THE LIFE HISTORY OF THE SPOTTED SAND BASS (*PARALABRAX MACULATOFASCIATUS*) WITHIN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Spotted sand bass (*Paralabrax maculatofasciatus*) are under increasing angling pressure in the shallow waters off southern California. In southern California, spotted sand bass are largely restricted to shallow, warm-water areas such as bays, estuaries, and harbors, which appear to serve as warm-water refuges for this basically subtropical species. Rod-and-reel sampling from June 1991 to August 1993 yielded 639 individuals from seven locations. Specimens ranged from 51 to 400 mm SL, with only 8 fish below 150 mm SL and 10 above 330 mm SL. Analysis of otolith sections revealed that a single opaque zone was laid down each summer. The oldest fish was 14 years old; the vast majority of the large specimens were 6 to 10 years old. Growth rate was sharply asymptotic, with some fish reaching 200 mm SL in their first year. Because growth rates varied significantly among the four locations tested, the overall growth model was highly variable (R^2 = 0.67). Half of the female spotted sand bass matured very early (age class 0) and at a small size (155 mm SL). Males matured later (50% maturity at 1.4 years) and at a somewhat larger size (50% at 180 mm SL). Gonosomatic indices indicated that spawning occurred from June through August in southern California.

Spotted sand bass inhabiting the northern Gulf of California are believed to be protogynous hermaphrodites, and populations from San Diego Bay showed an age/sex composition pattern consistent with protogyny. However, populations from the six other southern California locations had roughly equal representation of the sexes throughout the age structure, and many of the oldest individuals were females. This pattern is more consistent with gonochorism or "partial" protogyny. Southern California spotted sand bass seem to have a complex reproductive strategy which may include flexible rates of female sex change among populations and sneaking males that mimic females within spawning aggregations.

Back-calculation of annual recruitment success from otolith data revealed that almost all of our fish came from two pulses during 1984–85 and 1989–90. These pulses occurred during post-El Niño years. Recruitment into southern California during El Niño years (1982–83, 1986–87, and 1992–93) appears to have been extremely low to nonexistent. However, summer sea-surface temperatures at the Scripps Pier peaked one to two years after these El Niño events, resulting in a highly significant correlation (r = 0.723, df = 13, P = 0.002) between recruitment (corrected for mortality) of spotted sand bass and mean summer sea-surface temperature off southern California over the past 15 years.

[Manuscript received January 30, 1995.]

INTRODUCTION

Historically, spotted sand bass (*Paralabrax maculatofasciatus*) have ranged as far north as San Francisco Bay and south to Mazatlán, Mexico. Dense populations also occur in the northern portions of the Gulf of California (Sea of Cortez). Typically, spotted sand bass are rarely seen north of Santa Monica Bay. Early records of occurrence at more northern locations often came from El Niño and other warm-water periods. In southern California, spotted sand bass are restricted to shallow, warm-water areas such as bays, harbors, and quiet, protected areas of the coast that contain structure in the form of eelgrass, surfgrass, and rock relief (Fitch and Lavenberg 1975). These areas act as warm-water refuges for this generally subtropical species (Allen 1985).

While protected from commercial exploitation, spotted sand bass have come under increasing recreational angling pressure off southern California in recent years. Landings are greatest from private boats and rental skiffs fishing such prominent bay and estuarine habitats as Newport Bay, Mission Bay, and San Diego Bay (Love 1991; Ono 1992). The California Department of Fish and Game conducted a survey of skiff fishing and estimated that the annual catch of spotted sand bass in southern California waters ranged from 12,790 to 23,933 fish between 1976 and 1981. Subsequent estimates of sport catch, based on data from boat and shore fishing, indicated that between 53,000 and 170,000 spotted sand bass were taken per year from 1980 to 1989 (Ono 1992). Although the annual catch of spotted sand bass is considerably lower than the catches of its sympatric relatives the kelp bass (*Paralabrax clathratus*) and the barred sand bass (*P. nebulifer*), the fishing pressure on spotted sand bass must be considered significant because of their restricted habitat in southern California waters.

Prior to the current investigation, very little was known about the biology of this important sport fish. The largest spotted sand bass on record measured 450 mm standard length (SL) and weighed 2.6 kg (Miller and Lea 1972), but specimens longer than 330 mm SL are very rare. Before this study, the only information available on age came from a single specimen, 380 mm total length (TL), aged at 5 years (Fitch and Lavenberg 1975). The larval and juvenile stages of spotted sand bass have been described from laboratory-reared specimens by Butler et al. (1982). In southern California, these fish appear to form spawning aggregations at the mouths of embayments during the late spring and summer. The eggs are pelagic and enter the plankton in coastal waters. Studies of the spotted sand bass population in the northern Gulf of California indicated that fish from that location appear to be sequential, protogynous hermaphrodites (Hastings 1989). According to Hastings, most fish mature first as females and later change into males, although primary males may also exist. In a recent paper, Oda et al. (1993) presented limited evidence that individuals from Mission Bay in southern California were also protogynous hermaphrodites.

The primary purpose of our study was to provide basic information on the life history and ecology of spotted sand bass from southern California. This paper summarizes information on (1) length frequency, (2) length-weight relationship, (3) age and growth, (4) food habits, (5) reproductive cycles, (6) age at first maturity, (7) sex composition with age, and (8) annual recruitment patterns of spotted sand bass within the Southern California Bight.

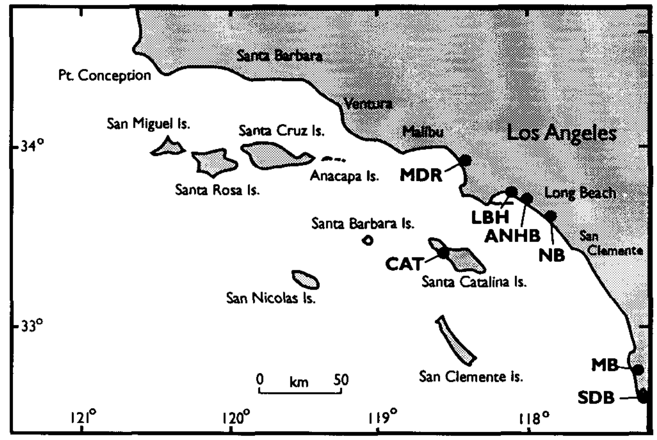

Figure 1. Mainland and Catalina Island locations where spotted sand bass were collected during 1991–93. *ANHB* = Anaheim Bay; *CAT* = Catalina Harbor; *LBH* = Long Beach Harbor; *MDR* = Marina del Rey; *MB* = Mission Bay; *NB* = Newport Bay; *SDB* = San Diego Bay.

