Abstract.-White seabass, Atractoscion nobilis, is a valuable recreational and commercial species, but much of its early life history is undescribed. The coast and two bays of San Diego County were sampled each month for two years with a depth-stratified sampling design to determine habitat, food habits, age, and growth rate of recently settled fish. Age was estimated from otolith increments and validated with fish of known age, reared in the laboratory. A few recently settled fish were caught in the bays at depths <1 m, but most inhabited shallow water (4-8 m) along the coast from May to October. This depth distribution coincides with that of the mysid Metamysidopsis elongata. Fish abundance in this zone was low, however, reaching a maximum of 24/ha in July. The smallest white seabass collected were about 7 mm SL and 26 d old, but previous studies indicate that smaller and presumably younger fish were probably extruded through the trawl. According to combined results, most larvae settled 2-3 weeks after being spawned. Juveniles remained at a depth of 4-8 m for 2-3 months, fed primarily on abundant mysids, and associated with drifting macrophytes (r=0.52, P=0.015, n=21). Growth during this period was 1.3 mm/d, similar to that observed in the laboratory. At about 100 mm SL (~100 d old), juveniles appeared to move out of the area. The shallow waters just beyond the breaking waves may be preferred by young white seabass because abundant food and warm water promote rapid growth and drifting macrophytes provide a refuge from predators.

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Age, growth, distribution, and food habits of recently settled white seabass, Atractoscion nobilis, off San Diego County, California

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White seabass. Atractoscion nobilis (family Sciaenidae), is a highly desired recreational and commercial species found in waters off the coasts of southern and Baja California as well as in the Gulf of California. Adults inhabit the nearshore zone over rocky bottoms and in kelp beds and can attain a weight of 38 kg (Young, 1973). Population size has not been estimated, but since the 1920's, commercial and recreational landings off California have continued to decline and the range of the species has contracted (Collins, 1981; Methot, 1983). Management efforts to stabilize and restore the population have been largely unsuccessful. Reductions in the catch and distribution of white seabass have been attributed largely to overfishing (Thomas, 1968; Vokovich and Reed, 1983; MacCall, 1986), but the importance of other mechanisms, such as increased natural mortality of fish at early life history stages, has not been evaluated.

Despite the historic value of this species, much of its early life history was unknown until recently. Moser et al. (1983) described the development of the early life stages and historic distribution of larvae in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) sampling area off southern and Baja California. In several laboratory studies, growth, survival, energetics, and feeding behavior of larvae have been examined (Kim, 1987; Dutton, 1989; Orhun, 1989), as well as the development of sensory systems and predator-avoidance behavior (Margulies, 1989).

Less is known about the early iuvenile stage because few early juveniles have been caught until recently. Early studies suggested that juveniles inhabit either the surf zone or kelp canopy along the open coast, or bays and estuaries (Thomas, 1968; Feder et al., 1974; Maxwell¹). Allen and Franklin (1988, 1992) have since demonstrated that late larvae and early juveniles inhabit shallow water along the open coast of southern California and **Channel Islands and semiprotected** embayments in the vicinity of Long Beach Harbor. However the nursery area for white seabass has not been clearly defined and the relative importance of the open coast and bays as nurseries has not been

¹ Maxwell, W. D. 1977. Progress report of research on white seabass, *Cynoscion nobilis*. Calif. Dep. Fish Game, Mar. Resour. Admin. Rep. 77-14, 14 p. [Available from Calif. Dep. Fish Game, 330 Golden Shore, Suite 50, Long Beach, CA 90802.]

evaluated. In addition, food habits, age, and growth of these fish in the wild have not been examined.

The specific goals of this study were to determine 1) the depth distribution of early juvenile white seabass along the open coast and in bays of San Diego County, 2) size-specific food habits of white seabass, and 3) age and rate of growth.

