula with a beveled tip was inserted through the needle and several cm into the dorsal aorta. Cannulae were filled with heparinized saline in a ratio of 1,000 international units (IU) sodium-heparin to 10 ml elasmobranch saline (Hoar and Hickman 1983), and secured by suturing to the skin. Mean surgery time, including anesthesia, was 22 minutes. Rays were placed individually in covered 210 L circular tanks with aerated, flowing seawater (11 ±1°C and 33 ±1 ppt) and allowed to recover for 2.5 days.

Blood sampling and hematological analyses.

An initial 0.8 ml blood sample was taken from each ray to determine blood gas and hematological conditions at 11°C. PO_2, PCO_2, and pH were measured with a Radiometer PHM 73 analyzer and thermostated electrodes (E5046, E5036, and G297/K497 respectively). Blood lactate was determined enzymatically (Yellow Springs Instruments (YSI) model 27 analyzer), hematocrit (Hct) by centrifugation at 10,400 x G for 3 min, and hemoglobin concentration ([Hb]) by the cyanmethemoglobin method (Sigma kit #525-A). The remaining blood was centrifuged (5 min at 3,800 x G) and the plasma aspirated and frozen for later analysis of: urea (colorimetrically, Sigma kit #535), glucose (enzymatically, YSI model 27 analyzer), osmolality (vapor pressure, Wescor 1500B), Cl^- (coulometric titration, Radiometer CMT 10), Na^+ and K^+ (photometrically, Instrumentation Laboratories 343 flame photometer).

Tonometry.

Blood (78 ml) from 4 individuals was pooled with 1,000 IU sodium-heparin in a large flask. Samples of the well-mixed, pooled blood were immediately taken to determine nucleoside triphosphate (NTP) (enzymatically, Sigma kit #366-UV), lactate, Hct, and [Hb]. Blood was loaded into two glass rotating tonometers (Hall 1960) or kept on ice for 20-40 min before being loaded into a second pair of tonometers. Tonometers were situated in a temperature-controlled water bath at 8, 14, 20 or 26 ± 0.2°C. Tonometer pairs received either humidified air from an air pump and humidified N_2 from a cylinder (low PCO_2 curves) or humidified gas mixtures (1% CO_2 with balance either air or N_2) from Wüsthoff gas mixing pumps (high PCO_2 curves). Blood was equilibrated for 30-40 min, after which samples of oxygenated and deoxygenated blood were withdrawn from the tonometers and mixed in a gas-tight glass syringe with a mixing bead (technique reviewed in Wells and Weber 1989). A Lex-O_2-Con (Lexington Instruments) was used to verify the O_2 content (CBO_2, in mmol/L) of oxygenated (100% saturation) and deoxygenated (0% saturation) pools. PO_2 was measured for each mixture, and pH was measured for each 50% mixture. Several lactate measurements were made on tonometered blood while curves were being constructed to ensure that there was no significant metabolic acidosis, e.g. in the deoxygenated tonometers. From time of sampling to completion of a pair of oxygen equilibrium curves required less than 2 hr.

Bohr factor (Ø), was calculated from $Ø = \Delta \text{Log P50}/\Delta \text{pH}$. The apparent heat of oxygenation, (ΔH, in kcal/mol), was calculated using a form of the van't Hoff equation:

$\Delta H = 4.578 \bullet (\Delta \text{Log } P_{50}/(\Delta 1/T) \bullet 1000)$, where P_{50} is from low PCO_2 curves in kPa and T is temperature in ^{o}K (Wyman 1964; Powers et al. 1979). Whole blood non-bicarbonate buffer value

(β in mmol HCO_3-$\bullet$pH unit$^{-1} \bullet L^{-1}$, or slykes) was calculated from:

$\beta = \Delta[HCO_3^-]/\Delta pH$. $[HCO_3^-]$ was calculated using pH and PCO_2 data in the Henderson-Hasselbalch equation (Davenport 1974) with constants for elasmobranchs published by Boutilier, Heming, and Iwama (1984). Hb subunit cooperativity (n_{50}) was determined from the slope of Log (y/100-y) versus Log p, where y = percent saturation between 10 and 90%, and p = PO_2 in kPa (Riggs 1970; Jensen 1991). Root effect was calculated as the percent loss in CBO_2 between a low and high PCO_2 pair.

A Pearson's correlation coefficient matrix was constructed for all measured and calculated variables to test for significant effects at the $p < 0.05$ level. Linear least squares regression was used to relate temperature and pH. Statistical tests were performed with SYSTAT 4.0 (Wilkinson 1988).

Results.

Resting, in vivo, blood gas and hematological characteristics of bat rays (Table 1) were similar to those of other cannulated elasmobranchs; Squalus (Lenfant and Johansen, 1966), Dasyatis (Cameron, Randall, and Lewis 1971), Scyliorhinus (Butler and Taylor 1975), Torpedo (Hughes and Johnston 1978), Negaprion (Bushnell et al. 1982), Raja (Graham, Turner, and Wood 1990), and Triakis (Lai, Graham, and Burnett 1990), with the exception that blood urea and osmolality levels were low for an elasmobranch acclimated to full seawater (33 ppt), and [Hb] was high. The low [lactate] and [glucose] (Table 1) indicated a negligible secondary stress response (Wedemeyer, Barton and McLeay 1990) and that these fish had recovered from surgery. Thus, blood from these fish was suitable for constructing O_2 equilibrium curves indicative of bat rays in the wild.

The P_{50}, Ø, and CBO_2 of both low PCO_2 and high PCO_2 curves were greatest at 20°C, where corresponding pH values were lowest (Table 2). NTP, [Hb], and ß were similar across all temperatures. ΔH was greatest between 14 and 20°C indicating a greater sensitivity to Hb-O_2 loading and unloading in this range as compared to the relative temperature independent binding at 8-14°C and 20-26°C ranges. Increasing PCO_2, from 0.03 to 1.01 kPa, significantly decreased blood pH (negative correlation, $p < 0.01$) and increased P_{50} (positive correlation, $p < 0.01$) at each temperature.

Blood oxygen dissociation curves (Figure 1,A-D) were approximately hyperbolic ($n_{50} \leq 2$) with low P_{50}'s, large CBO_2, ß, and Ø, and negligible Root effects (Table 2). Lactate measurements of tonometered blood never exceeded 1.0 and 1.2 mmol/L in 0.03 and 1.01 kPa PCO_2 respectively, which was close to that of in vivo measurements from resting fish (Table 1). While Root effect was significantly negatively correlated with temperature ($p < 0.05$), no other correlations between temperature and any variable in Table 2 over the 8-26°C range were significant. Dafré and Wilhelm (1989) considered a Root effect of $\leq 10\%$ to be insignificant and we will follow their convention. In addition, neither regression slope relating pH and temperature was significantly different from 0 ($p > 0.1$ for 0.3 kPa PCO_2, and $p > 0.03$ for 1.01 kPa PCO_2).

Discussion.

Temperature Effects.

Although fish acclimate their Hb-O_2 binding abilities to warmer temperatures in several ways, the results are due primarily to alterations in allosteric phosphate cofactors and [Hb] (reviewed in Powers 1980; Weber and Wells 1989). In our study, rays were captured and held at about 11°C, and Hct, [Hb], and NTP were constant; thus our results are free of complicating acclimatory changes and reflect the sum of the molecular and cellular effects of temperature on bat ray red blood cell O_2 binding.

In ectotherms, an acute temperature rise decreases O_2 affinity directly due to the exothermic nature of Hb-oxygen binding, and indirectly due to the associated pH decrease (reviewed in Johansen and Weber 1976; Weber and Jensen 1988). Bat ray blood O_2 binding was temperature-independent (low ΔH) in the 8-14 and 20-26°C ranges, but showed a similar temperature effect to that of other fishes between 14-20°C (Table 2,3, Powers 1980). Bat rays are most abundant in Tomales Bay from April to November, when temperatures are typically between 14 and 24°C (Smith et al. 1991) and it is in this temperature range that bat rays show their greatest change in resting O_2 uptake/°C (14-20°C:Q_{10} = 6.52 (Hopkins and Cech 1993). Thus, between 14-20°C bat rays appear to sacrifice O_2 uptake ability (by decreasing affinity) in order to increase O_2 offloading ability to supply metabolically active tissues.

Blood O_2 affinity in bat rays tended to drop with increasing temperature with one exception, the 20-26°C range. Blood pH at both PCO_2 levels fell between 0.02-0.04 pH unit/°C between 8 and 20°C and then increased 0.01 pH unit/°C between 20-26°C (Table 2) a trend which mirrored that of affinity. In addition, the large (25%) drop in CBO_2 between 20 and 26°C may be an indication of a decrease in the functional ability of a hemoglobin fraction to carry O_2 at elevated temperatures. Because NTP, [Hb] and Hct were constant across temperatures, we suspect that a Hb heterogeneity may be responsible for this reverse trend.

A functional Hb heterogeneity extends the range of conditions under which the composite pigment executes its O_2 transporting and other functions, thus enlarging the habitable environment and serving changing physiological needs (Weber 1990). Hb heterogeneity is common among teleosts (Brittain 1991) and has been documented in several elasmobranchs (Anderson et al. 1973; Bonaventura, Bonaventura, and Sullivan 1974; Pennelly et al. 1975; Brittain et al. 1982; Weber, Wells, and Rossetti 1983). Thus, the presence of a high affinity Hb, functional at elevated temperatures would preserve the bat ray's ability to withstand hypoxia and to supply increased metabolic demands at warmer temperatures. We suspect that two Hbs are present; one which was dominant in the 8-20°C range, and another with a higher affinity, which was dominant at 26°C, although we have only indirect evidence for this hypothesis.

Ecological Implications.

The blood of bat rays has comparatively high affinity, a large Bohr factor (Ø), blood O_2 carrying capacity, non-bicarbonate buffering capacity (ß), and a low cooperativity (Tables 2,3, Figure 1). Among teleosts, high affinity, hyperbolic blood O_2 binding curves and large ß values are associated with hypoxia and hypercapnia tolerance (Wood, McMahon, and McDonald 1977; Johansen and Weber 1976; Powers 1980). Conversely, reduced affinity, large Bohr factor, and high blood O_2 carrying capacity are typical of active poikilothermic teleosts (Satchell 1991). The situation is not as clear in elasmobranchs however, as species with widely differing aerobic scopes show similar blood O_2 characteristics (Table 3, Tetens and Wells 1984). By teleostean standards then, bat rays appear well adapted for hypoxia and hypercapnia (low P_{50} and n_{50}, high ß), and high activity levels (high CBO_2 and large Ø). In fact, the blood O_2 carrying capacity, Bohr factor, and whole blood ß are among the largest recorded for a poikilothermic elasmobranch (Table 3).

Bat rays are seasonally common in bays and estuaries where they prey upon benthic infauna in shallow (often < 1 m) mudflats or eelgrass beds (Karl and Obrebski 1976; Love 1991). In a telemetry study in Morro Bay, California, Dubsky (1974) tracked a bat ray moving an average of 0.74 km/hr and frequenting the shallow parts of the bay, "...where hovering and short bursts of speed were observed."(Dubsky 1974, pg. 27). This behavior pattern and movement rate is similar to that of telemetered bat rays in Tomales Bay (Hopkins unpublished), and to that of the cownose ray, Rhinoptera bonasus, in the Chesapeake Bay (MacLean 1981; Smith and Merriner 1985, 1987).

The cownose ray (family Rhinopteridae) is a morphologically and ecologically similar species which also forages in intertidal mudflats and eelgrass beds (Orth 1975; Smith and Merriner 1985, 1987). Both cow nose rays and bat rays have a unique ball and socket joint connecting their pectoral fins to the vertebral column (McEachran 1990) which contributes to their unique swimming mode (Heine 1990). In addition, both species outmigrate during the winter months (Ridge 1963; Love 1991) and the long range migrations of the cownose ray are well studied (Smith and Merriner 1987). Although the winter movements of bat rays are undocumented, large schools have been sighted near the Channel Islands off southern California (Odenweller 1975; Hall 1990; Love 1991).