METHODS AND MATERIALS

Collection of Specimens

Spotted sand bass are structure-oriented, fairly sedentary fish that are virtually impossible to capture with standard scientific collecting methods (trawls, seines, and gill nets). Rod-and-reel (light tackle) sampling with artificial lures is the only efficient method for collecting large numbers of spotted sand bass. To this end, a professional fishing guide, Mike Gardner, was contracted to make twelve monthly sampling trips using rod and reel between March 1992 and February 1993. On these twelve trips we sampled spotted sand bass at the following locations within the bight (figure 1): Anaheim Bay, Long Beach Harbor, Marina del Rey, Newport Bay, and San Diego Bay. These collecting trips yielded about 40 spotted sand bass each month, except for January 1993, when no fish were caught following 13 straight days of rainfall. Additional collections were made with rod and reel from 6 m Boston whalers launched from the R/V *Yellowfin* operated by the Ocean Studies Institute of the California State University. These collections were taken at Catalina Harbor, Newport Bay, Mission Bay, and San Diego Bay from July 1991 through August 1993. National Marine Fisheries Service, Long Beach, provided five young-of-the-year spotted sand bass collected by beach seine from Mission Bay in April 1993. Finally, a number of large specimens were donated by local anglers in response to flyers distributed throughout southern California. Overall, 639 fish were included in this study.

Specimens were either returned to the research vessel or placed on ice and returned to the laboratory for workup. Donated fish were typically accepted in a frozen state and thawed before workup. Each fish was numbered, measured to the nearest mm (both SL and TL), and weighed to the nearest 0.1 g. Both sagittae were removed, cleaned, air-dried, and stored in labeled envelopes. Finally, the digestive tract and gonads were dissected out and preserved in 10% Formalin and seawater in individual zip-lock bags for later analysis.

All data were entered into Reflex 2.0 (Borland International Inc., Scotts Valley, CA) database form on an MS DOS desktop computer system for storage and subsequent analysis. Data summary and analyses were carried out with the Complete Statistical System (CSS; Statsoft Inc., Tulsa, OK).

Age and Growth

The left sagitta (in most cases) of each specimen (N = 634) was sectioned with a Buehler Isomet low-speed saw. Otoliths were attached to wood blocks with cyanoacrylate (Super glue). Each block with its sagitta was placed on the saw, and a dorsal–ventral, 0.5 mm section was cut through the otolith, with two diamond-edged blades separated by a stainless steel shim. Sections were placed in a black-bottomed watch glass filled with water and read under a dissecting scope at 50× magnification. Each otolith was read twice, by two different readers. When readings did not agree, the otolith was read again. The value of two concordant readings was accepted as the best estimate of age. Less than 0.1 percent of the otoliths had to be excluded from analysis because of difficulty in recognizing annuli.

Many fish lay down an opaque and a hyaline (translucent) band in their otoliths on a seasonal basis. We attempted to validate that these bands were formed annually by calculating the percentage of fish taken each month from April 1992 to February 1993 that had opaque and translucent margins (edges) on otoliths. It is reasonable to assume that band deposition was seasonal if the bands were present during only one portion of the year.

Lengths at age were estimated by taking the means of the standard lengths by age class as determined from direct reading of the otoliths. Growth was assumed to be described by the von Bertalanffy growth curve model using FISHPARM (Elsevier Scientific Publishers Co., Bronxville, NY):

$$L_t = L_\infty\,(1 - \exp - k(t - t_0))$$

where

L_t = length at time t

L_∞ = theoretical maximum length

k = constant expressing the rate of approach to L_∞

t_0 = theoretical age at which $L_t = 0$.

First, a growth model was determined for all fishes collected from southern California. Secondly, due to the high variance of age-specific lengths of fish from different locations, individual growth models were also calculated for the four locations (Anaheim Bay, Catalina Harbor, Newport Bay, and San Diego Bay) where sample sizes were adequate to allow such a treatment. Growth rates at these four principal locations were compared by means of analysis of covariance (ANCOVA) of length-at-age data for individual fish. Thirdly, growth curves for males and females were calculated separately and also compared by means of ANCOVA.

Food Habits

The contents of 534 preserved spotted sand bass stomachs were examined. Artificial lures were used almost exclusively in the capture of specimens, thereby avoiding any bias introduced by the use of organic baits. Each item found was identified to the lowest taxon possible, counted, and weighed (wet weight) to the nearest gram. After data collection, items were grouped into higher-level taxonomic categories, and prey importance was represented using the Index of Relative Importance (modified from Pinkas et al. 1971):

$$\mathrm{IRI} = (N + W)\,F$$

where N = % numerical occurrence;
W = % wet weight;
F = % frequency of occurrence.

Timing of Maturation and Reproduction

To determine the duration of the spawning season, we calculated the gonosomatic index (gonad weight/total body weight × 100) for each specimen to quantify changes in gonad size over the months of the year.

We determined length and age at first maturity by classifying the gonads of 358 specimens collected during the peak breeding season (May–August) as immature or mature (male or female) based on the techniques of Bagenal and Braum (1971). The relationships between length and maturity and age and maturity were established with a transformation of

$$P_x = \frac{1}{1 + e^{ax+b}}$$

(Gunderson et al. 1980) to yield

$$ax + b = \ln\left(\frac{1}{P_x} - 1\right)$$

where P_x = the proportion mature at length or age x. We plotted x against

$$\ln\left(\frac{1}{P_x} - 1\right)$$

with stepwise linear regression (SPSS, version 2.1) to obtain values for a and b. We determined fifty percent maturity by calculating values for a and b and $P_x = 0.50$ to solve for x.

Sex Composition

Gonads were examined macroscopically. In cases where sex was uncertain, the gonads were teased apart under a dissecting microscope to verify sex class. Length frequencies of immature, male, and female fishes were plotted to examine relationship between length and sex for all southern California fish combined (n = 634).

Evidence of sexual strategies in this species was obtained by determining sex ratios over age classes for all southern California spotted sand bass, and for the two major populations studied (where $N > 100$) from Newport Bay and San Diego Bay. This technique should function as an indirect measure of sexual strategy.

Annual Recruitment Patterns

Annual recruitment patterns within the Southern California Bight were estimated from year-class strength as determined by the aging of individual fish. Year of birth was back-calculated for each fish that was successfully aged. The resultant year-class strength information for the last 15 years was presented graphically. The annual recruitment as measured by year-class strength was corrected for mortality with a general equation for mortality and survivorship (modified from Ricker 1975):

$$N_t = N_0 \left(\frac{1}{S}\right)^t$$

where

N_0 = number of fish in a year class at $t = 0$
N_t = estimated number of recruits at t years in past corrected for mortality
S = annual estimated survivorship (complement of mortality).