Materials and methods

Sampling design

Most white seabass were obtained from a survey originally designed to sample settled California halibut, *Paralichthys californicus* (Kramer, 1990). Two bays (Mission Bay and Agua Hedionda Lagoon) and the open coast of San Diego County were sampled monthly from September 1986 to September 1988 with a depth-stratified sampling design. The coast was sampled at four primary sites with a 1.6 m \times 0.35 m beam trawl (Fig. 1). At each site, four benthic tows were made in each of three bottom depth intervals (strata): 4–8, 9–11, and 12–14 m. A few tows were made in water as shallow as 3 m on days when the sea was calm. Tows were made parallel to shore at about 0.6 m/s for 10 min. The exact depth of tows within each stratum was chosen at random. Sampling depth was maintained along the chosen 1-m depth contour with the aid of a fathometer. An odometer attached to the trawl recorded tow distance, which ranged from 250 to 450 m. An additional four sites were sampled from April to October 1988 by biologists at San Diego State University (SDSU) with identical gear, but only at the 4–8 and 9–11 m depth strata.

A similar sampling design was used to sample the two bays. Mission Bay and Agua Hedionda Lagoon were subdivided into five and three blocks respectively to sample the various habitats adequately within each bay (Fig. 1). Each block was further subdivided into three depth strata: 0-1, 1-2, and 2-4 m. Within each stratum and block, three benthic tows were made at random locations with a $1.0 \text{ m} \times 0.35 \text{ m}$ beam trawl equipped with an odometer. In the two deeper strata, the trawl was towed by a 5-m skiff for 5 min, covering a distance of 100-250 m. In the 0-1 m stratum, the trawl was towed by hand for a measured distance of 20-50 m. The 0-1 m depth stra-



Figure 1

Map of San Diego County showing location of the eight coastal sites and sampling areas (blocks) within Mission Bay and Agua Hedionda Lagoon. Four coastal sites were sampled by Kramer (1990) and four were sampled by San Diego State University (SDSU). The sampling design used along the coast is also shown.

tum was also sampled with a $1 \text{ m} \times 6 \text{ m}$ beach seine. Three hauls were made in each block over a measured distance of 15–50 m with the width of the seine fixed at 4 m. In addition, three tows were made each month in blocks 2–5 of the 2–4 m stratum in Mission Bay with the 1.6-m beam trawl (Fig. 1). The mesh size of all three nets was 3 mm. All hauls were made during the day. Monthly sampling in Agua Hedionda Lagoon was not initiated until March 1987.

Tow distance, water temperature, and the presence and type of drift macrophytes in the net were recorded at the end of every tow. Beginning in April 1988, the weight of drift macrophytes in each tow was also recorded at the four coastal sites sampled by SDSU biologists. White seabass were either frozen or preserved in 80% ethanol and later measured to 0.1 mm standard length (SL) in the laboratory. Lengths of alcohol-preserved fish were adjusted by 3.6% to compensate for shrinkage. Average shrinkage was estimated by measuring a subsample of white seabass before and several months after preservation in ethanol. Sagittae and stomach contents were removed and stored in 80% ethanol. Fish were then dried at 60°C for two days and weighed.

White seabass were also obtained opportunistically (i.e. sporadically) from the coastal habitat with a 7.6-m headrope otter trawl and a 15.2-m beach seine (6-mm mesh). These fish were used only in the food habits and growth portions of this study.

Distribution and abundance

Abundance was calculated as the number of fish caught divided by the product of tow distance (from odometers) and net width. Mean abundance of fish along the coast was calculated for each site by depth stratum (n=4 tows). Monthly differences in abundance among the three depth strata were compared by using the Kruskal-Wallis test, with a=3 depths, and n=4 (1987) or n=8 (1988) sites (Sokal and Rohlf, 1981). Monthly mean abundance in bays was calculated for each bay by block and depth stratum. Block means were averaged to produce a mean for each bay and the two bays were averaged to yield a grand mean for each depth stratum. Because estimates of monthly mean abundance did not differ among the two gear types (paired *t*-test; mean difference=0.50 fish/ha, t=0.27, df=8, P=0.79), trawl and seine samples within the 0-1 m depth stratum were pooled to produce an improved estimate of abundance.

The relation between abundance of white seabass and drift macrophytes was estimated by testing for a correlation between abundance of white seabass and drift macrophytes in each tow and for a correlation between mean abundances at each site (n=4 tows). Abundance of macrophytes (g/m^2) was logtransformed prior to analysis. Biomass of macrophytes was recorded only from April to October 1988 at the four secondary sites along the coast that were sampled by SDSU biologists.