Because both bat rays and cownose rays actively forage in shallow areas where the possibility of encountering elevated temperatures and hypoxia is high, and may migrate long distances during parts of the year, it is not surprising that their blood-oxygen binding characteristics are a similar (Scholnick and Mangum 1991). Furthermore, the high blood buffering capacity and the large Bohr factor seen in bat rays supports the hypothesis of Dobson et al. (1986) that a high blood buffering capacity is an important strategy for extending muscle performance. However, a scaled-up blood buffering capacity requires an increased pH sensitivity of Hb for releasing O_2, otherwise O_2 delivery to the tissues during exercise will be compromised. Thus, a large Bohr factor would facilitate O_2 delivery from the blood to the aerobic muscles for a small change in blood pH during exercise.

While our blood O_2 binding data are an instantaneous sample of a system which can be altered over various time scales (Jensen 1991); the hematological characteristics of bat rays are sufficient to allow activity in reduced oxygen conditions over a broad temperature range, to sustain metabolically or environmentally produced hypercapnia, and to undertake long-term aerobic activity such as migrations. Thus, we reject our hypothesis that the diel movements of bat rays in Tomales Bay were solely due to limitations in their ability to reversibly bind oxygen and carbon dioxide, or tolerate mild hypoxia.

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Table 1. Mean *in vivo* arterial blood and plasma characteristics (standard error in parentheses) from seven cannulated, resting rays acclimated to 11°C and 33 ppt.

PaO_2 (kPa)	11.66 (1.35)
$PaCO_2$ (kPa)	0.08 (0.01)
pH	7.929 (0.04)
Hct (%)	19.31 (1.02)
Hb (mg/dL)	5.81 (0.35)
Na^+ (mmol/L)	239.0(8.16)
K^+ (mmol/L)	3.61 (0.26)
Cl^- (mmol/L)	242.3 (5.61)
Osm (mOsm/kg)	747.0 (23.82)
Urea (mmol/L)	269.8 (11.45)
Lactate (mmol/L)	0.74 (0.15)
Glucose (mg/dL)	103.5 (22.69)

Table 2. Effects of temperature and CO_2 on bat ray blood-oxygen equilibrium characteristics.

Temp °C	PCO_2 kPa	pH	P_{50} kPa	CBO_2 mmol/L	n_{50}	NTP µmol/g	Hct %	Hb mg/dl	Ø	ß slykes	Root %	ΔH kcal/mol
8	0.3	8.37	0.8	3.7	1.0	0.16	23	5.4	-0.45	-16.43	5	
8	1.0	7.63	1.7	3.5	1.2							-5.96
14	0.3	8.33	1.0	3.6	1.0	0.16	23	5.8	-0.47	-16.07	2	
14	1.0	7.55	2.3	3.5	1.2							-16.17
20	0.3	7.92	1.8	4.1	1.6	0.17	23	5.5	-0.52	-16.13	1	
20	1.0	7.45	1.8	4.1	1.7							-3.44
26	0.3	7.99	1.6	3.1	2.0	0.16	20	5.2	-0.47	-14.25	0	
26	1.0	7.51	2.7	2.1	1.8							

Table 3. Blood-oxygen equilibrium curve characteristics of selected elasmobranchs. Units are defined in Table 2.

Species	Temp	pH	P_{50}	Ø	Hct	$CB0_2$	n_{50}	ß	ΔH	Ref*
Skates and Rays										
Rhinoptera bonasus	20	7.7	1.5	-0.41	16		1.5			1
Raja clavata	15	7.7	4.0	-0.25		1.6	2.5			2
Raja ocellata	12	7.8	3.7	-0.29	12	1.6	1.8	11.0		3
	10		2.7			2.7	2.0		-2.28	4
	25		6.0				1.9			4
Dasyatis	25		3.3		14	1.2	1.7			6
Torpedo marmorata	15	7.8	2.7	-0.32		1.6	1.4			7
	20		3.7				1.5			7

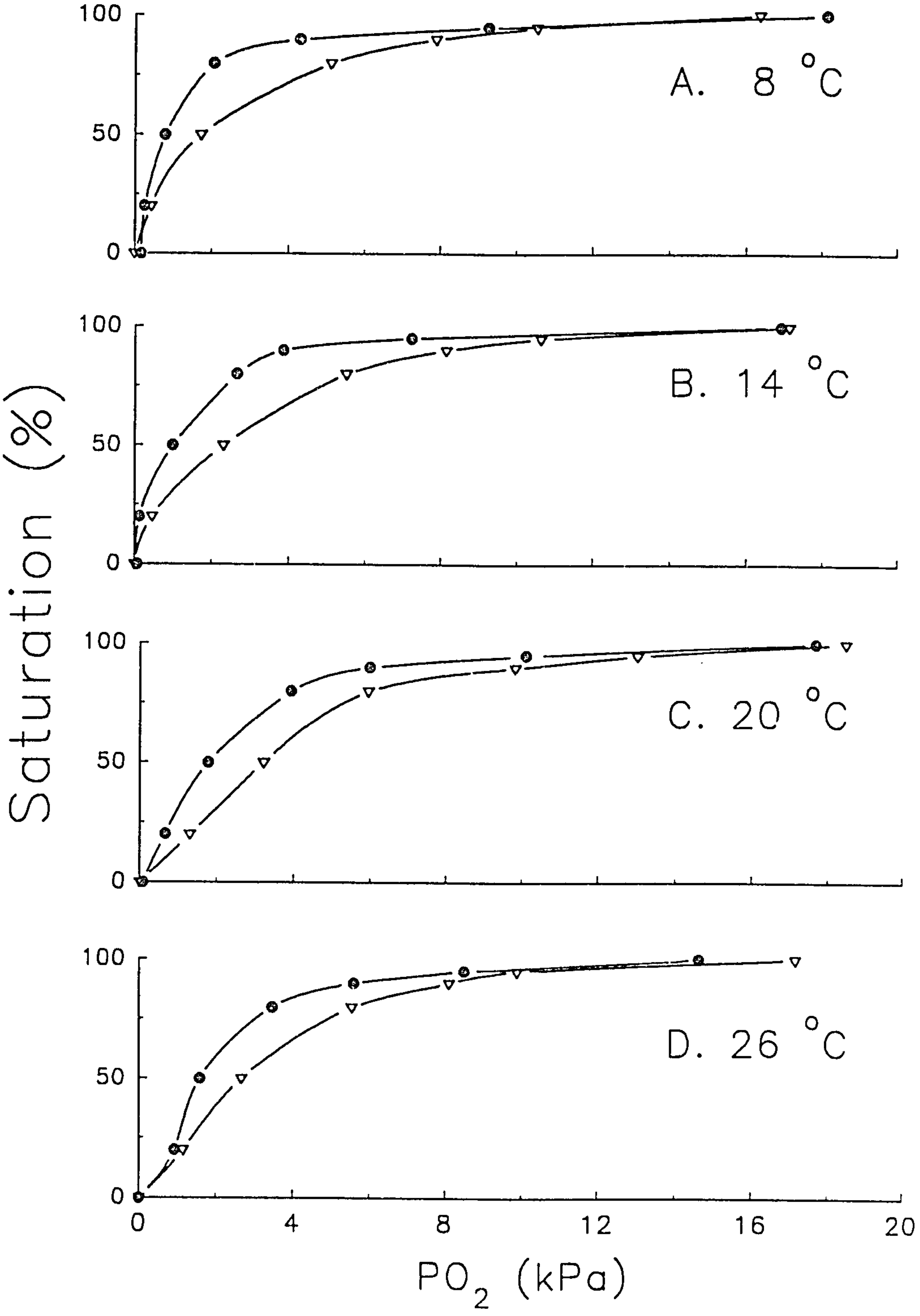
Table 3 (continued).

Poikilothermic Sharks

Triakis semifasciata	20		2.0		18	2.8	1.1	9.3		8
Squalus acanthias	15	7.8	1.8	-0.28	12	1.6-2.0	1.6			9
Cephaloscyllium isabella	5	7.7	1.1	-0.32	15		1.5			10
	15	7.7	0.7	-0.49	15				-8.7	10
Negaprion brevirostris	24	7.7	1.6	-0.36	16	1.4	1.7			11
Scyliorhinus canicula	17	7.6	2.9	-0.43	22		1.7			12
Scyliorhinus stellaris	17	7.6	2.1		16	1.9	1.8			13

References: [1]Scholnick and Mangum 1991, [2]Hughes and Wood 1974, [3]Graham et al. 1990 ,[4]Dill, Edwards, and Florkin 1932, [5]Cameron et al. 1971,[6]Hughes 1978, [7]Lai et al. 1990, [9]Wells and Weber 1983, [9]Tetens and Wells 1984, [10]Bushnell et al. 1982, [11]Pleschka, Albers, and Spiach 1970, [12]Piiper and Baumgarten-Schumann 1968.

Figure 1. Bat ray blood-oxygen equilibrium curves at 8, 14, 20, and 26°C with 0.03 kPa PCO_2 (circles), and 1.01 kPa PCO_2 (triangles).


Saturation (%)
A. 8 °C
B. 14 °C
C. 20 °C
D. 26 °C
0
50
100
0
4
8
12
16
20
PO$_2$ (kPa)

The Influence of environmental variables on the distribution and abundance of three elasmobranchs in Tomales Bay, California.

Abstract.

Using monthly longline samples over a 20 month period I tested the hypothesis that temperature, salinity, and dissolved oxygen affect elasmobranch distrib ution and abundance in Tomales Bay, California. I used a Poisson regression under generalized least squares and found that temperature and salinity were the most important factors determining the distribution and abundance of the three most common elasmobranch species, bat ray, Myliobatis californica, leopard shark, Triakis semifasciata, and brown smoothhound shark, Mustelis henlei. Females of all three species were more abundant than males throughout the bay, and were most abundant in the warmer more saline inner bay. All three species left Tomales Bay in late fall as water temperatures in the bay decreased < 10-12°C, and returned in early spring after temperatures increased > 10°C. Three out of 432 bat rays tagged in Tomales Bay were recaptured, all within 1 km of their tagging location despite having been at large for 103-583 days.

Introduction.

Abiotic factors such as temperature, salinity, and dissolved oxygen, are important in determining the distribution and relative abundance of temperate bay and estuarine fishes (Gunter 1961, Kinne 1964, Recksiek and McCleave 1973, Allen and Horn 1975, Hoff and Ibara 1977, Weinstein et al. 1980, Allen 1982, Mulligan and Snelson 1983, Onuf and Quammen 1983, Coutant 1985, Kennish 1990, Loneragan et al. 1986, 1987, Yoklavich et al. 1991, Pearson 1989, Cyrus and Blaber 1992, Breitburg 1992). However, most studies have focused on teleosts and have largely ignored elasmobranchs (sharks, skates, and rays).

Elasmobranchs are fundamentally different from teleosts in their life history, behavior, and physiology (Hoenig and Gruber 1990, Pratt and Casey 1990, Nelson 1990). They are slow growing, late maturing, have long gestation periods, produce few young, and attain a large body size (Hoenig and Gruber 1990). While less numerous in most systems than teleosts, they forage near the top of the food chain (Compagno 1990) and may account for a significant portion of the total biomass in a system (e.g Horn 1980, Recksiek and McCleave 1973). In addition, they may segregate by sex and by size on both local and regional scales (Pratt 1979, Castro 1983). Many species use bays and estuaries for part of the year and depart during the winter months (Steven 1932, Bearden 1959, Jensen 1965, Struhsaker 1969, Sage et al. 1972, Snelson and Williams 1981, van der Elst 1981, Smith and Merriner 1987, Rousset 1990).

Previous studies on elasmobranchs have implied that temperature and salinity play a role in their distribution (Smith and Merriner 1987, Struhsaker 1969, Funicelli 1975, Sage 1972, Bearden 1959, Snelson et al. 1988, Snelson et al. 1989, Rousset 1990) but the effects of these environmental factors has not been quantified. From a physiological standpoint, temperature, salinity, and dissolved oxygen should, alone or in concert, influence the distribution of elasmobranchs. The majority of nearshore elasmobranchs are ectothermic and changes in the environmental temperature are rapidly transferred to the body of the animal where nearly every physiological process is affected (Prosser and Heath 1991). Furthermore, elasmobranchs use various end products of nitrogen metabolism as osmotically active solutes to maintain themselves hyperosmotic to their environment (reviewed by Perlman and Goldstein 1988), but they are unable to maintain this balance in the face of decreased salinities (reviewed by Pang et al. 1977). Finally, seasonal or diel dissolved oxygen depressions (hypoxia) are common in shallow bays and estuaries (Loesch 1960; Taft et al. 1980; Day et al. 1989) and constitute an important physical disturbance to aquatic communities (Coutant 1985; Kennedy 1990; Breitburg 1992). Hypoxia adaptations in elasmobranchs are complex and can be altered over several time scales (e.g. hours, days, months; Jensen 1991) so that their general response to this factor are highly variable (Johansen and Weber 1976, Butler and Metcalf 1988).