We estimated an annual mortality of 0.16 ($S = 0.83$) for spotted sand bass populations from southern California based on the frequency of fish in the 2 through 10 age classes. To err on the conservative side, we corrected annual recruitment by assuming a constant mortality rate and using the rounded-off value for annual survival, $S = 0.8$ ($M = 0.2$, $-Z = 0.2231$). To examine the possible relationship between annual recruitment success and sea temperature, we ran a Pearson's correlation analysis comparing the annual corrected recruitment with mean summer (June–September) sea-surface temperatures taken at the Scripps Pier for the years 1978 to 1992.

RESULTS

Length Frequency

The 639 specimens collected from 1991 through 1993 ranged from 51 to 400 mm SL; only 8 fish were smaller than 150 mm, and 10 were larger than 330 mm (figure 2). Overall, 72% of the fish ranged from 200 to 299 mm; the modal size class was 240–249 mm. The largest fish in our collection (400 mm SL) was donated by a local angler and stands as the current California state record fish.

Standard length (SL) was found to be about 80% of the total length (TL) across size classes; the two measures were related by the equation $TL = 1.233\ SL + 2.444$.

Length-Weight Relationship

We used 507 fish in the length-weight analysis. We included males and females with immature fish in this analysis since it made little sense to separate sexes in potentially hermaphroditic populations. The relationship between length and weight fit the relationship $W = aL^b$, where W = weight in grams, L = standard length in mm, and a and b are constants, with values determined by the nonlinear regression subroutine in CSS (figure 3). The length-weight function for this data set was $W = 0.000026L^{3.0187}$. Over 97% of the variance in the data was explained by the model ($R^2 = .9739$).

Age and Growth

Spotted sand bass appear to lay down opaque bands on a seasonal basis, beginning in spring and extending through the summer months (figure 4). We therefore judge the bands to represent annual rings. The focus of the average otolith was very wide; the first opaque ring did not form until the otolith was about 3 mm wide. Subsequent rings were typically closely packed and very readable. Initial readings by two independent readers were in 75% agreement. Reevaluation resolved all but a few cases.

The oldest fish encountered was a 14-year-old female from Newport Bay. The oldest male came from Anaheim Bay and was determined to be 13 years old. The vast majority of fish, however, were 10 years old or less

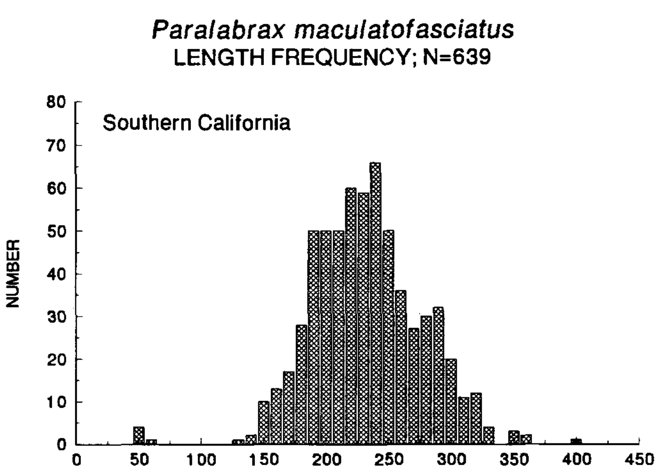

Figure 2. Length frequency of 639 spotted sand bass (*Paralabrax maculatofasciatus*) from all southern California locations combined, 1991–93, in length increments of 10 mm.

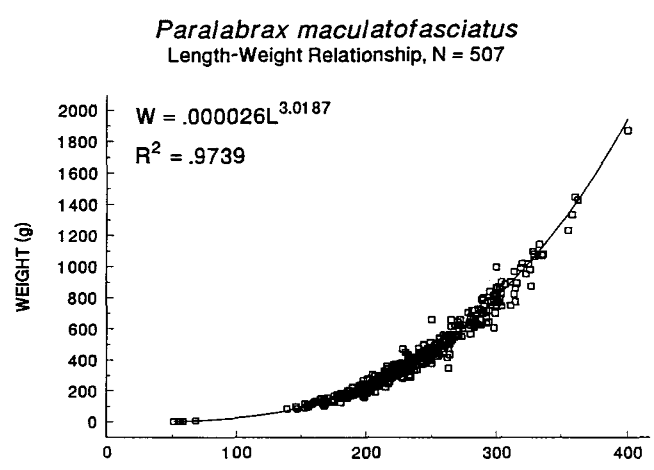

Figure 3. Length-weight relationship of 507 spotted sand bass (*Paralabrax maculatofasciatus*) collected from 1991 through 1993 from the Southern California Bight.

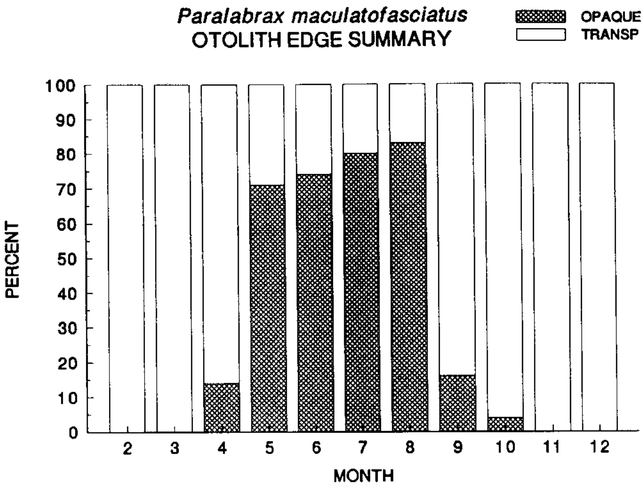

Figure 4. Otolith edge summary (opaque versus transparent ring at edge of otolith) of spotted sand bass (*Paralabrax maculatofasciatus*) captured each month from April 1992 through February 1993 from southern California. (No fish were taken in January 1993.)

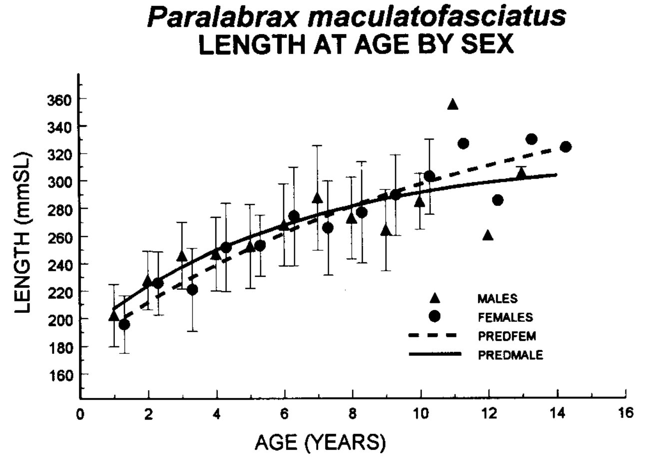

Figure 6. Mean length (mm SL) at age for female (n = 367) and male (n = 218) spotted sand bass (*Paralabrax maculatofasciatus*) from southern California. *Error bars* represent 1 standard deviation. *Curves* were fitted using the von Bertalanffy growth equation. *PREDFEM* = predicted curve for females; *PREDMALE* = predicted curve for males.