Food habits

The stomach contents of 142 white seabass collected in bays and along the coast with all gear types were examined. For each fish, prey items were identified, counted, sorted into one of ten major prey categories, dried at 60°C for 1–2 d, and weighed to either 1 µg (for samples <25 mg) or to 0.1 mg (for samples >25 mg). White seabass were grouped into six length classes: 6– 10, 10–18, 18–25, 25–35, 35–55, and 55–150 mm SL. Class intervals were chosen so that each interval contained similar numbers of fish. Mean prey weight and frequency of occurrence of each prey category were calculated for the six length classes. Six individuals with empty stomachs were excluded from calculations of frequency of occurrence and mean weight of prey.

Age and growth

The ageing method was validated by using laboratory-reared fish of known age. Eggs obtained from captive broodstock were placed in 7-m³ flow-through tanks and reared at 17-20°C on a diet of marine rotifers, brine shrimp, euphausids, and chopped mackerel. White seabass were sacrificed at irregular intervals between 13 and 76 d after hatching and stored in 80% ethanol. Sagittae were mounted in Eukitt mounting media and ground in the sagittal plane with 15-µm grit sandpaper and polished with 0.3-µm grit lapping film. Increments were counted on the right sagitta from the central primordium to the midventral margin. Each sagitta was read in one session by one observer, with neither age nor length of the fish known to the reader. The rate of increment deposition and age at first increment formation were estimated by linear regression.

A subsample of 50 wild larval and juvenile white seabass was aged with the technique described above. Individuals were selected at random from several length classes to represent equally the size range of fish collected. The subsample included fish caught in bays, on the coast, and in both years. Growth rates were estimated by fitting a Gompertz function ($L_t = L_o e^{G(1-e^{-gt})}$) to length-at-age and weight-at-age data. The ages of the remaining individuals were estimated from the resulting age-length relation. The date each fish was spawned was calculated by subtracting the age of the fish and an additional two days (incubation time at ~16°C; Orhun, 1989) from date of capture. The error associated with the estimated spawn dates is therefore the same as that associated with the age-length relation.

Growth of wild white seabass was compared with growth of three groups reared in the laboratory. Eggs spawned on 8 May, 24 June, and 25 September 1989 were reared as described above. Mean length-at-age was estimated from random subsamples (n=16-76 fish) taken at irregular intervals during rearing. Linear growth models were fitted to the length-at-age data for both reared and wild fish to facilitate statistical comparisons of growth rates with ANCOVA. Although growth of white seabass from hatching to 150 mm SL was nonlinear, growth over a smaller size range of 6–104 mm SL was described equally well by linear models ($r^2 \ge 0.94$).

Results

Distribution and abundance

The overall abundance of white seabass in the bays and along the coast of San Diego County was low.



Figure 3

Distribution of white seabass and the mysid *Metamysidopsis elongata* along the coast in relation to depth. White seabass abundance is the mean $(\pm 1 \text{ SE})$ during months fish were captured (Jun-Aug 1987, May-Oct 1988). Number of tows at each depth during this period is indicated at the top of the graph. Mysid data are redrawn from Clutter (1967) and represent total number of *M. elongata* caught from 1960 to 1962 at a site ~3 km south of the Torrey Pines 2 site (Fig. 1). Sampling effort for mysids was similar for all depths.



Length-frequency distributions of white seabass caught during regular sampling along the coast of San Diego County with a 1.6-m beam trawl and in Mission Bay and Agua Hedionda Lagoon with 1.6-m and 1.0-m beam trawls and a 6-m beach seine.

During regular sampling, a total of 112 white seabass were caught in 1,250 tows along the coast and 10 white seabass were caught in 2,527 tows in the bays.

> Most tows caught no white seabass. Lengths of fish ranged from 6.2 to 149 mm SL (x=30.2 mm SL), but 80% were smaller than 40 mm SL (Fig. 2). About 40 fish (33%) were smaller than 15 mm SL, the approximate length at metamorphosis (Moser et al., 1983).