The purpose of this study was to establish the relative importance of temperature, salinity, and dissolved oxygen in determining the distribution and abundance of the three most common elasmobranchs in temperate Tomales Bay in northern California.

Study Organisms.

I focused our analysis on the three most commonly captured elasmobranchs in northern California bays, the bat ray (Myliobatis californica), the brown smoothhound shark (Mustelus henlei), and the leopard shark (Triakis semifasciata) (Herald and Ripley 1951, Herald et al. 1960, Karl 1979, Talent 1982, Talent 1985, Armor and Hergesell 1985, Pearson 1989, Love 1991, Herbold et al. 1992)

Bat rays.

Bat rays range from Oregon to Baja California, and forage for clams, crabs, shrimps, and the echiuroid worm Urechis caupo in sand or mud substrates (MacGintie 1935, Ridge 1963, Karl 1979). Bat rays are viviparous and 50% of all females are mature at a disc width (DW) of 88 cm and all females studied by Martin and Cailliet (1988a) over 100 cm DW were sexually mature. Males are fully mature by 68 cm DW. Gestation lasts 9-12 months and 2-12 young (DW 22-30 cm) are born in spring or summer (Martin and Cailliet 1988a). Females can live at least 24 years and attain a DW of 183 cm, while males can live at least 6 years and reach a DW of 100 cm (Martin and Cailliet 1988b). Large schools of bat rays have been sighted off southern and central California (Odenweller 1975, Hall 1990, Love 1991).

Brown smoothhound sharks.

Brown smoothhounds range from Coos Bay, Oregon, south to the Gulf of California (Love 1991). They consume mainly crabs, shrimp and small fish, and are very abundant in San Francisco Bay (Herald et al. 1960, Russo 1975, Talent 1982, Herbold et al. 1992). They frequent nearshore waters during spring and summer and move offshore during winter (Compagno, 1984). Brown smoothound females mature between 1 and 4 years of age and females give birth to 1-8 young which are about 20 cm TL (Yudin and Cailliet 1990, Love 1991). Females mature between 51-63 cm TL, live 13 years, and can reach 100 cm TL. Males mature between 52-66 cm

TL, can live 7 years, and can reach 90 cm TL (Yudin and Cailliet 1990, Compagno 1984).

Leopard sharks.

Leopard sharks range from Oregon to Baja California including the Gulf of California and are the most studied California nearshore shark (Cailliet 1992). They eat crabs, shrimp, clam siphons, fish, and small sharks and rays (Russo 1975, Talent 1976). Females mature between 11-21 years of age (100-129 cm TL), live about 30 years (Ackerman 1971, Smith and Abramson 1990) and can reach 200 cm TL. Gestation takes about 12 months and females produce 3-11 young which are born during spring and summer (Love 1991). Males mature between 76-120 cm TL.

Study Site.

Tomales Bay is a 20 km long straight basin which averages 1.4 km in width and 3 m in depth formed by the intersection of the San Andreas fault with the northern California coastline (Hollibaugh et al. 1988) (Figures 1,2). The bay watershed covers about 570 km^2 and is almost entirely rural, with a population of about 10,000 persons and 20,000 cows (Smith et al. 1991). Most runoff enters from the two major streams in the eastern and southern portion of the watershed. The larger of the streams (Lagunitas Creek) enters the southern end, while the second (Walker Creek) enters along the east side of the bay, about 5 km from the mouth (Figure 1).

The bay is hydrographically simple and has been divided into two parts based on chemical and physical characteristics (Hollibaugh et al. 1988, Smith et al 1991). The bottom of the outer bay (12 km^2) is mostly fine sand and has 6 km^2 of dense seagrass beds. The inner bay (16 km^2) has extensive intertidal and shallow subtidal mudflats covered with macroaglae and 1 km^2 of seagrass beds (Ridge 1963, Spratt 1989)(Figure 1). Longitudinal gradients of hydrographic variables are large relative to lateral and vertical gradients, and vertical stratification is weak and episodic (Smith et al. 1991). Exchange of water between the inner and outer bay during summer is near zero, and the inner bay tends to be 2-6°C warmer and 1-3 ppt more saline than the outer bay at this time of year (Ridge 1963, Smith et al. 1991). Mixing is greatest in winter due to increased runoff and the inner/outer bay temperature gradient disappears. Inner bay salinity is largely a function of runoff from Lagunitas Creek, while Walker Creek has little impact on the salinity of the outer bay.

Materials and Methods.

Data Collection.

Sharks and rays were collected by longlines fished monthly from September 1990 through April 1992 at stations located 2 km apart in Tomales Bay (Figures 1,2). A longline consisted of a 9.53 mm diameter braided polypropylene mainline 34 m long anchored at both ends with 20 m float lines attached to each anchor. Each longline held about 20 gangions which were spaced 1.2 m apart. Each gangion consisted of a heavy-duty stainless steel quicksnap with 1/0 swivel, 0.5 m of 41 kg test coated stainless steel leader, another 1/0 swivel and a 0.8 m leader ending in a 12/0 Mustad Kirby hook. Longlines were baited with 1-2 squid (Loligo sp.) per hook and set soon after dawn and fished on the bottom for 4-6 hr. I sampled the inner and outer bay with about equal intensity (e.g. outer bay, 3 longline stations/km^2; inner bay, 3.2 longline stations/km^2).

I recorded: location, start and finish times for setting and hauling operations, number of hooks fished, and tide height and stage (rising, falling, slack) as determined from published tide tables, for each longline set. The sex and characteristic length (TL or DW) of all captured sharks and rays was recorded. All sharks were immediately released, while bat rays were tagged prior to release with a numbered spaghetti tag (Floy FT-4 lock-on) placed through a hole made by passing a 17 gauge hypodermic needle through the chondrocranium 2 cm proximal to the spiracle on the ray's right side. Sharks or rays which broke the gangion or dislodged the hook after being brought alongside were counted as a catch and noted as a "lost" fish.

Vertical profiles of temperature, salinity, and dissolved oxygen concentration were recorded from surface to bottom at 1 m intervals at each longline station using a Hydrolab Surveyor II approximately 24 hr prior to longlining.

Modeling.

The following variables were considered for our model: location (inner/outer bay), season 1 = January-March, season 2 = April-June, season 3 = July-September, season 4 = October-December, tide stage, and the mean inner bay and outer bay values for: tide height, number of hooks fished, number of sharks or rays captured (males and females combined), and set time. Mean temperature and salinity were calculated from vertical transect data using values recorded 1 m off the bottom. Dissolved oxygen was not included in the model as concentrations in the bay never fell below 75% of air saturation, a level not considered stressful for bat rays or leopard sharks (Chapman 1986, Lai et al. 1990, Hopkins, unpublished)(Figure 3).

I used a Poission regression under generalized least squartes to construct our model of bat ray distribution and abundance because the mean number of rays captured was approximately normally distributed and encompassed a small range of values. I used Akaike's information criterion (AIC) (Akaike 1969), C_p, and r^2adj (Neter et al. 1985) as selection criteria to determine the best main effects model without interaction terms using all possible subsets. Interactions were added to the resulting main effects model individually, and each new model was re-evaluated using these same criteria. These selection criteria either increase or decrease as variables are added to the model allowing one to determine the most powerful model (one which best describes the data) using the least number of variables and interaction terms. Normality of the final model residuals was tested using a Shapiro-Wilk statistic (Shapiro and Wilk 1965), and a normal scores plot (Neter et al. 1985)

The large number of low or zero catches of leopard and brown smoothhound sharks prohibited us from using this approach in constructing models for these species. Instead, we fit the model derived for bat rays using generalized least squares with Poisson error terms and calculated asymptotic confidence intervals (Neter et al. 1985).

Modeling and statistical work was performed using PC-SAS version 6.04 with significance judged at the 0.05 level. An analysis of variance (ANOVA) was used to detect differences in the size of males and females of each species based on capture location. A chi-square test for goodness of fit (X^2) was used to determine if, for a given species, equal numbers of each sex were captured in the inner and outer bay.

Results.

Longline catch.

A total of 257 bat rays, 80 brown smoothhound sharks, 66 leopard sharks, four angel sharks (Squatina californica), three sevengill sharks (Notorynchus cepedianus), three spiny dogfish (Squalus acanthias), two soupfin sharks (Galeorhinus galeus), two thornback rays (Platyrhinoidis triseriata) and one white sturgeon (Acipenser transmontanus) were caught. No teleosts were captured. Bat rays comprised 62% of the catch by numbers, leopard sharks and brown smoothhound sharks made up 19% and 16% respectively, and the remaining elasmobranchs (grouped) made up 3% of the total longline catch. Since our sampling effort was similar in both parts of the bay our catches in each area are directly comparable.

Male and female bat rays arrived in Tomales Bay in early spring and were present throughout the bay until late fall although females were always more common than males (Figure 4). Significantly more males and females were captured in the inner bay (X^2, $P < 0.003$ for each) although the males and females captured in the outer bay were significantly larger (greater DW) than those captured in the inner bay (ANOVA, $P < 0.02$, $P < 0.001$, respectively, Figure 5).

No leopard sharks were captured during December, January or February in either 1990/1991 or 1991/1992 (Figure 6). Both sexes were more abundant in the inner bay (X^2, both $P < 0.003$) but we found no differences in the TL of each sex in the inner and outer bay (Figures 6,7). Both males and females entered the bay in spring and female abundance in the inner bay peaked in August 1991, after which the numbers of both sexes declined (Figure 6).

Brown smoothhound sharks were common in Tomales Bay only during spring and late summer (Figure 7). Females were most abundant in the inner bay (X^2, $P < 0.001$) and we found no significant difference in the abundance of males by capture location; nor was there a difference in the size of each sex based on capture location (Figure 7,8).

The sevengill sharks, thornback rays, and soupfin sharks were captured in the inner bay, the white sturgeon and spiny dogfish were captured in the outer bay, and angel sharks were equally divided between the inner and outer bay.

Tag Returns.

432 bat rays were tagged between August 1990 and April 1992; 257 during monthly longline surveys and 175 during other operations in the bay. Only three fish were recaptured as of January 1993. The rays were at large for 106, 359, and 583 days each (sex and DW at release were: male, 81 cm; female, 114 cm; and male 72 cm, respectively). All were recaptured within 1 km of their tagging location in Tomales Bay. Unfortunately, anglers did not record disc widths from recaptured rays so we were unable to estimate growth rates.

Modeling.

The best model predicting the distribution and relative abundance of bat rays in Tomales Bay accounted for 77% of the variation in our data (Table 1, Figure 9). The main effect terms in this model were (in decreasing order of importance) temperature, salinity, season 1, season 3, location, set time, and season 2. Eight interaction terms were judged important by our selection criteria (Table 1).

Mean bat ray catches for the outer bay in November 1991 and the inner bay for September 1990, December 1990, and July 1991 fell outside the 95% confidence intervals of our model (Figure 10). Every fall, during October-November, the horizontal gradient of temperature and salinity in Tomales Bay breaks down as the inner bay water density exceeds that of the outer (Smith et al. 1991). Since the timing of this event differs from year to year, and we used only an average temperature and salinity for each month to predict the mean catch, the fault may lie in our data rather than with the model. September 1990 was our first sampling period and it is likely that we were less efficient in baiting and setting the longlines, as evidenced by the low catch in the outer bay as well (Figure 10). The model may have over-estimated the predicted mean catch for December 1990 because salinity of the inner bay remained higher during this January than it did in any year between 1988 and 1992 (Figure 3). I have no explanation for the discrepancy between the actual and predicted inner bay catch for July 1991.

The bat ray model, when fitted to data for leopard and brown smoothhound sharks, described 72% of the variation in the leopard shark data and 65% of the variation in the brown smoothhound data (Tables 1, and Figures 10,11).