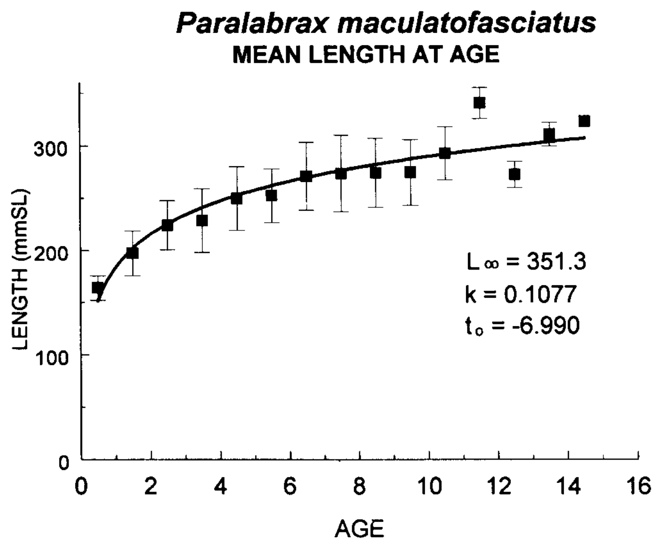

Figure 5. Mean length (mm SL) at age for spotted sand bass (*Paralabrax maculatofasciatus*) from southern California. *Error bars* represent 1 standard deviation. *Curve* was fitted using the von Bertalanffy growth equation. Von Bertalanffy parameters are listed on the right in the figure.

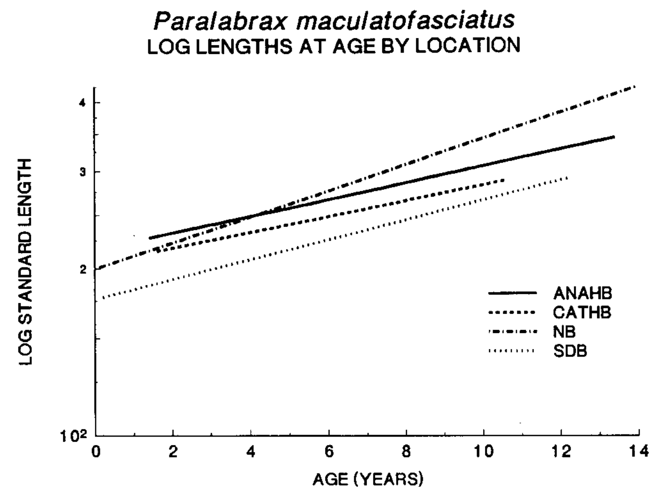

Figure 7. Growth rates (log-transformed) of spotted sand bass (*Paralabrax maculatofasciatus*) from four southern California locations. *ANAHB* = Anaheim Bay (n = 96); *CATHB* = Catalina Harbor (n = 41); *NB* = Newport Bay (n =264), *SDB* = San Diego Bay (n = 138).

(figure 5); only eight individuals (1.3%) were 11 years or older.

Growth rate for all southern California fish combined was sharply asymptotic, with some fish reaching as much as 200 mm SL in their first year (figure 5). Fish in their first two years grew extremely fast, with the mean length of age-1 fish being 197 mm SL. The von Bertalanffy parameters for all fish were determined to be L_∞ = 351.3, k = 0.1077, and t_0 = −6.990. Growth rates of males and females were not significantly different (ANCOVA; df = 1, 517; F = 2.79; P = 0.09). But a slight trend toward very fast, early growth was evident in some males (figure 6).

Variance in age-specific length data was high (R^2 = 0.67) when fish from all locations were considered together (figure 5). Log-transformed growth rates differed significantly (ANCOVA, df = 3, 541; F = 134.03; P < 0.001) among the four principal locations: Anaheim Bay, Catalina Harbor, Newport Bay, and San Diego Bay (figure 7). Of these, San Diego Bay fish exhibited the slowest overall growth rate; the Catalina Harbor, Anaheim Bay, and Newport Bay populations showed progressively faster growth rates.

Food Habits

Brachyuran crabs (IRI = 2020) and bivalve mollusks (IRI = 1326) were by far the most important food items

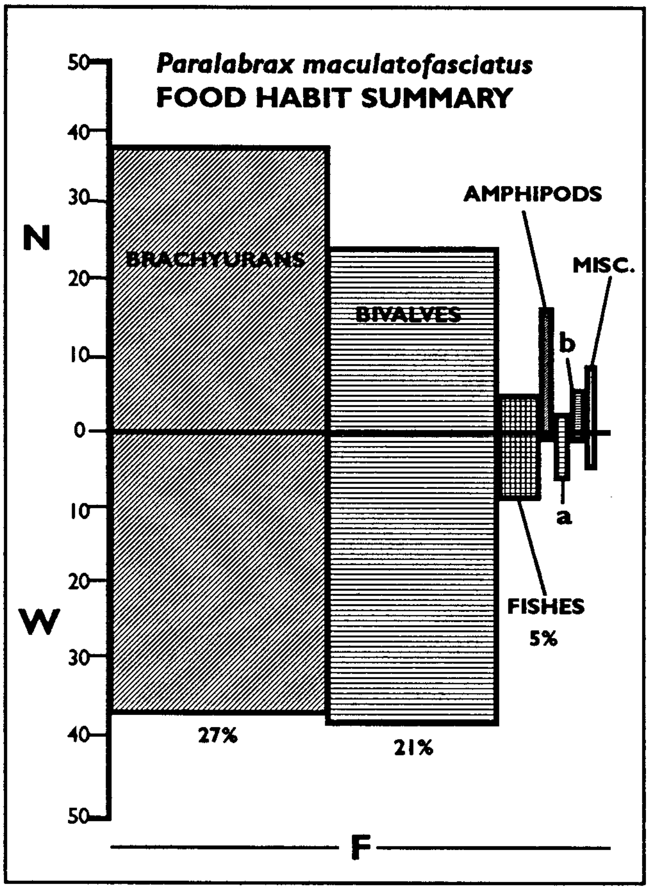

Figure 8. Relative importance of various food items found in the stomachs of 443 spotted sand bass (*Paralabrax maculatofasciatus*) from southern California. *N* = % number; *W* = % wet weight; *F* = % frequency of occurrence; *a* = Echiuroids; *b* = Gastropods (after Pinkas et al. 1971).

found in spotted sand bass (figure 8), followed much less commonly by bony fishes (IRI = 67) and amphipods (IRI = 28). In all, twelve taxonomic groups of mainly benthic organisms were identified from gut contents. Of the guts examined, 201 (38%) were found to be empty, probably because of the high incidence of regurgitation of gut contents during capture.