> White seabass were caught primarily in shallow water in both coastal and bay habitats. Along the coast, nearly all white seabass (97%) were collected in the shallowest (4-8 m) depth stratum, with the highest density at 6 m (Fig. 3). Only three fish were taken in deeper water and these were among the largest caught, ranging from 92 to 149 mm SL. In the bays, all ten fish were caught in the shallowest (0-1 m) stratum.

> Settled (demersal) white seabass were present in shallow strata only during spring and summer, although one fish, the 149-mm-SL juvenile, was caught in January 1988. Along the coast, white seabass were caught from June to August 1987, and from May to October 1988, when sampling ended (Fig. 4). In both years, abundance was highest in July, with mean densities of 15/ha (1987) and 24/ha (1988). White seabass were found in 54 of 210 tows (26%) made in the 4–8 m

stratum during these nine months. Because most tows in the 4–8 stratum caught no white seabass, the variance associated with the estimates of abundance within the stratum was high. As a result, abundance in the 4–8 m stratum did not differ statistically from that in the 9–11 and 12– 14 m strata (generally zero) except in June 1987 and from June to July 1988 (Kruskal-Wallis test, P<0.05, n=4 or 8). The temperature in the 4–8 m stratum during the summer ranged from 16 to 20°C, an average of 1.2 and 1.8°C warmer than the two deeper strata.

Although the relative abundance of settled white seabass was lower in the bays than along the coast, the two estimates could not be compared statistically because different nets were used to sample the two habitats. In addition, only 10 fish were caught in the two bays, making estimates of abundance sensitive to capture of individual fish. Estimates of mean density in the 0–1 m stratum in the bays from April to August ranged from 0 to 5 per ha in 1987 and from 0 to 10 per ha in 1988 (Fig. 4). The high April 1988 estimate resulted from a single fish caught in a short tow. Mean abundance during these five months (total catch + total area swept) was 1.3/ha in 1987 and 3.1/ha in 1988. Monthly estimates for bays were about 0.8-12 times

lower than estimates for the coast during the same period.

Abundance of white seabass within the 4-8 m coastal stratum was related to the abundance of drift macrophytes. Drift macrophytes were common in the 4-8 m stratum and were recorded in 188 of 205 tows (92%) made during the nine months when white seabass were present. Macrophytes were present in 49 of 52 tows (94%) that caught white seabass. The drift material was mainly giant kelp (Macrocystis pyrifera) and surf grass (*Phyllospadix torrevi*), but filamentous red and other brown algae were dominant at times. In 1988, weight of macrophytes in each tow was recorded at the four sites sampled by SDSU biologists. At these sites, abundance of white seabass in each tow was weakly correlated with the abundance of drift macrophytes in each tow in the 4-8 m coastal stratum (n=77, r=0.29, P=0.01, Fig. 5A). Because white seabass were not abundant, an average of the four tows made at each site was also calculated. Mean abundance of white seabass at each site (n=4 tows) and mean abundance of drift macrophytes were more strongly correlated (n=21, r=0.52,

P=0.015, Fig. 5B). Drift macrophytes were also present in the two deeper strata, but only three white seabass were caught at those depths.

Food habits

Along the coast, white seabass of all length classes fed almost exclusively on mysid crustaceans. For each length class, mysids composed from 74% to 99% of the diet by weight and were found in 78–100% of stomachs that contained food (Table 1). These mysids were not identified to species but were probably *Metamysidopsis elongata*, the numerically dominant mysid in the nearshore coastal habitat (Clutter, 1967; Roberts et al., 1982). Larger white seabass ate larger mysids, although fish >0.2 g dry weight (~40 mm SL) fed on mysids of similar mean weight (Fig. 6). Mysids also dominated the diet of the 10 fish caught in the bays.