Discussion.

Temperature and salinity are the most important environmental factors determining the distribution and abundance of bat rays in Tomales Bay (Table 1). In addition, the good fit of the bat ray model to the brown smoothhound and leopard shark data indicates that the factors which influence bat ray distribution and abundance in Tomales Bay also affect these species (Figures 10,11). While the importance of environmental variables in the distribution and abundance of teleosts is well known (Kennish 1990), this is the first rigorous test focusing on nearshore elasmobranchs.

Season 1 (January-March) and season 3 (July-September) were also important factors in our bat ray model, but their importance may be inflated somewhat due to the relationship between salinity and temperature. Late in season 1 (March) in 1991 and 1992, the temperature in both parts of the bay began rising, and salinity in the inner bay increased steadily (Figure 3) and the first and second highest catch of bat rays occurred. During season 3 the inner bay temperature remained consistently above that of the outer bay, and the inner and outer bay salinities diverged, as the inner bay became slightly hypersaline. Also, during July-September 1991 the catch of bat rays in the inner bay declined steadily, while outer bay catches increased slightly (Figure 4).

Location also played a significant part in our bat ray model. However, temperature and salinity are incorporated into the definition of location (inner and outer bay, Smith et al. 1991) and since they are important in our model, it is not surprising that location is also important.

Dissolved oxygen was not used in our model because it was always well above stressful levels (Chapman 1986, Lai et al. 1990, Hopkins, unpublished)(Figure 3). Our sampling protocol would not have allowed us to detect short-term oxygen depressions, such as those occurring nightly or lasting only a few days, or those restricted to small areas of the bay. Oxygen depressions are widespread phenomena (Loesch 1960, Taft et al. 1980, Coutant 1985, Day et al. 1990, Breitburg 1992) and while undocumented in Tomales Bay, may nevertheless contribute to the distribution of elasmobranchs in some systems.

The composition of our longline catch was similar to that of the July 1975 shark tournament in Tomales Bay (Karl 1979). Our catch consisted of 62% bat rays, 19% leopard sharks, 16% brown smoothhounds and 3% other species, while the 1975 shark derby catch was 59% bat rays, 14% leopard sharks, 16% brown smoothhounds, 9% spiny dogfish, and 2% other species (Karl 1979). Derby participants probably did not restrict their efforts to inside Tomales Bay, as we did, and several local fisherman have told one of us (T.E.H.) that spiny dogfish are commonly caught while fishing off the mouth of Tomales Bay, but rarely captured inside the bay.

Few studies have been conducted for long periods over broad geographic ranges so that the true population sex ratio is unknown for most elasmobranchs. To date, only Ridge (1963), de Wit (1975) and this study have reported sex ratios from sampling programs lasting more than one year in northern or central California. Published sex ratios for our three target species have varied greatly (Table 2), most likely due to differences in sampling techniques. Sampling in shallow bays is hampered by biases associated with the collection techniques which vary with season, life stage, and location (Pierce et al. 1990, Weinstein and Davis 1980, Horn and Allen 1985, Livingston 1987). Otter trawls and beach seines can over-inflate the relative importance of small gear-susceptible species or life stages, and underestimate the abundance of larger, faster life stages (Yoklavich et al 1991). Gill nets, with several different-sized panels, may capture a broad range of size classes, but are often fatal for sharks unless fished with great care. In addition, gill nets may not capture rays unless they become entangled by their dorsal spines (Talent 1985). Longlines are a good alternative unless diets are to be studied because only foraging individuals are captured. However, longlines will only capture certain size classes and more mobile species so that hook size and bait selection are important considerations. Shark derbies typically yield a large number of specimens but sex ratios are apt to be skewed because derbies are highly localized, short-term collections, and participants are less likely to report smaller individuals. Finally, Russo and Herald (1968) took advantage of an unusual occurrence, an elasmobranch kill of unknown cause, and recorded data from 10,338 elasmobranchs during an 11 day period in San Francisco Bay. Regardless of sampling bias, sex ratios are difficult to interpret because many elasmobranchs have seasonal movement patterns and school by sex or size, especially in spawning or nursery areas (Castro 1983, Compagno 1984).

Between 35% and 67% of the female bat rays captured in Tomales Bay were sexually mature (50% mature at 88 cm DW, 100% are mature at 100 cm DW; Martin and Cailliet 1988a) and 63% of all males captured were sexually mature (> 62 cm DW)(Figure 5). In comparison, only 8-12% of the females and 27% of the males captured by Ridge (1963) were sexually mature. Ridge (1963) also sampled throughout the year, and while his sample size is 2.4 times larger than ours, most rays were supplied by commercial gill-netters targeting smaller sharks so that his data may be biased toward smaller less mature rays.

Ninety-five percent of the female brown smoothhounds captured in Tomales Bay were sexually mature (> 63 cm TL, Figure 8)(Compagno 1984). During April-May 1991 and September-October 1991, when most of the females were captured, many were gravid and several gave birth to 5-10 near-term or full-term young while on the boat. Males, while much less common than females, were most abundant in April-May 1991, and all were sexually mature (> 66 cm TL, Figure 7). A 90 cm TL male was captured during October 1991 in the inner bay (15 km from the mouth) which increases the maximum recorded size for a male of this species by 10.5 cm (Yudin and Cailliet 1990).

Of the 66 leopard sharks captured 15% of the females (>100 cm TL) and 80% of the males (> 76 cm TL) were sexually mature (Smith and Abramson 1990)(Figure 8). The paucity of reproductive age females has been noted previously (Smith and Abramson 1990, King and Cailliet, unpublished), and may be due to an increase in commercial and recreation fishing pressure (Smith and Abramson 1990, Cailliet 1992).

Female rays captured in the outer bay were significantly larger than those captured in the inner bay (anova, $P < 0.001$). Several studies of teleosts have demonstrated ontogenetic shifts in thermal preference such that older individuals tend to prefer cooler temperatures (Magnuson et al. 1979, McCauley and Huggins 1979, Coutant 1985, Kennish 1986). It is possible that larger rays prefer the cooler deeper water near the mouth of Tomales Bay. There is some evidence that bat rays behaviorally thermoregulate (Hopkins unpublished). During June and July 1991 several telemetered rays were tracked moving from the inner to the outer bay late in the day and returning to the inner bay early the next morning, a round trip distance of about 16 km (Hopkins unpublished). I have hypothesized that the rays may be thermoregulating or avoiding nightly hypoxia (Hopkins and Cech 1993).

Bat rays, brown smoothhounds, and leopard sharks tend to move out of bays and estuaries during winter months (Compagno 1984, Ridge 1963), although winter outmigrations are less common in southern and central California bays where winter temperatures are warmer and salinities are less variable. All three species left Tomales Bay sometime between late November and early February in each year of this study. Hopkins (unpublished) used bat rays with implanted ultrasonic transmitters and showed that they are not present in Tomales Bay during the winter months. Five of five rays with transmitters disappeared in late-November 1990 when inner bay temperatures were between 10-12°C, and reappeared in early February 1991, about a week after the inner bay rose above 10°C (Hopkins, unpublished data). How far any of these species travel during their outmigration, and what occurs during these movements (e.g. mating) is unknown.

Karl (1979) found that of 90 rays tagged in June 1975, one was captured two weeks later in Tomales Bay, and two were captured in San Francisco Bay, 25 km south, one month later. Smith and Abramson (1990) found that leopard sharks tended to move out of San Francisco Bay during fall and winter; one tagged individual was recaptured 140 km south in Elkhorn Slough, California. Talent (1985) mentions that a leopard shark tagged in Elkhorn Slough was later captured in San Francisco Bay and Compagno (1984) reported that a tagged brown smoothound migrated 160 km in three months. Of the 432 bat rays tagged during this study, only three were recaptured (as of January 1993). All three rays were recaptured within 1 km of their tagging location in Tomales Bay. This suggests that bat rays may possess the ability to return to specific areas within Tomales Bay on a yearly basis.

In conclusion, temperature and salinity are important factors determining the distribution and abundance of the most common elasmobranchs in Tomales Bay. Because physical factors in nearshore environments fluctate on a daily, seasonal, and yearly basis, and little is known about the influence of biotic factors (e.g. competition, predation) which can limit an elasmobranchs ability to occupy its entire physiological niche, elasmobranch distributions in nearshore habitats are best delineated by abiotic factors (Roughgarden and Diamond 1986, Huey 1991, Dunson and Travis 1991).

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Table 1. Parameters and goodness of fit criteria for models of distribution and relative abundance of three elasmbranchs in Tomales Bay, California.

Parameter	Bat Ray	Leopard Shark	Brown Smoothhound
Intercept	16.7493	-11.4120	9.6878
Temperature (Temp)	-2.3000	0.5622	-0.8009
Salinity (Sal)	-0.6006	0.2597	-0.2442
Location (Loc)	1.7282	0.8913	-0.7483
Set Time	0.7233	0.4101	-0.1186
Season 1	-6.4487	2.1820	-3.1906
Season 2	3.0970	3.7788	6.0185
Season 3	3.0891	-5.7729	-0.7478
Temp*Salinity	0.0732	-0.0153	0.0300
Temp*Salinity*Season 1	0.0187	-0.0042	0.0068
Temp*Salinity*Season 2	-0.0065	-0.0074	-0.0122
Temp*Salinity*Season 3	-0.0082	-0.0101	0.0015
Temp*Salinity*Location	-0.0055	-0.0024	0.0012
Temp*Sal*Loc*Season 1	-0.0019	-0.0004	0.0004
Temp*Sal*Loc*Season 2	-0.0001	-0.0009	-0.0008
Temp*Sal*Loc*Season 3	-0.0006	-0.0009	0.00002
r^2	0.77	0.72	0.65
r^2adj	0.61		
AIC	-0.40		
Cp	8.88		

Table 2. Sex ratios for three species of elasmobranchs from bays and estuaries in northern and central California.

Species	Male:Female	N	Capture method	Source
Bat Ray				
	1:4.5	33	longline, rod-reel	1
	1:4.2	257	longline	2
	1:2.0	2960	derby	3
	1:1.2	422	derby	4
	1:1.1 adult	621	gill net, rod-reel	5
	1:1	?	shark kill	6
	1:0.6 embryo	10	gill net, rod-reel	5
Brown Smoothhound				
	1:4.5	492	shark kill	6
	1:4.3	80	longline	2
	1:2.3	131	trawl	7
	1:2.2	89	longline, rod-reel	1
	1:0.3	872	longline	1
Leopard Shark				
	1:2	156	longline, rod-reel	1
	1:1.6	?	derby	1
	1:1.6	66	longline	2
	1:1	?	shark kill	6
	1:1	92	trawl	7
	1:0.9	1194	derby	3
	1:0.9	948	longline	8

1/Ebert 1986, 2/this study, 3/King and Cailliet unpublished, 4/Karl 1979, 5/Ridge 1963, 6/Russo and Herald 1968, 7/deWit 1975, 8/Smith and Abramson 1990.

Figure 1. Map of Tomales Bay, California showing station locations (km from the bay mouth). Outer bay is stations 1-4, inner bay is stations 5-9.