The prominent brachyuran crabs included the genera *Hemigrapsus*, *Pachygrapsus*, *Cancer*, and *Loxorhynchus*. The main bivalves were members of the genera *Tagelus* and *Laevicardium*. Identifiable fishes were mainly gobies (Gobiidae) and northern anchovies (*Engraulis mordax*).

Maturation and Reproduction

Female spotted sand bass matured very early and at a small size (figures 9 and 10); half matured before the end of their first year at a length of 155 mm SL. All females one year old or older were found to be mature. Males matured later (50% being mature in 1.4 years) and at a somewhat larger size (50% at 180 mm SL). The impact of potential sex change, if any, on these values is unknown.

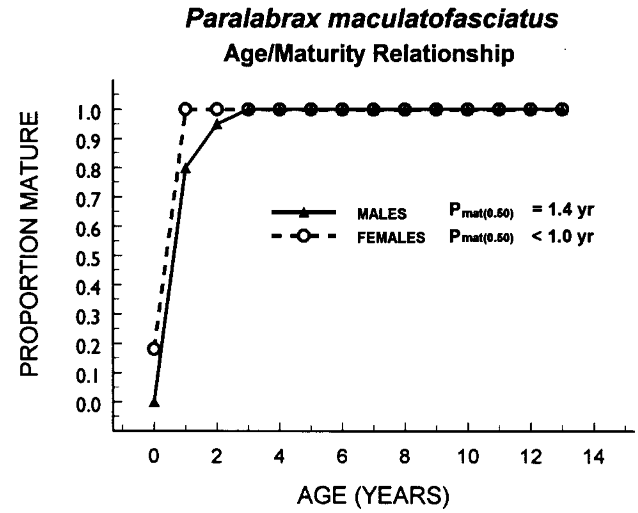

Figure 9. Age-maturity relationships for 585 male and female spotted sand bass (*Paralabrax maculatofasciatus*) from southern California, including the ages at which 50% of the males and females were mature.

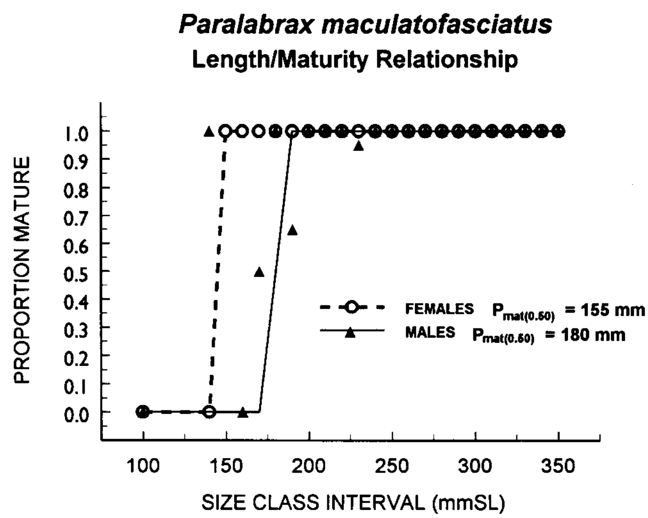

Figure 10. Length-maturity relationships for 585 male and female spotted sand bass (*Paralabrax maculatofasciatus*) from southern California, including the lengths (mm SL) at which 50% of the males and females were mature.

Analysis of gonosomatic indices throughout the year indicated that spotted sand bass spawn from June through August in southern California (figure 11). Female gonosomatic indices peaked in June (GSI = 6.2%) and decreased thereafter through August (2.9%). Male GSIs increased dramatically in June (3.6%), peaked in July (3.7%), and then declined through August (2.1%). Fall, winter, and early spring GSIs ranged from 0.1% to 0.4% body weight in males and 0.3% to 0.7% in females.

Sex Composition

The capture of breeding (ripe and running) spotted sand bass revealed the significance of the various color patterns in southern California populations. The large, high-contrast, black-and-white individuals with white

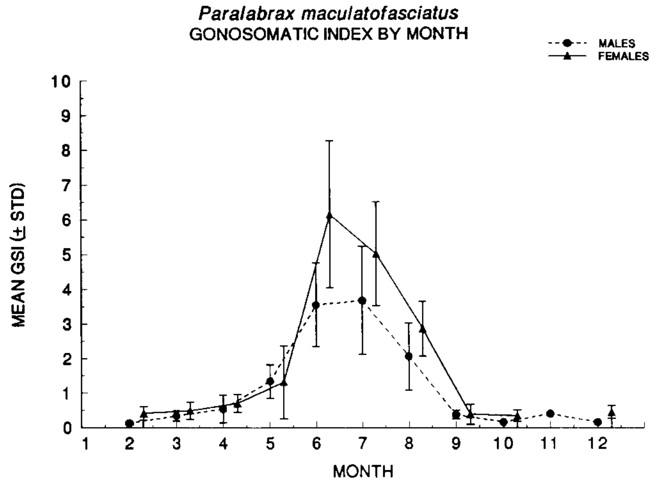

Figure 11. Gonosomatic indices for 168 male and 290 female spotted sand bass (*Paralabrax maculatofasciatus*) from southern California by month of capture from February 1992 to February 1993. Values are means ±1 s. (No fish were taken in January 1993.)

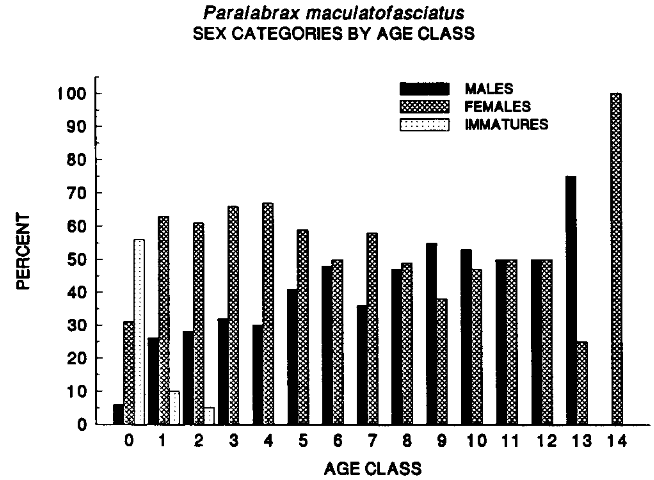

Figure 13. Percentage of 639 immature, female, and male spotted sand bass (*Paralabrax maculatofasciatus*) classified by age for all locations within southern California.