Prey of secondary importance varied with white seabass length class. Larvae (6-10 mm SL) fed on copepods, fish of intermediate length (10-55 mm SL) fed on gammarid amphipods, and larger juveniles



(35–150 mm SL) preyed on shrimp and fishes. Most fish in the stomachs were well digested and difficult to identify, but the sagittae closely resembled those of white croaker, *Genyonemus lineatus*, and queenfish, *Seriphus politus*. One case of cannibalism was observed; a 7-mm larva was eaten by a 35-mm juvenile. Most shrimp were well digested, but at least two individuals were identified as belonging to the genus *Crangon*. Other items found in the stomachs included nematodes, bits of algae and surf grass,



Figure 5

Relations between (A) abundance of drift macrophytes and abundance of white seabass in each tow, and (B) mean abundance of drift macrophytes and mean abundance of white seabass at each site (n=4 tows) in the 4-8 m stratum from April to October 1988 at the four coastal sites sampled by SDSU. Sample size, Pearson correlation coefficient (r), and *P*-values are shown. portions of crustaceans, and sand. The stomachs of six white seabass (5%) were empty or contained only nonfood items such as sand.

Age and growth

Otolith increments formed daily in sagittae of laboratory-reared white seabass (Fig. 7). The slope of the regression of observed number of increments on age was 0.96 and did not differ from unity (r^2 =0.96, n=25, P<0.01, 95% confidence limits on slope: 0.89 and 1.04 increments/d). The first increment formed 3–4 d after hatching, a period that corresponds to yolk absorption and onset of feeding (Kim, 1987; Orhun, 1989).

Age was estimated for 50 wild white seabass ranging from 6.2 to 104 mm SL. The ten smallest fish that were aged ranged from 6.2 to 9.2 mm SL and were estimated to be 26–32 d old (Fig. 8). The age of a fish that was 15 mm SL, the length at metamorphosis, was estimated to be about 40 d. The largest juvenile aged (104 mm SL) was estimated to be 108 d old. The range of estimated ages suggests that white seabass remain in the nursery for 2–3 months after settlement. It should be noted that the oldest validated age was 76 d. A 149-mm-SL juvenile was not aged because it was probably much older than the oldest validated age.

Growth of these fish was rapid in terms of length and weight. The parameters of the Gompertz model relating age and length were estimated as $L_0=0.202$, G=6.64, and g=0.0273, where L_0 is length at time t_0 , G is the instantaneous growth rate at time t_0 , and gis the rate of decrease of G (Fig. 8A). This equates to a maximum growth rate of 1.57 mm/d at 70 d. Weight also increased rapidly. The parameters relating weight and age were $W_0=2.72 \times 10^{-7}$, G=17.58, and g=0.0256, where W_0 is weight at time t_0 (Fig. 8B).

Wild fish between 6 and 104 mm SL grew at rates similar to those of laboratory-reared fish. Wild fish grew at a linear rate of 1.31 mm/d, compared with laboratory rates of 1.15, 1.32, and 1.04 mm/d for groups spawned in May, June, and September 1989 (Fig. 9). Linear growth models were used to facilitate statistical analysis by ANCOVA. Linear models fitted the data well, with coefficients of determination (r^2) of 0.94–0.99 for the four groups. The rate of growth (slopes) did not differ among the four groups (ANCOVA, F=1.40, P=0.25). However, the June laboratory group was significantly larger at a given age than the wild fish (ANCOVA, F=5.05, P < 0.01; Tukey pairwise comparison), but the remaining groups did not differ in their length-at-age.

The distribution of spawning dates, based on counts of otolith increments, indicated that spawning occurred from March to July in 1987, and from

Table 1

Mean dry weight in micrograms (μg) and as a percentage of total weight (in parentheses) and frequency of occurrence of prey items in stomachs of white seabass caught along the coast. Six fish with empty stomachs were excluded from the analysis. n = sample size.

Prey category	Length class and mean length (mm SL)					
	6–10 (7.9)	10–18 (13.7)	18–25 (21.8)	25–35 (29.1)	35–55 (44.8)	55–150 (79.2)
Mean Dry Weight in µg and (%)						
Mysids	46 (75)	154 (91)	467 (99)	1,417 (99)	2,329 (78)	8,270 (74)
Copepods	10 (16)	2(1)	_	_	_	· _
Gammarid amphipods		7 (4)	_	5 (<1)	11 (<1)	—
Fish		_	4(1)	_	97 (3)	768 (7)
Shrimp		-			186 (6)	211 (2)
Nematodes		-	_	-	6 (<1)	15 (<1)
Macrophytes		—	<1	_	55 (2)	647 (6)
Crustacean parts	5 (8)	2(1)		5 (<1)		459 (4)
Sand		_		1 (<1)	185 (6)	
Unidentified		5 (3)		_	99 (3)	814 (7)
Total	61	170	471	1,428	2,968	11,184
Frequency of occurrence (%)						
Mysids	78	91	100	96	100	100
Copepods	11	5		—	_	_
Gammarid amphipods	_	5	-	11	5	_
Fish		_	5	_	25	25
Shrimp					5	5
Nematodes		—	_	_	5	10
Macrophytes		—	5		25	50 [.]
Crustacean parts	11	5		4	5	15
Sand		—		4	5	
Unidentified		5	_	-	15	10
n	18	22	20	27	20	20