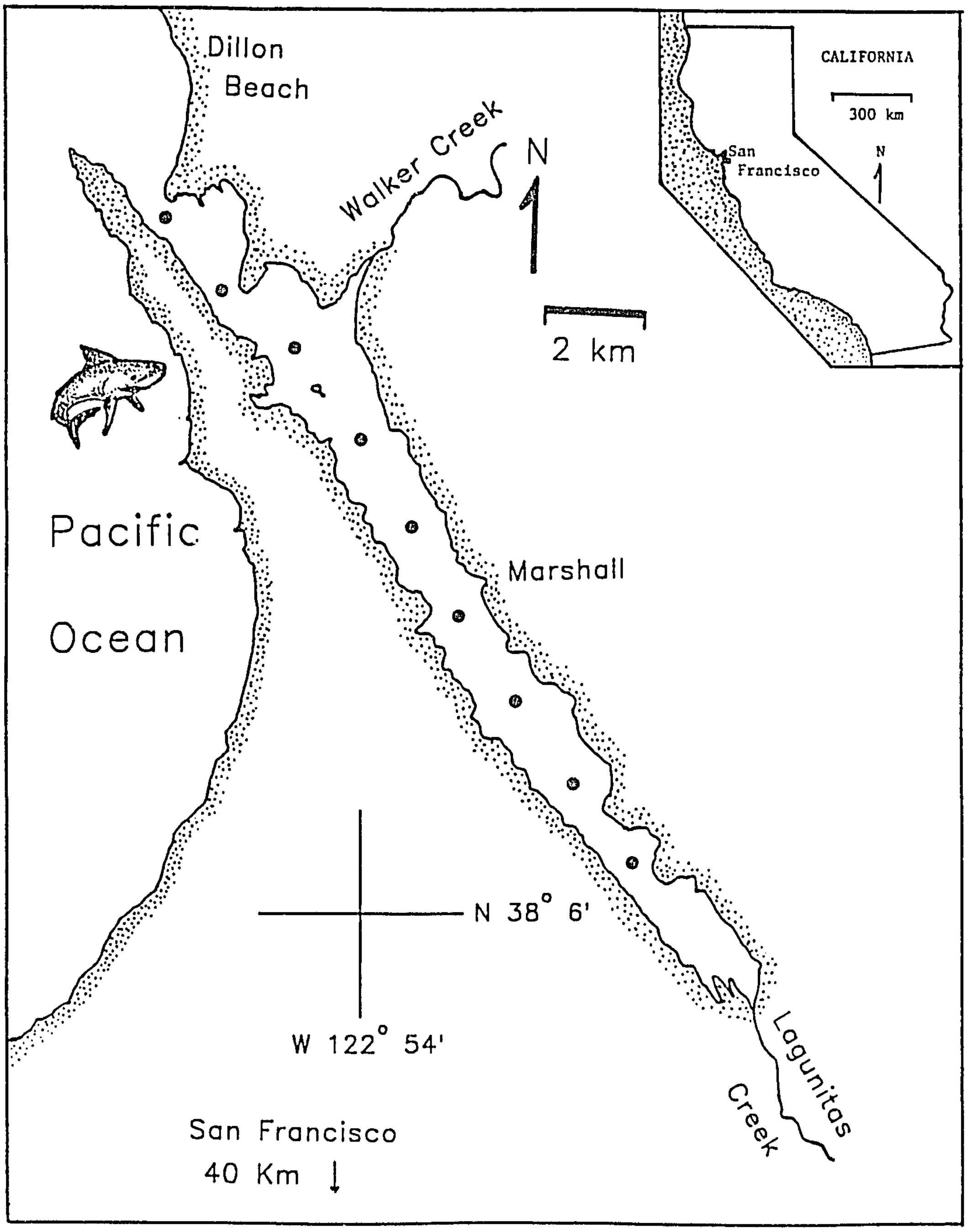

Dillon
Beach
Walker Creek
N
2 km
Pacific
Ocean
Marshall
N 38° 6'
W 122° 54'
Lagunitas
Creek
San Francisco
40 Km ↓
CALIFORNIA
300 km
N
San
Francisco

Figure 2. Tomales bay depth profile and sampling stations.

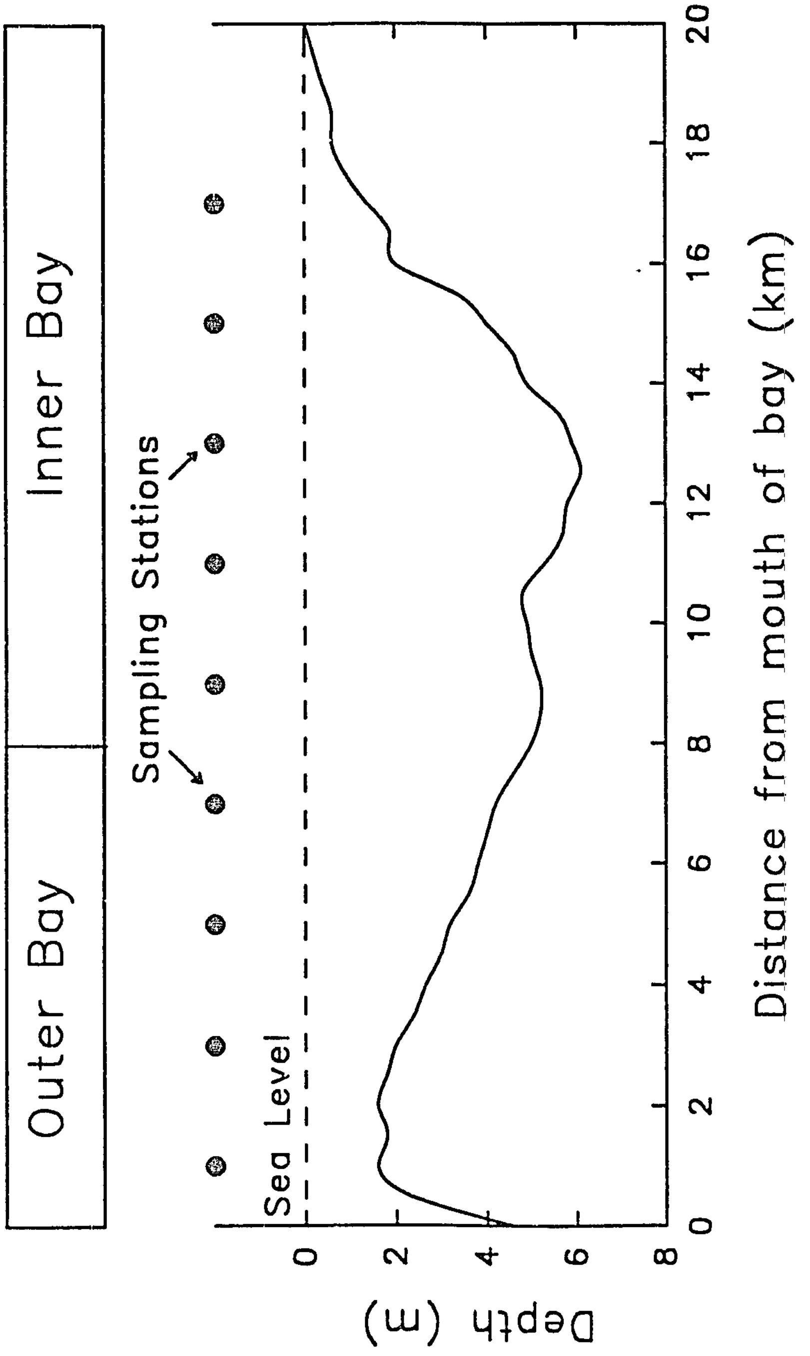

Outer Bay
Inner Bay
Sampling Stations
Sea Level
Depth (m)
0
2
4
6
8
Distance from mouth of bay (km)
0
2
4
6
8
10
12
14
16
18
20

Figure 3. Tomales Bay temperature (A), salinity (B), and dissolved oxygen (C) September 1990-April 1992. Dashed lines are bay outer bay values and solid line represents inner bay values. Temperature data are daily average bottom temperature at the mouth (km = 0) and the inner bay (km = 12). Salinity data are from the same stations, but taken about every 2 weeks. Dissolved oxygen data are average outer and inner bay values from monthly vertical transects. Temperature and salinity data are unpublished data from S. Smith and J. Hollibaugh (U. HI and SFSU, respectively).

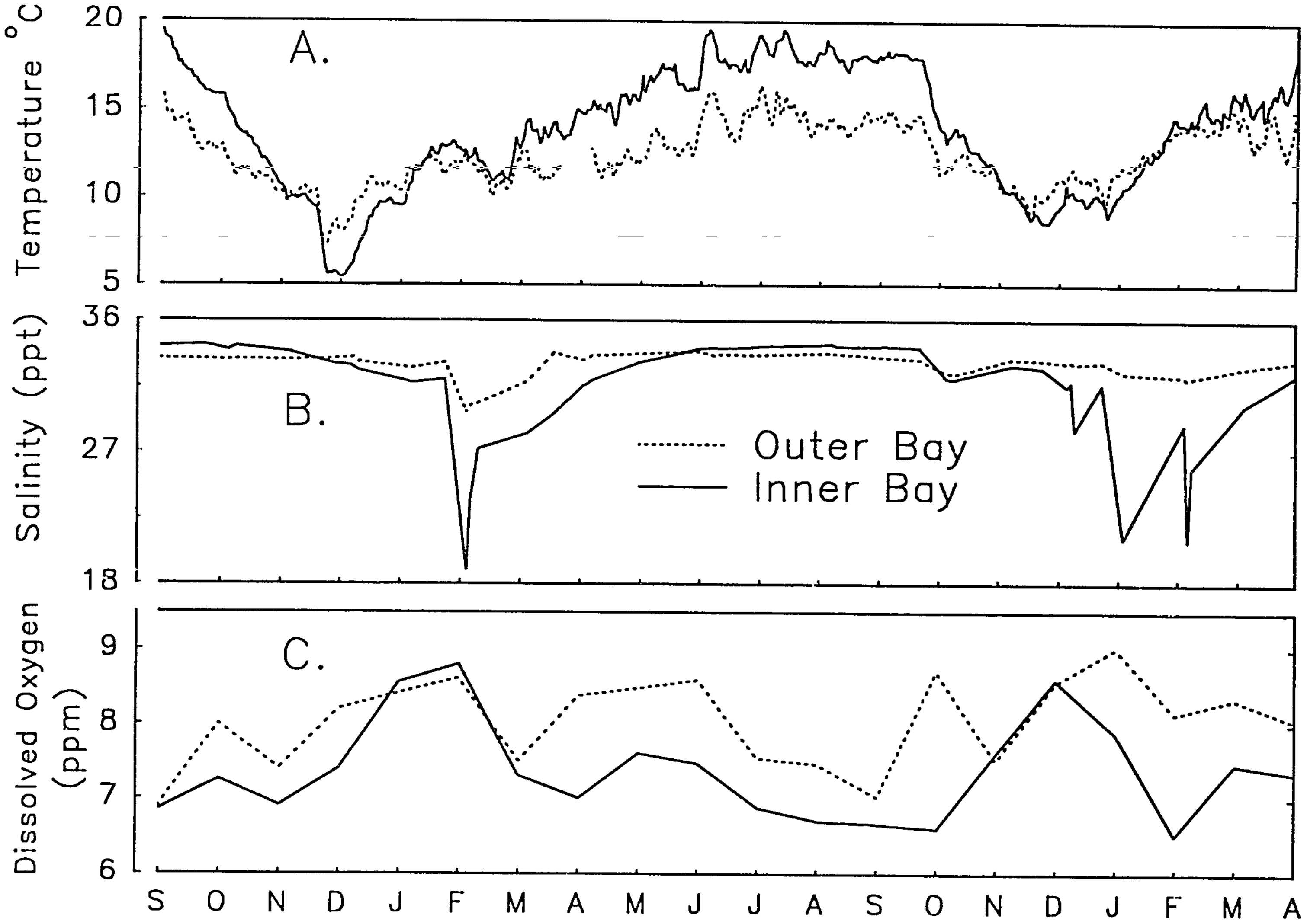

A.
Temperature °C
20
15
10
5
B.
Salinity (ppt)
36
27
18
Outer Bay
Inner Bay
C.
Dissolved Oxygen (ppm)
9
8
7
6
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A

Figure 4. Mean outer Bay (A) and inner bay (B.) catches of bat rays (males closed circle, females open triangle), September 1990-April 1992.