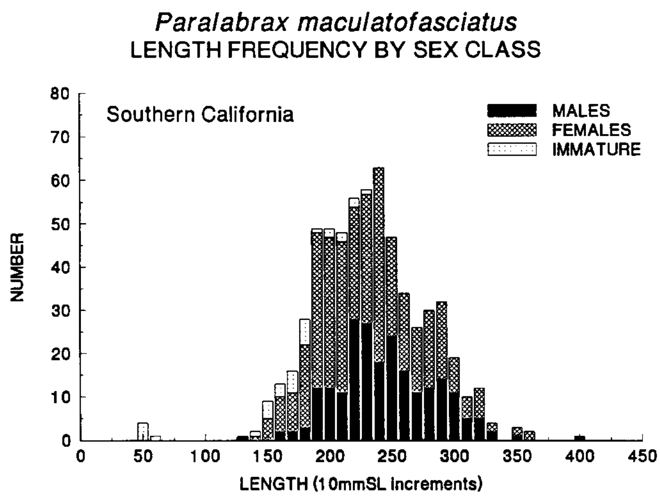

Figure 12. Length frequencies of all 639 spotted sand bass (*Paralabrax maculatofasciatus*) taken from southern California, classified by sex.

chins and jaws and prominent white spots below their dorsal fins are always males. Smaller fish with golden hues and yellow chins and jaws are usually females. However, some relatively large yellow fish turned out to be females, and small yellow fish were found to be males with extremely large testes. These observations suggest a complex mating system.

If southern California fish are functioning hermaphrodites practicing strict protogyny, all small fish should be either immature or females. As females grow, an ever greater number of them would change sex, making all large fish males. Length-frequency analysis by sex of a protogynous species should show a very large proportion of females in the smaller size classes, whereas males should dominate the larger size classes. However, both males and females were consistently represented throughout the size classes when all southern California fish were considered (figure 12). In fact, about half of the largest fishes in our samples turned out to be females. Immature fishes were represented into the 230 mm SL size class. Identifiable females appeared as far down as the 140 mm size class, and males as far down as the 130 mm class. A female bias in sex ratio was evident from 150 mm up through 240 mm. Thereafter, sex ratios appeared to be fairly equitable.

Sex composition by age class (figure 13) for all fish in the sample showed patterns similar to those for length. Females are well represented into the oldest age groups; the oldest fish aged (14 years) was female. Males were identified as early as age-0 (young-of-the-year, YOY) and were represented in all other age classes save the fourteenth. Thirty percent of the YOY fish were determined to be females; again, an early bias toward females is evident up to five or six years. Sex ratios appear to be about 50:50 throughout the older (7–10 year) age classes. Age classes 11, 12, and 14 were each represented by only one or two specimens. Immature fish were restricted to the first three year classes (0–2).

Preliminary examination of sex composition by age separately within Newport Bay and San Diego Bay indicated radically different patterns in the different populations. We believe that only two of the locations, Newport Bay and San Diego Bay, have been sampled sufficiently to warrant separate consideration at this time. A comparison between these two habitats is particularly instructive, since the Newport Bay fish were shown to be the fastest growing and the San Diego fish the slowest growing of all of the southern California populations considered.

In Newport Bay, female spotted sand bass are represented in all age classes present except 11 (figure 14).

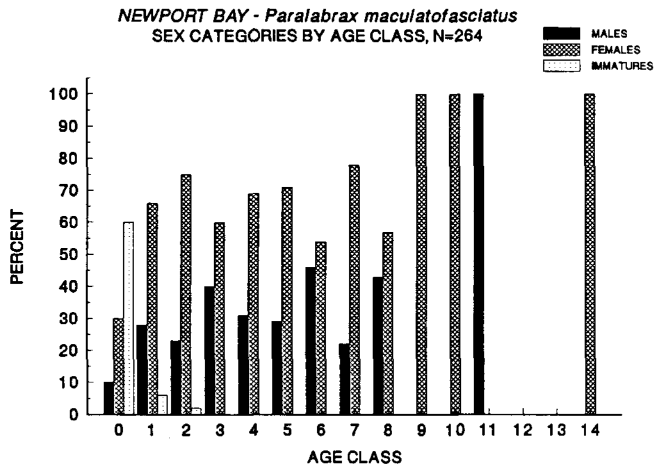

Figure 14. Percentage of 264 immature, female, and male spotted sand bass (*Paralabrax maculatofasciatus*) classifed by age, from Newport Bay only.

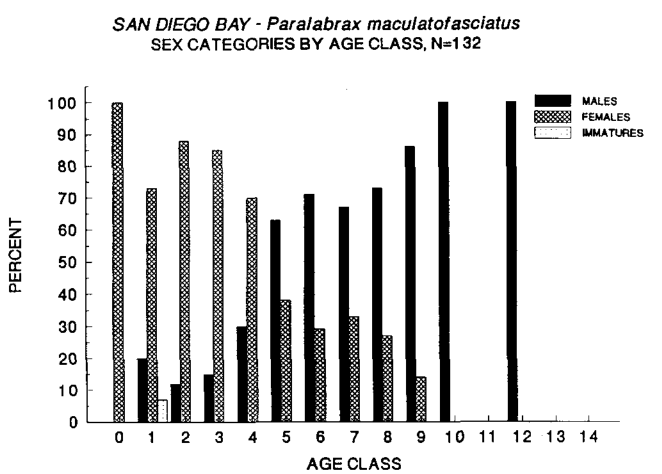

Figure 15. Percentage of 132 immature, female, and male spotted sand bass (*Paralabrax maculatofasciatus*) classified by age, from San Diego Bay only.

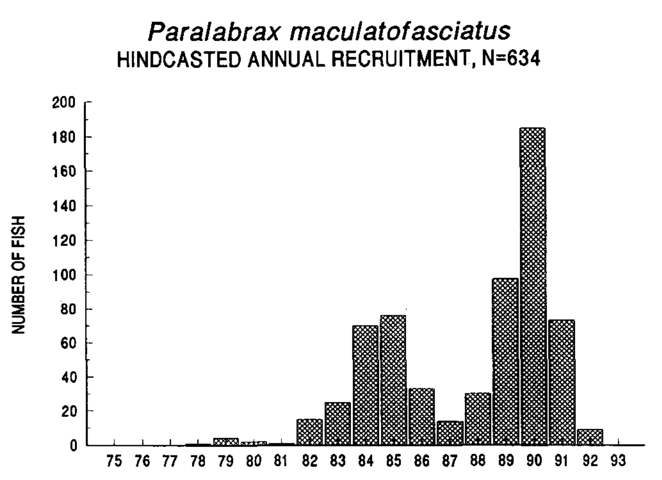

Figure 16. Annual recruitment of 634 spotted sand bass (*Paralabrax maculatofasciatus*) from southern California, 1975–93, as back-calculated from otolith age data not corrected for mortality.