March to the beginning of September in 1988 (Fig. 10). In both years, most of the young white seabass collected were spawned in June. The distribution of spawning dates derived from estimated ages agreed closely with those based upon direct ageing.

Discussion

Spawning season

Larval and juvenile white seabass collected off San Diego County were spawned from March to September, with the greatest number spawned in June in both years (Fig. 10). This seasonal pattern of spawning, inferred from counts of otolith increments, agrees with previous estimates based on larval abundance and adult spawning condition. Moser et al. (1983) observed that eggs and larvae were most abundant in CalCOFI





plankton samples in July and that 95% of fish were captured between May and August. Adults begin to mature in early March (Clark, 1930) and spawn off southern California from April to August. Peak spawning activity is in May and June (Skogsberg, 1939).

Size and age at settlement

The smallest larvae caught during the present study were 6–7 mm SL, which would seem to indicate that white seabass begin to settle at about this size. However, white seabass as small as 4.2 mm SL were collected along the open coast north of San Diego County in 1988 and 1989 with a trawl containing 2-mm mesh in the codend (Allen and Franklin, 1992); therefore the smallest settled larvae were probably not retained by our net. More than 20% of the individuals collected in that study were <5 mm

SL and 50% were <7 mm SL. This size distribution suggests that many larvae caught off San Diego County had settled at lengths of 4–5 mm SL. Larvae up to 7.2 mm SL have been collected from the water column (Moser et al., 1983), indicating that some individuals settle at >5 mm SL.

Given that many white seabass settled at 4–5 mm SL, the average age at settlement must be less than one month. The 10 smallest fish caught and aged in this study ranged from 6.2 to 9.2 mm SL and were 26–32 d old (Fig. 8). Although smaller (4–5 mm SL) fish were not aged, they were probably much younger. In the laboratory, white seabass reared at 15°C hatch at a length of 2.8 mm SL after 2 d and grow to 4 mm SL in 10 d and to 5 mm SL in 15–19 d (Moser et al., 1983; Orhun, 1989). At this rate of growth, a 4–5 mm SL settled fish would have spent only 12–21 d in the pelagic habitat.

Allen and Franklin (1992) hypothesized that most white seabass larvae that settle along the coast of southern California are spawned off Baja California and advected northward. However, a short pelagic phase of 2–3 weeks suggests that many of these larvae are spawned within the Southern California Bight (SCB). The direction of larval transport is difficult to predict because the behavior and position of white seabass larvae in the water column is unknown. During spring and early summer, polewardflowing undercurrents over the continental slope and equatorward-flowing surface currents over the continental shelf (Hickey, 1993) could transport larvae along the coast in either direction. However, mean



seasonal current velocities in the SCB region in spring and early summer are generally less than 20 cm/s, although short-term velocities can be higher (Hickey, 1993). At 20 cm/s, larvae could be transported a maximum of 200–360 km in 12–21 d. It therefore seems unlikely that the 4–5 mm SL white seabass caught in the northern and middle SCB by Allen and Franklin (1992) were spawned off Mexico. These larvae, which represented a large proportion of the total catch, were almost certainly spawned off California. Of course older larvae collected in the middle SCB or young larvae caught off San Diego County could have been spawned off either California or Mexico.