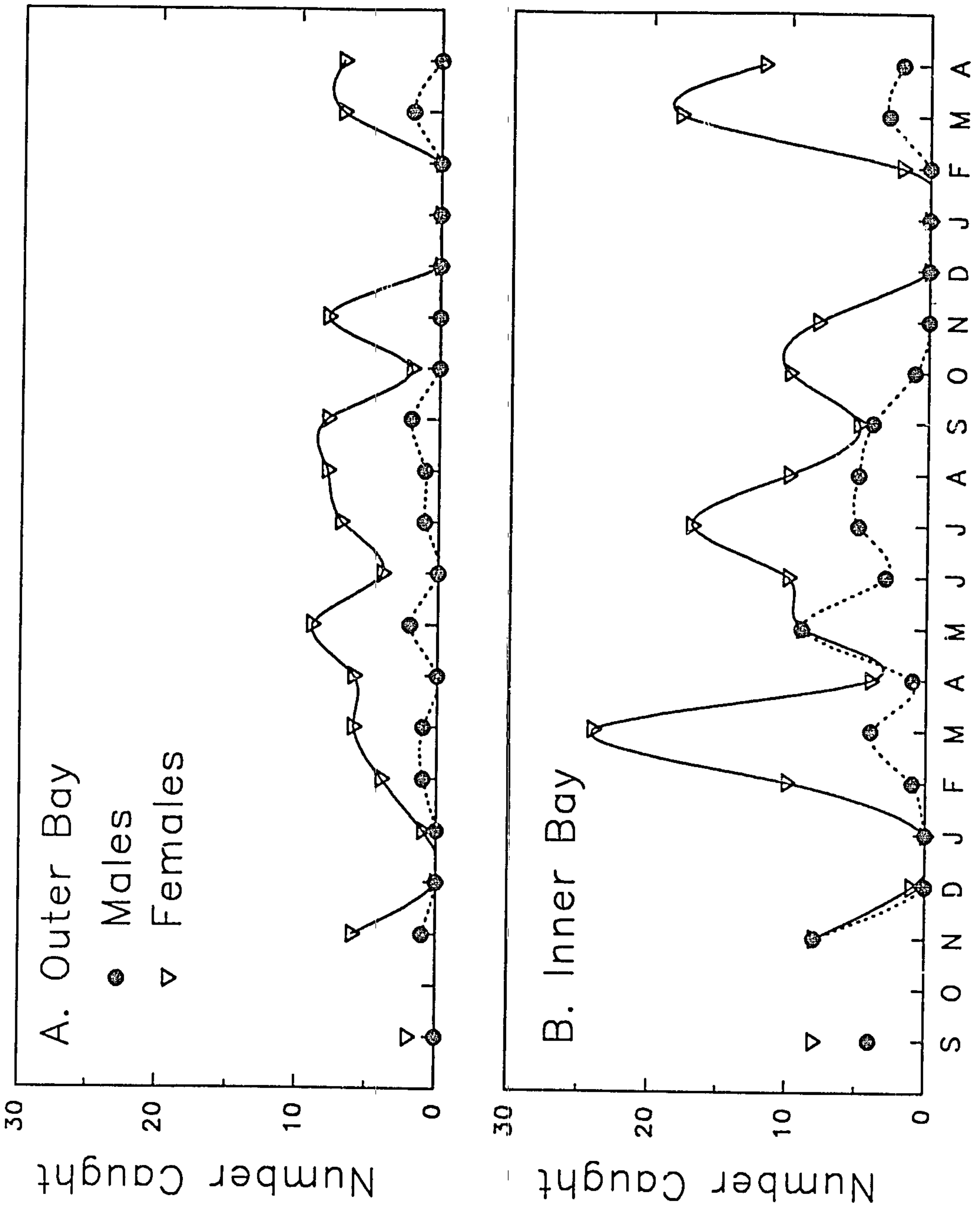

A. Outer Bay
Males
Females
B. Inner Bay
Number Caught
Number Caught
0
10
20
30
0
10
20
30
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A

Figure 5. Length frequency of male (hatched) and female (solid) bat rays captured in outer (A) and inner (B) Tomales Bay. N in parentheses.

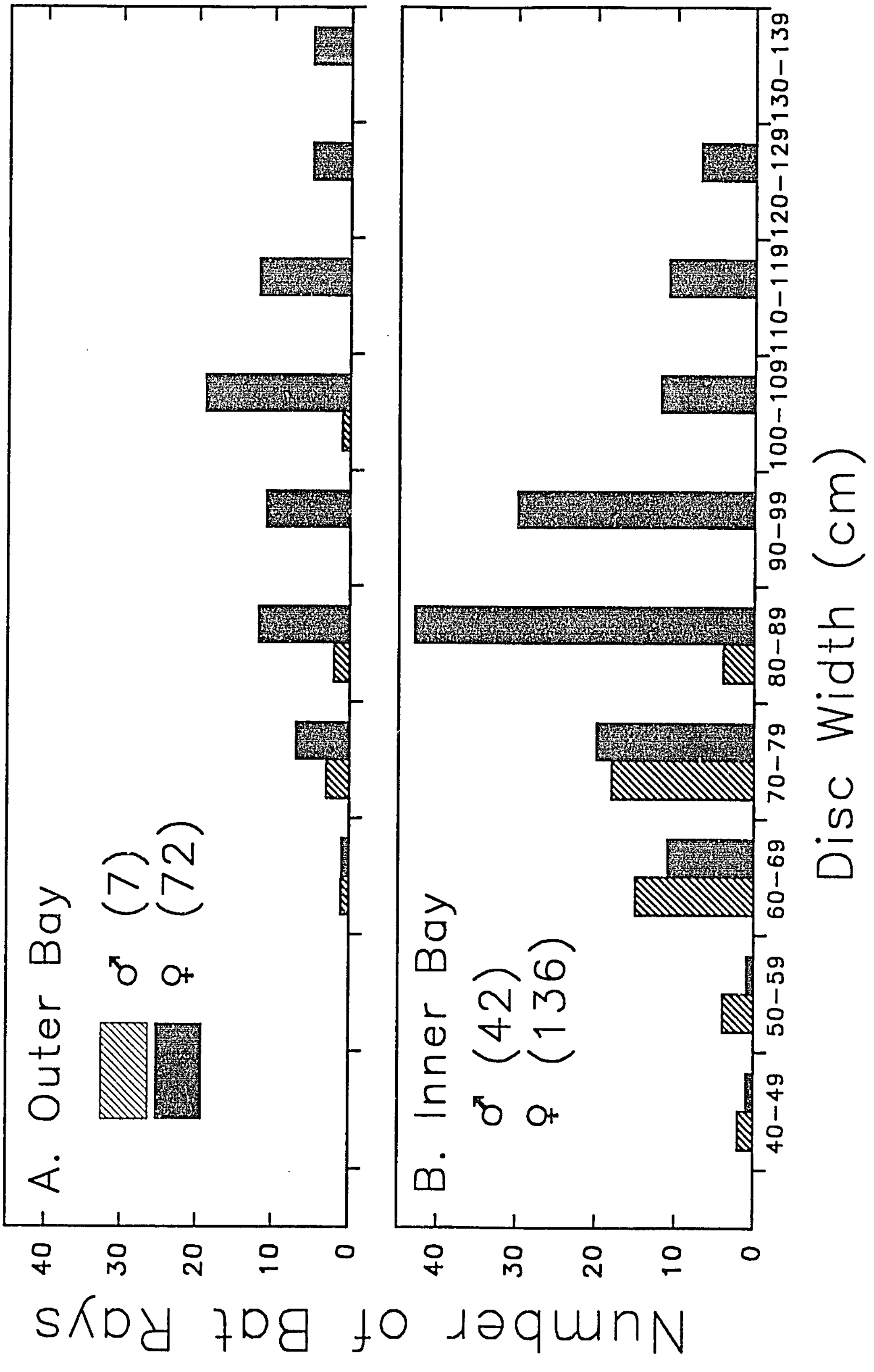

A. Outer Bay
♂ (7)
♀ (72)
B. Inner Bay
♂ (42)
♀ (136)
0
10
20
30
40
Number of Bat Rays
40-49
50-59
60-69
70-79
80-89
90-99
100-109
110-119
120-129
130-139
Disc Width (cm)

Figure 6. Mean outer Bay (A) and inner bay (B) catches of leopard sharks (males closed circle, females open triangle), September 1990-April 1992.

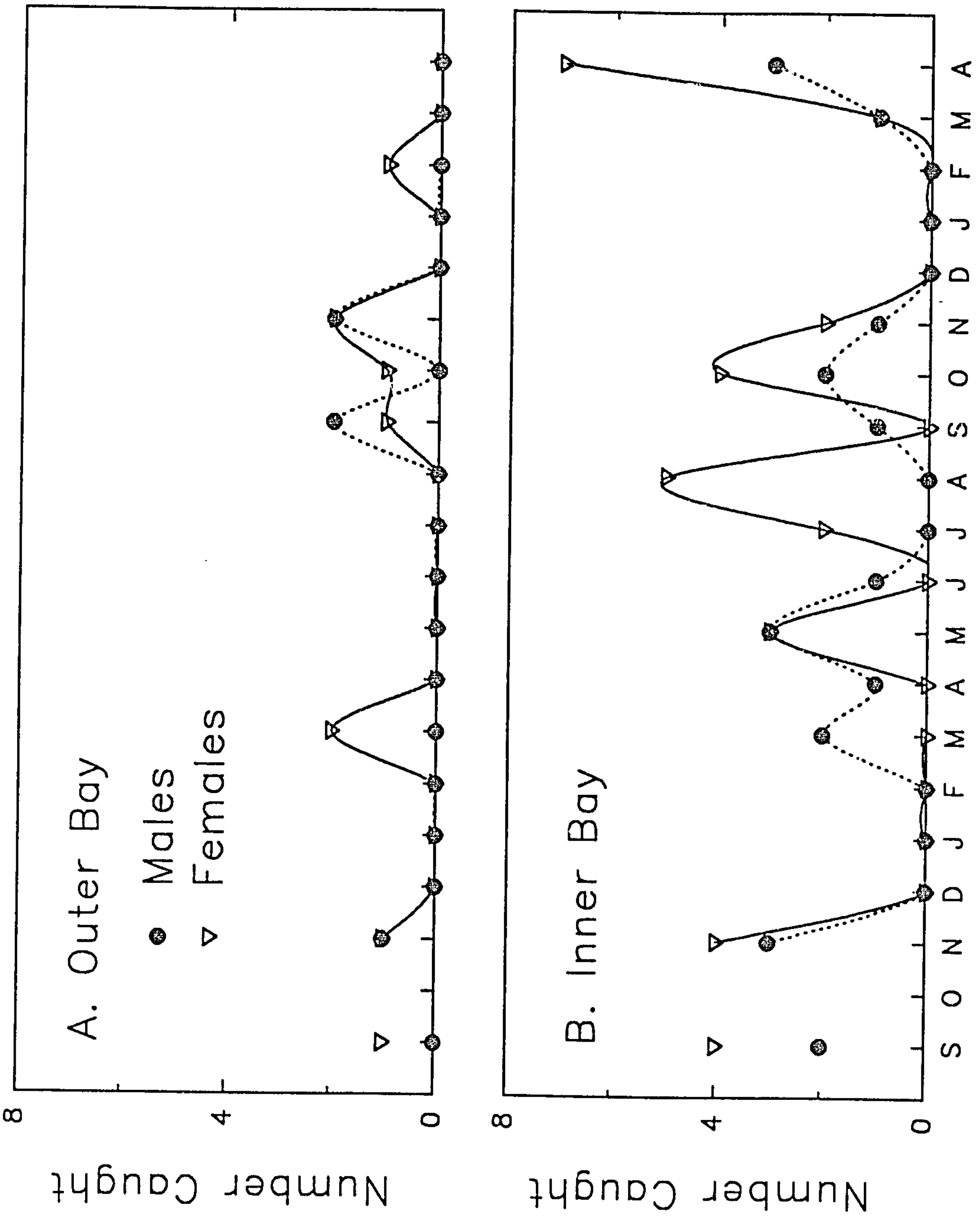

A. Outer Bay
● Males
▽ Females
B. Inner Bay
Number Caught
Number Caught
0
4
8
0
4
8
S O N D J F M A M J J A S O N D J F M A

Figure 7. Length frequency of male (hatched) and female (solid) leopard sharks captured in outer (A) and inner (B) Tomales Bay. N in parentheses.