Almost all of the 264 individual fish were eight years old or less. Males are represented in all age groups up to 8, but a pronounced bias toward females appears throughout the age structure. The overall sex composition of the Newport fish was 70% females versus 30% males.

On the other hand, the San Diego Bay population showed a strikingly different pattern of sexual composition over age classes (figure 15). In San Diego Bay, females dominate the younger age classes (0–4) and decline thereafter. In age classes 5 through 10, males dominate after constituting only a small proportion of the younger age groups.

Annual Recruitment Patterns

The 15-year pattern of annual recruitment for 634 fish, based on back-calculated year of birth (not corrected for mortality) was distinctly bimodal, with most of the fish coming from the very successful recruitment periods of 1984–85 and 1989–91 (figure 16). A small number of older fish (13–14 years) in the populations were recruited in 1979 and 1980. Notable depressions in recruitment appear to have occurred in 1981–82, 1987, and 1992–93.

Patterns of recruitment within five locations showed a similar pattern, with some notable exceptions (figure 17). The locations in figure 17 are shown in, roughly, north-to-south order, with Marina del Rey (MDR) being the northernmost site where fish were collected and San Diego Bay the southernmost. The recruitment peaks in 1984–85 and 1989–90 were evident in most locations, but recruitment seemed highly variable at this scale of resolution. Recruitment appeared to be highly successful in 1984–85 in Catalina Harbor (CAT), Anaheim Bay (ANB), and San Diego Bay (SDB), but not as evident in Marina del Rey and Newport Bay (NB). The 1989–90 recruitment appeared relatively strong at all locations except Catalina Harbor. Marina del Rey exhibited a relatively strong 1988 year class, while recruitment appeared to be very low in the other four locations. Finally, the San Diego Bay populations appeared to have experienced moderate recruitment in 1987, while all other populations did not, and San Diego Bay showed low recruitment in 1990 when Anaheim Bay, Newport Bay, and Marina del Rey had strong year classes.

For a closer examination of the variation in annual recruitment success and its relationship to sea temperature, we had to correct birth-year distributions for mortality, because fish recruited closer to the time of collection (young fish) have experienced lower mortality in their lifetime than older fish in the sample (figure 18). The pattern of annual recruitment corrected for mortality was distinctly trimodal. The years 1984 and 1985 were the best recruitment years for spotted sand bass since

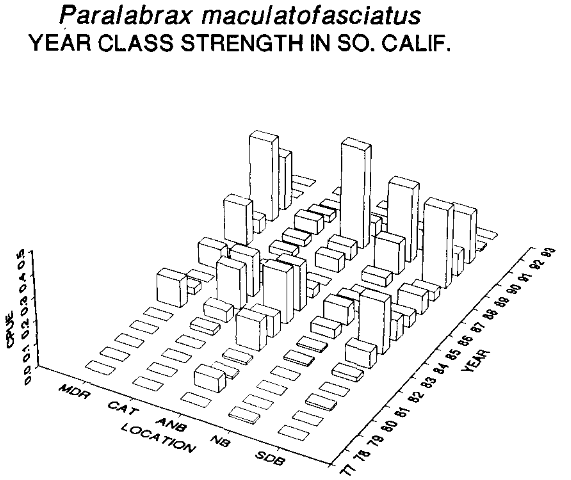

Figure 17. Estimated year-class strength (annual recruitment) for spotted sand bass (*Paralabrax maculatofasciatus*) from five locations in southern California, 1977–93. Catch-per-unit-effort was calculated by dividing the number of fish recruited (determined from back-calculating from otolith age data) by the number of angler hours spent at each location. Locations are ordered approximately north to south: *MDR* = Marina del Rey (n = 36); *CAT* = Catalina Harbor (n = 41); *ANB* = Anaheim Bay (n = 97); *NB* = Newport Bay (n = 270); and *SDB* = San Diego Bay (n = 138).

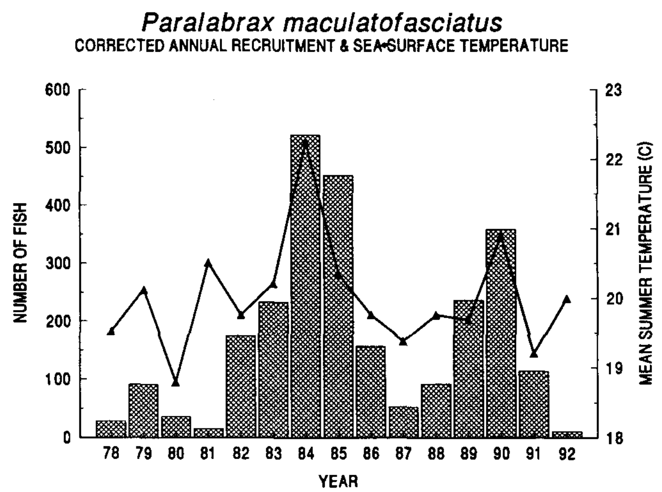

Figure 18. Annual recruitment (corrected for mortality) of 632 spotted sand bass (*Paralabrax maculatofasciatus*) from southern California compared to mean summer sea-surface temperature recorded at Scripps Pier, 1978–92.

1978, followed by 1989 and 1990. The third (smaller) peak, centered in 1979, is now more evident.

Mean summer sea-surface temperatures for the same 15-year period as measured at the Scripps Pier (figure 18) exhibit a similar pattern. In fact, corrected annual recruitment correlated significantly ($r = 0.723$; df = 13; $P < 0.002$) with mean summer sea-surface temperature.

DISCUSSION

Age and Growth

Spotted sand bass are fast-growing, short-lived fishes compared to their southern California close relatives, the kelp bass and barred sand bass. An average 1.5-year-old spotted sand bass (mean = 253 mm TL) was found to be about 1.6 times longer than the same-aged kelp bass (165 mm TL) or barred sand bass (166 mm TL; Love et al., in press). Maximum age for spotted sand bass (14 yr) in southern California is about 0.4 times that of kelp bass (33 yr) and 0.6 times that of barred sand bass (24 yr; Love et al., in press). The characteristics of fast growth and relatively short life span are usually associated with tropical fishes; in retrospect, it should not be surprising to have found these characteristics in what is basically a subtropical form living in a warm, temperate coastal zone.

The virtual absence of small (<150 mm SL) individuals in our samples was probably due more to very low recruitment of spotted sand bass in 1991 and 1992 than to sampling bias. The rapid growth in YOY and one-year-old fish plus the failed recruitment years largely explain the substantial gap in frequencies of small size classes that we observed. Spotted sand bass are aggressive carnivores which will bite lures at almost any size. We have caught hundreds of YOY and one-year-old fishes along both coasts of Baja California; if these small size classes had been available in southern California during our sampling, we would have collected them. Moreover, a beach seine study from 1989 to the present in San Diego Bay (Robert Hoffman, NMFS, unpublished data) yielded large numbers of YOY spotted sand bass in 1989–91 and none in 1992–93.