Nursery location

The depth distributions of settled white seabass on the coast and within bays suggests that these fish prefer shallow water beyond the surf zone. Along the open coast, nearly all fish were caught at depths of 4-8 m, a region which begins just beyond the breaking waves. In the bays, all 10 fish were caught just beyond the shore break at a depth of 0-1 m. Previous observations in other regions are consistent with this conclusion. Settled white seabass have been collected beyond the breaking waves along semiprotected and exposed shores in and around Long Beach Harbor (Allen and Franklin, 1988). White seabass were not collected along protected shores, but depths <1.5 m were not sampled. On the open coast north of San Diego County, settled white seabass were also more abundant along the 5-m depth contour than along the 10-m contour (Allen and Franklin, 1992). Although this distribution supports the conclusion that white seabass prefer shallow water, 30-40% of the settled fish were caught at the 10-m contour (Allen and Franklin, 1992). Most of the fish collected at 10 m were taken along one section of coastline between Ventura and Point Dume; thus the preference for shallow water may be modified by local conditions.

Greater densities of settled fish along the open coast than in the bays suggests that the primary nursery for white seabass is the open coast. However, this difference in densities may reflect lower capture efficiencies of the 1.0-m trawl and beach seine in comparison with the 1.6-m trawl used on the coast. Although net efficiencies could not be estimated for white seabass because of low abundance, Kramer (1990) found no difference in efficiency of these same nets for California halibut <40 mm SL. Net efficiencies probably did not differ greatly for small white seabass either, and thus the low catch of settled fish in the two bays was due to low abundance. In ichthyofaunal surveys of other southern California bays over the last several decades, only a few early juvenile white seabass have been caught (Dixon and Eckmayer, 1975; Klingbeil et al., 1975; Horn and Allen, 1981). Although depths of 0–1 m may not have been sampled intensively, data from these surveys support the view that bays as a whole are not important nurseries for white seabass.

The small size of southern California bays must also limit their importance as nursery areas for white seabass. As an example, Kramer (1990) estimated there were only 92 ha of habitat available between 0 and 1 m in Mission Bay and only 10 ha in Agua Hedionda Lagoon, compared with roughly 2,500 ha of habitat available between 5 and 8 m along the coast of San Diego County. Most of the remaining bays on the southern California coast are also small and many are periodically closed off from the sea by shifting sandbars (Zedler, 1982).

Nursery features

The narrow depth distribution of settled white seabass along the coast suggests that one or more fea-



tures of this zone enhance survival of young fish. Survival in shallow nurseries may be higher because of faster growth resulting from abundant food or warmer water, or lower predation rates (Bergman et al., 1988; Karakiri et al., 1989). Two features of the white seabass nursery that may promote rapid growth of juveniles are the abundant mysids and warmer water. Mysids, the principal prey of all sizes of white seabass collected, appear to be much more abundant within the nursery than at adjacent depths. Clutter (1967) sampled mysids at depths of 2-14 m during 1960-62 at a site 3 km south of the Torrey Pines 2 site (Fig. 1). Although the center of the depth distribution varied among months by 1-2m, the mysid Metamysidopsis elongata was most numerous in the middle of the white seabass nursery

(Fig. 3). Other species of mysids were much less abundant. Density of M. *elongata* within the nursery can be quite high. Clutter's data indicate that the mean density of mysids at 6 m was over $4,000/m^3$, whereas Roberts et al. (1982) estimated that the mean density of mysids at 6 m near the San Onofre site was over $100/m^3$. Mysids are also about an order of magnitude more abundant during spring and summer, when white seabass are in the nursery (Clutter, 1967).

Mysids are not only abundant within the nursery; their broad size distribution makes them suitable prey for both recently settled larvae and much larger juveniles. Mature *M. elongata* brood and release relatively large young that remain in shallow water (Clutter, 1967). This reproductive strategy results in a population of mysids in the nursery that ranges over 100-fold in individual weight (Fig. 6). Although larger fish eat larger mysids, juveniles >40 mm SL can apparently feed on the largest mysids available (Fig. 6). At about this size, a transition from mysids to larger prey

such as fish and shrimp also begins. The diets of other closely related sciaenids show a similar shift. Small (10-40 mm SL) sand seatrout, *Cynoscion arenarius*, small (15-30 mm SL) spotted seatrout, *C. nebulosus*, and juvenile (50-129 mm SL) weakfish, *C. regalis*, all feed extensively on mysids and at larger sizes shift to eating fish (Stickney et al., 1975; Sheridan, 1979; McMichael and Peters, 1989). Large juvenile, subadult, and adult white seabass feed principally on fish (Quast, 1968; Thomas, 1968).