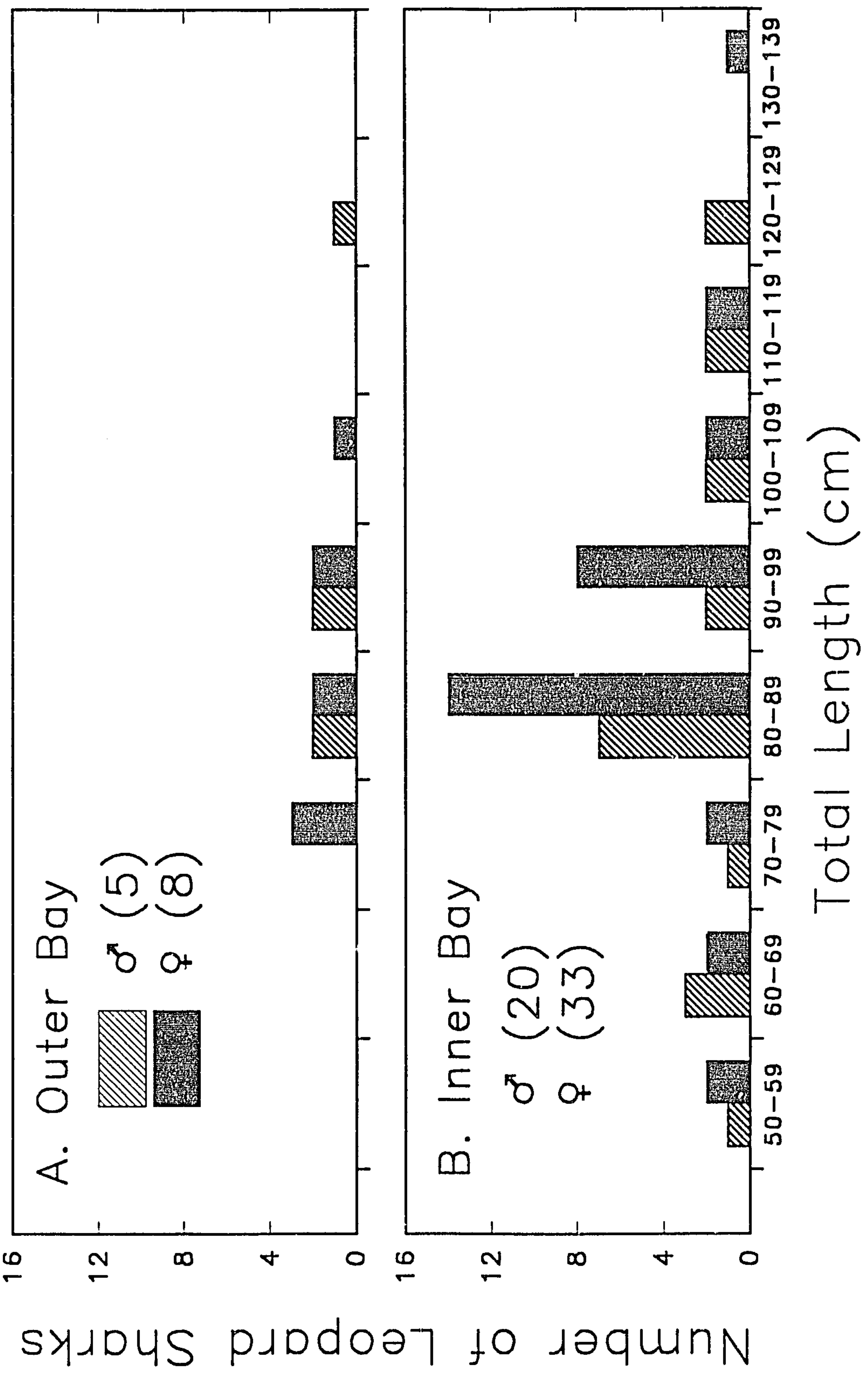

A. Outer Bay
♂ (5)
♀ (8)
B. Inner Bay
♂ (20)
♀ (33)
0
4
8
12
16
Number of Leopard Sharks
50-59
60-69
70-79
80-89
90-99
100-109
110-119
120-129
130-139
Total Length (cm)

Figure 8. Mean outer Bay (A) and inner bay (B.) catches of brown smoothhound sharks (males closed circle, females open triangle), September 1990-April 1992.

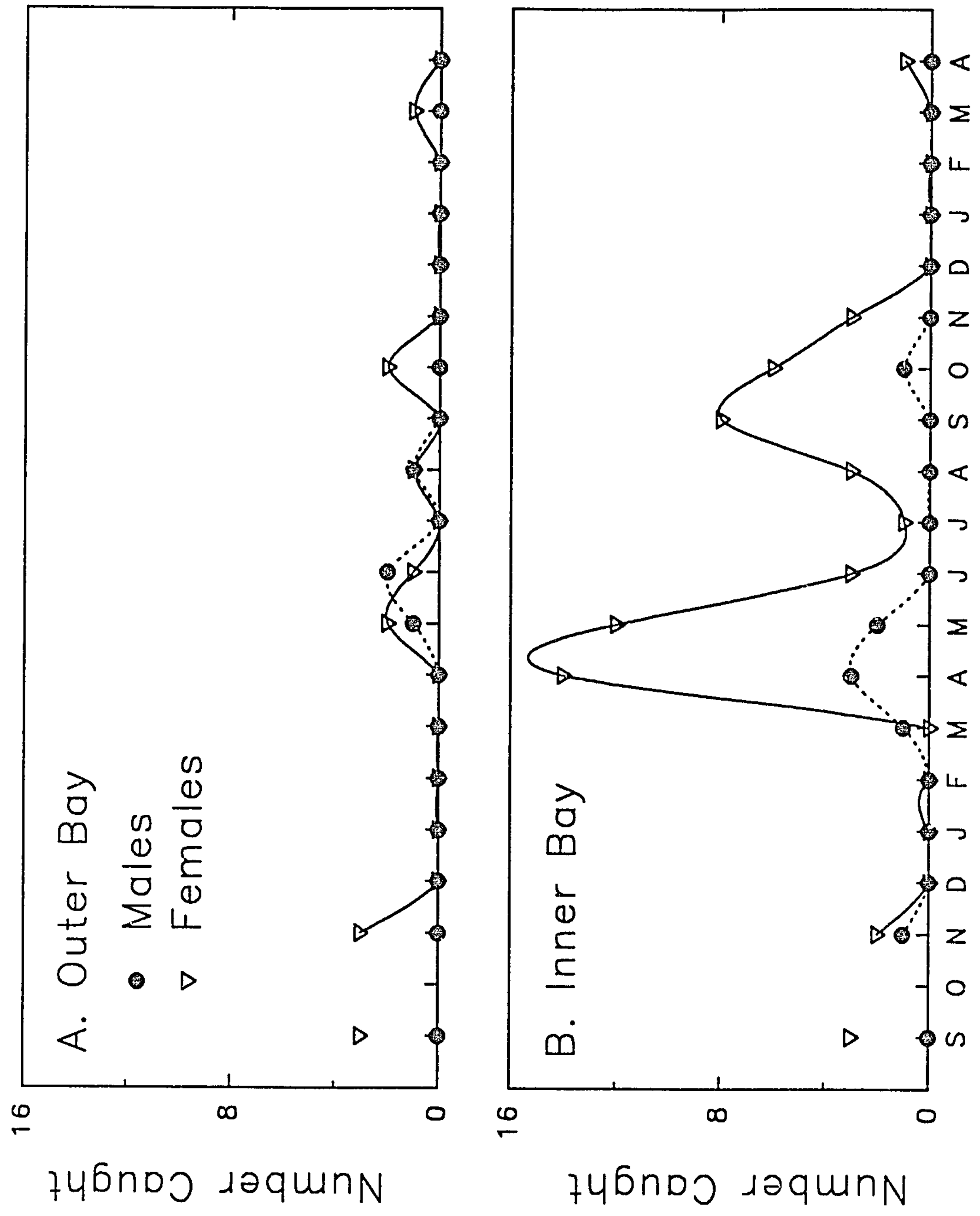

A. Outer Bay
Males
Females
B. Inner Bay
Number Caught
Number Caught
16
8
0
16
8
0
S O N D J F M A M J J A S O N D J F M A

Figure 9. Length frequency of male (hatched) and female (solid) brown smoothound sharks captured in outer (A) and inner (B) Tomales Bay. N in parentheses.

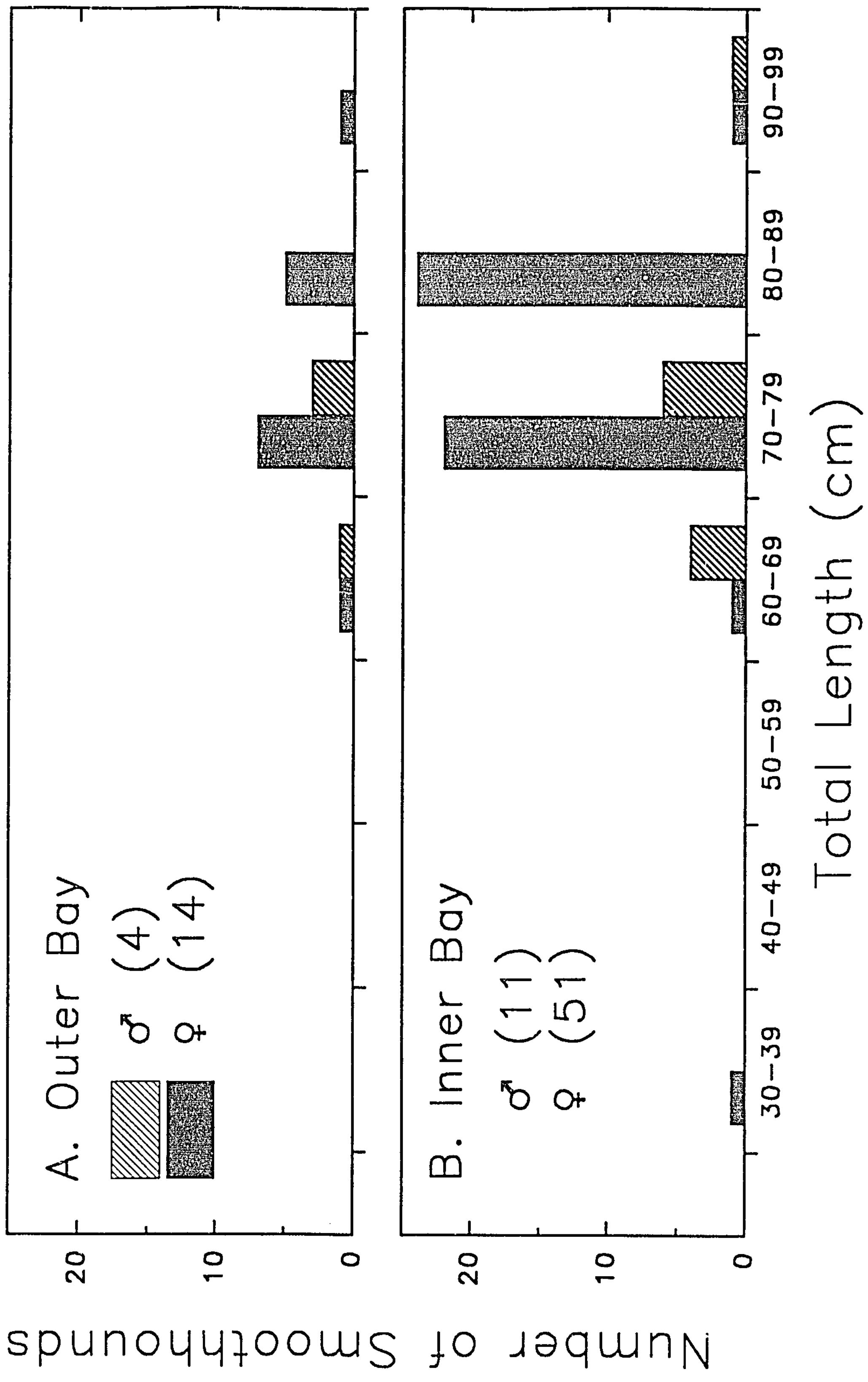

A. Outer Bay
▨ ♂ (4)
▩ ♀ (14)
B. Inner Bay
♂ (11)
♀ (51)
0
10
20
30–39
40–49
50–59
60–69
70–79
80–89
90–99
Total Length (cm)
Number of Smoothhounds

Figure 10. Actual catch (closed circles) and predicted catch (open triangles) with model 95% confidence limits for bat rays captured between September 1990 and April 1992.