Although different growth rates in different populations of the same species are well documented in freshwater species (see Wooton 1990) and coral reef fishes (Jones 1986), this is the first example of this phenomenon in a coastal marine fish from California. The significant differences in growth rate discovered among the four principal populations of spotted sand bass may have a number of causes. Wooton (1990) listed a number of factors, both exogenous and endogenous, which have been shown to affect growth rates in fishes. These include (1) temperature; (2) food quantity, quality, and size spectrum; (3) dissolved oxygen; (4) salinity; (5) social interactions; and (6) genetics. Any one, or a number, of these factors may be operating to vary the growth rates of populations in the different locations. The different embayments vary dramatically in size, depth, temperature regimes, and—probably—population density. San Diego Bay is by far the largest and deepest of these habitats. Catalina Harbor is the smallest and the farthest offshore. The temperature regimes are probably cooler overall in these two embayments than in the moderately sized, shallow habitats of Anaheim Bay and Newport Bay. The slower growth rates of spotted sand bass in San Diego Bay and Catalina Harbor may be attributable to the reduced temperature regime alone. But many other variables such as food supply, population density, and pollution levels must also be considered.

Food Habits

The southern California members of the genus *Paralabrax* have all been characterized as important predators in nearshore coastal waters. Kelp bass are active predators around kelp beds and rocky reef habitats, and feed on a variety of motile organisms including fishes, squids, octopi, and benthic crustaceans (Love et al., in press). A large portion of their prey is taken from the water column. Barred sand bass are more benthic in orientation than kelp bass and feed on an array of fishes, crabs, shrimps, octopi, and other substrate-oriented invertebrates.

Ono (1992) listed small fishes, cephalopods, and crustaceans as the major prey items of spotted sand bass. This characterization of diet seems to be in error. Our study represents the most comprehensive sample ever taken of spotted sand bass from their normal habitats. The results clearly show that crabs and clams, particularly jackknife clams (*Tagelus* sp.), dominate the diet of spotted sand bass from southern California waters. How spotted sand bass actually capture jackknife clams remains a mystery, since most of the time these clams are buried 15–18 cm deep in the mud. Fishes form a relatively small component of the spotted sand bass diet, especially when compared to the two other species of *Paralabrax* in southern California.

Reproductive Strategies

Strict protogynous hermaphroditism is apparently not a general characteristic of all populations of spotted sand bass. Data from our extensive collections in the northern Gulf of California have, so far, supported Hastings's findings (1989). We have been able to age northern gulf fish, which Hastings was not able to do with his preserved specimens. Sexual composition over age groups in our fish from the northern Gulf of California are completely consistent with a protogynous strategy. Virtually all of the very young fish were females, and nearly all of the large, old fish have been males. These data, coupled with the detailed histological examination of gonads presented by Hastings (1989), make it highly probable that the northern Gulf of California fish are protogynous. Our San Diego Bay population exhibited an almost identical age-sex pattern to the fish in the northern Gulf of California.

As a group, the populations from all locations in southern California other than San Diego Bay exhibit a pattern of female bias in sex ratios in young age groups which gradually disappears over time. There appears to be a relatively high proportion of primary males in these populations, and large, old females are quite common. When we examined the populations separately, it was evident that spotted sand bass in Newport Bay maintained female bias throughout all age classes.

Conclusions on the actual reproductive strategies of these populations will have to await completion of our ongoing histological analysis.

Annual Recruitment Patterns

Variation in recruitment to individual embayments was expected, since recruitment success in fishes has been shown to be a highly variable process, particularly in broadcast spawners with pelagic larvae (cf. Doherty 1991). Because spotted sand bass have pelagic larvae, variable recruitment into their restricted habitats is to be expected. The sporadic recruitment to Catalina Harbor during the last 15 years is probably the best example of how habitat isolation influences recruitment. Almost all of the spotted sand bass collected from this offshore habitat were found to be 7- and 8-year-olds from the strong 1984–85 recruitment period. The interpretation of back-calculated recruitment data from individual locations in southern California is, however, complicated by variable fishing pressure. Fishing mortality may be a particular problem in Newport and San Diego Bays, which are heavily fished by recreational anglers. Therefore the data on annual recruitment presented here must be viewed and interpreted with caution.

The overall, bimodal pattern of recruitment was at first puzzling because it seemed to be almost anti-El Niño in nature, showing relatively small year classes in 1982–83, 1987–88, and 1992–93. This possibility seemed counterintuitive because one would predict a subtropical species to recruit well to southern California coastal waters during El Niño years. But in southern California, summer sea-surface temperatures (as measured at the Scripps Pier) actually peak one or even two years after a recognized El Niño event. These lagged peaks coincide closely with peaks in spotted sand bass recruitment (corrected for mortality) within the Southern California Bight as a whole. The highly significant correlation discovered between corrected recruitment and mean summer sea-surface temperature at Scripps Pier leads us to conclude that spotted sand bass recruit best during summers when the nearshore ocean temperatures off southern California are warmest.

ACKNOWLEDGMENTS

A study of this magnitude could not have been accomplished without the support of many people. We thank those who ably assisted in the demanding field work, especially Cheryl Baca, Andy Barbarena, Michael Franklin, Tom Grothues, Jo Korting, Loretta Roberson, Bob Scott, Greg Tranah, and Carrie Wolfe. The crew of the R/V *Yellowfin*—Jim Cvitanovich, Paul Irving, and Danny Warren—assisted greatly through their capable handling of vessels, sampling nets, and rods and reels. Andy Brooks (University of California, Santa Barbara) performed the age- and size-at-first-maturity analysis. The authors also wish to thank the following organizations for their donations of equipment to aid this research effort: Shimano American Corp., Eagle Claw, AA Worms, and Izorline International. Special thanks must go to Big Mike Gardner, our professional fishing guide, for his dedication to this project. Without Mike's skill and expertise, far, far fewer spotties would have been available for study. Angler Pat Gorman donated his record fish for study. Mary Yoklavich generously shared her insights on how to correct for mortality when back-calculating annual recruitment. We also gratefully acknowledge the assistance provided by Chuck Valle and Dave Parker of the California Department of Fish and Game in procuring funds, reviewing the manuscript, and scaling many administrative obstacles. This research was funded through contracts with the Bay, Estuarine, and Nearshore Ecosystem Studies (BENES) program of the California Department of Fish and Game which, in turn, is supported by the Federal Aid to Sport Fish Restoration Program (Wallop-Breaux).

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