A second feature of the shallow nursery that may enhance growth and survival of settled white seabass is warm water. Temperatures in the 4-8 m stratum during the summer ranged from 16 to 20°C, an average of 1.2 and 1.8°C warmer than the two deeper strata. The effect of a 1-2°C increase on growth has not been calculated for juveniles, but Orhun (1989) observed that a temperature increase from 15 to 17°C resulted in an increase in growth rate (dry weight gain) from 13.8%/d to 16.7%/d in 4-21 d old larvae. Temperature may have less influence on growth of juveniles, but any increase in growth rate will accumulate over the 2-3 months that juveniles are in the shallow nursery. Houde (1987) has demonstated that a small increase in growth rate acting over a moderate time interval can reduce stage duration and theoretically result in substantial increases in survival and cohort size.



Estimated linear growth rates of wild white seabass (n=50) and three groups of juveniles spawned on 8 May, 24 June, and 25 September 1989 and reared at 17–20°C. Symbols represent the mean length $(\pm 1 \text{ SD})$ of a subsample of 16–76 reared fish. For clarity, symbols are not shown for wild fish. Slopes, adjusted least squares (ALS) means, and coefficients of determination (r^2) are shown.

Correlations between abundances of drift macrophytes and white seabass suggest that macrophytes are also an important feature of the nursery. Although the correlation among abundances in single tows was weak (r=0.29), the sensitivity of this analysis was poor because the catch of white seabass was low; a maximum of only two white seabass was caught in a single tow at these stations. The correlation among mean abundances in the four tows at each site-the mathematical equivalent of making longer tows—was stronger (r=0.52) and does suggest that white seabass are more common near drift macrophytes. Allen and Franklin (1992) also noted that white seabass were rarely caught unless drift algae was present. It is possible that white seabass are simply more vulnerable to the trawl when drift macrophytes are present, but numerous studies with drop nets and purse seines have demonstrated that many juvenile fishes associate with drift macrophytes (Kulczycki et al., 1981; Robertson and Lenanton, 1984; Kingsford and Choat, 1986). Small white seabass may associate with drift macrophytes because they harbor suitable prey or serve as a refuge from predation.

In addition, the nursery area may be preferred by white seabass because the risk of predation could be lower than at adjacent depths. Unfortunately this hypothesis is difficult to evaluate. Surveys of the nearshore areas of southern California show that predators of small benthic fishes are present both within the white seabass nursery and in deeper water (Love et al., 1986). Some of these predators, such as the California lizardfish (Synodus lucioceps), are less abundant within the white seabass nursery than at 12-18 m, whereas other species, such as California halibut (Paralichthys californicus), are more abundant within the nursery than in deeper water (Ford, 1965; Love et al., 1986; Allen, 1990). However predation risk will depend not only on the total number of vertebrate and invertebrate predators at a particular depth, but also on the size and ontogenetic distribution of predators as well as species-specific probabilities of encounter, detection, and capture (Bailey and Houde, 1989; Fuiman and Margurran, 1994). A detailed study is required to determine if the risk of predation to settled white seabass is lower in the nursery than in deeper waters.

Conclusion

The shallow water along the open coast just beyond the breaking waves appears to be the primary nursery for white seabass. Survival of young white seabass is probably influenced by the abundance of mysids and drifting macrophytes as well as by water temperature in the nursery during spring

and summer. However, it is not known if survival in the nursery is an important determinant of year-class success for white seabass. Year-class success in most marine fishes is generally believed to be set during the larval stage. However, poor correlations between larval abundance and subsequent recruitment for some species indicate that survival of older fish, perhaps early juveniles, may be equally important (Sissenwine, 1984; Bradford, 1992). Further studies are needed to evaluate the importance of survival of early life history stages in determining the distribution and abundance of white seabass populations off southern California.

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two-day incubation period (Orhun, 1989). The ages of 50 fish were estimated directly from otoliths, the others from the age-length relation shown in Figure 8.

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