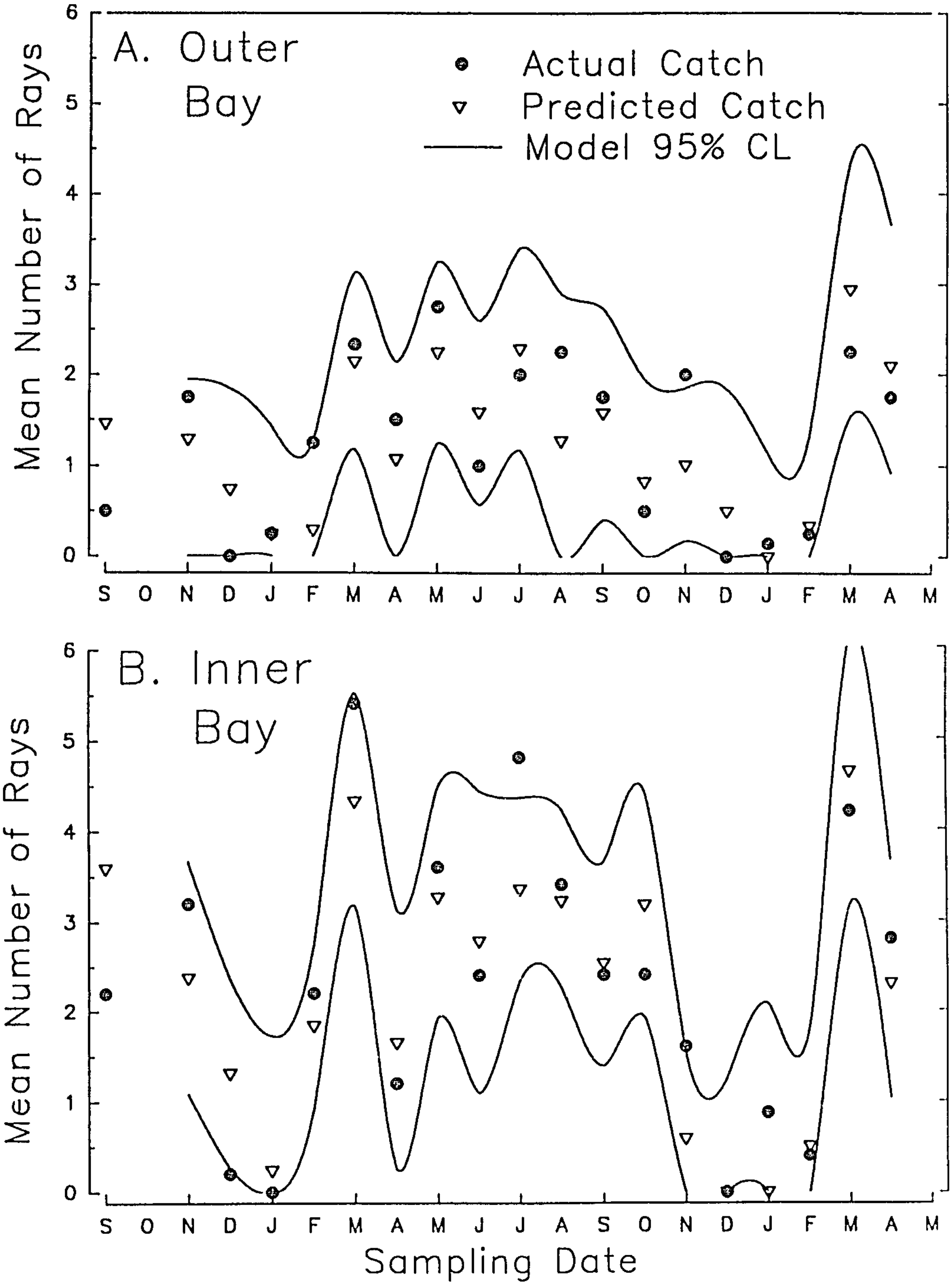

A. Outer Bay
Actual Catch
Predicted Catch
Model 95% CL
B. Inner Bay
Mean Number of Rays
0
1
2
3
4
5
6
S O N D J F M A M J J A S O N D J F M A M
Sampling Date

Figure 11. Actual catch (closed circles) and predicted catch (open triangles) with model 95% confidence limits for leopard sharks captured between September 1990 and April 1992.

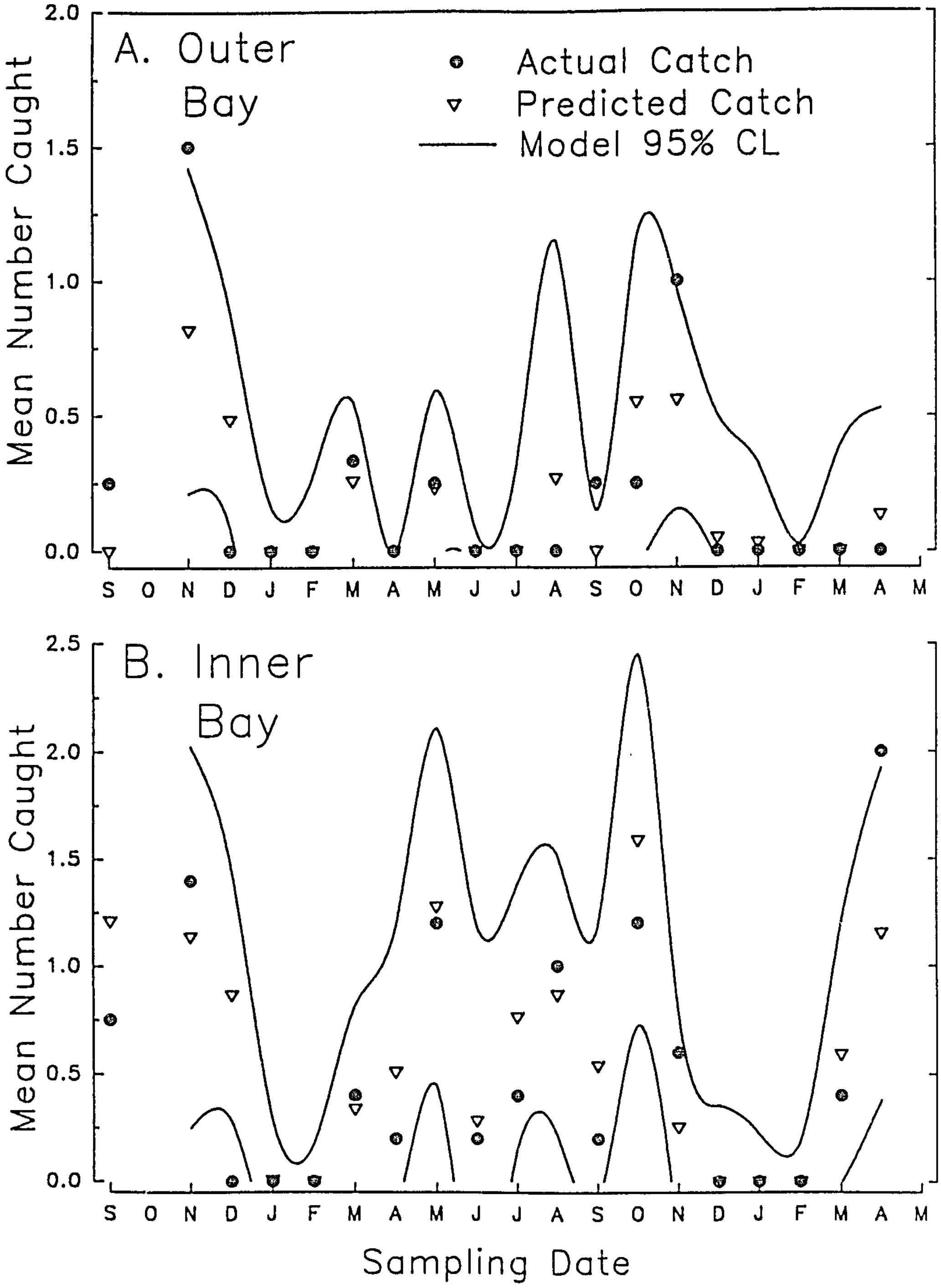
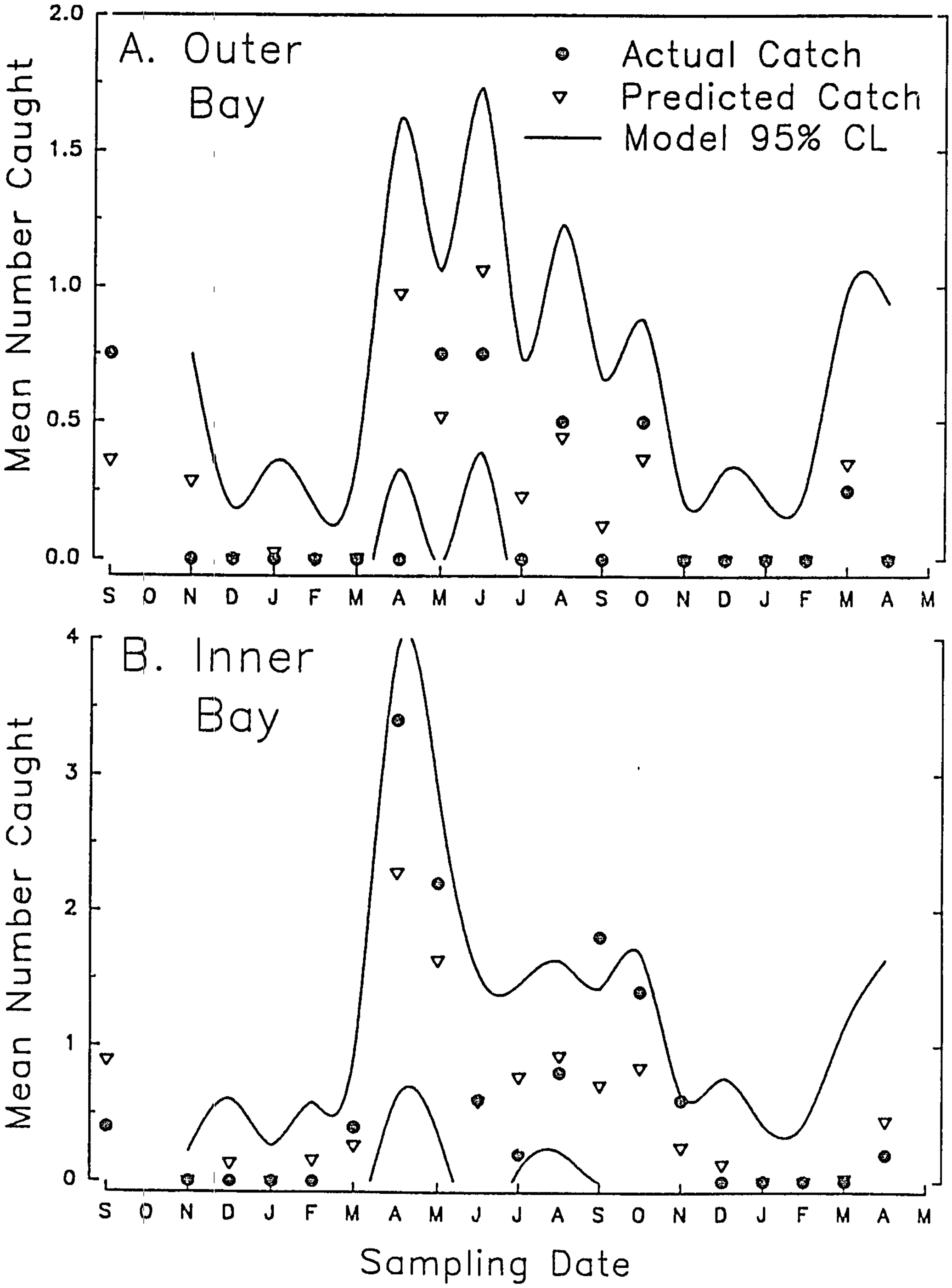

A. Outer Bay
Actual Catch
Predicted Catch
Model 95% CL
Mean Number Caught
2.0
1.5
1.0
0.5
0.0
S O N D J F M A M J J A S O N D J F M A M
B. Inner Bay
2.5
2.0
1.5
1.0
0.5
0.0
S O N D J F M A M J J A S O N D J F M A M
Sampling Date

Figure 12. Actual catch (closed circles) and predicted catch (open triangles) with model 95% confidence limits for brown smoothhound sharks captured between September 1990 and April 1992.


A. Outer Bay
B. Inner Bay
● Actual Catch
▽ Predicted Catch
Model 95% CL
Mean Number Caught
2.0
1.5
1.0
0.5
0.0
4
3
2
1
0
S O N D J F M A M J J A S O N D J F M A M
Sampling Date