

Size-Specific Vulnerability to Predation and Sensory System Development of White Seabass, *Atractoscion nobilis*, Larvae

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ABSTRACT: The size-specific vulnerability of white seabass, *Atractoscion nobilis*, larvae (2.5–15.0 mm SL) to two types of fish predators—adult northern anchovy, *Engraulis mordax*, and juvenile white seabass—was examined in laboratory predation trials. Concurrent analyses were made of the developmental ontogeny of larval visual and mechanoreceptive systems. The proportion of larvae responding to or escaping attacks by either predator increased with larval size. There were no significant differences in proportions of larvae responding to or escaping attacks of either predator until larvae were 6.0–7.5 mm SL (early postflexion stage). At this size, larvae were better able to evade the slower, more discontinuous attacks of juvenile white seabass compared with the faster attacks of adult anchovy. Major developmental events occur during this larval stage, including rapid improvement in visual acuity, visual accommodation to distant objects, growth and stratification of the optic tectum, and large increases in the numbers of free neuromasts on the head and trunk. It is likely that at larval sizes >7 mm SL, the slower attacks of juvenile white seabass allow more time for larvae to process and integrate visual and mechanoreceptive sensory input from several modalities. White seabass larvae (and sciaenids in general) become more demersal in distribution during the late larval stages in nearshore southern California waters. This ontogenetic shift deeper into the water column may be related to predator-avoidance capabilities of the larvae, since most demersal planktivores exhibit some type of hovering, ambush, or discontinuous mode of predation similar to that of juvenile white seabass and attack at much slower speeds than pelagic, shoaling fish predators. As they shift downward, older white seabass larvae may maximize their predator-detection capabilities when encountering demersal fish predators.

For most marine and estuarine fishes, predation-induced mortality during early life stages may be crucial in determining year-class

strength. Predation has long been recognized as an important potential regulatory mechanism in prerecruit life stages (Houde 1978, 1987; Hunter 1981, 1984), but many of the specific factors that influence predation rates on early life stages are not well understood (Bailey and Houde 1989).

One of the crucial aspects of predator/prey dynamics involves the developmental or physiological basis for capture and escape responses. Fish larvae possess several sensory systems presumed to be important in predator detection; these include visual, mechanoreceptive, and auditory systems. During early ontogeny, these sensory systems undergo rapid development, and the improvement in these systems is thought to be crucial in controlling vulnerability to predation (Hunter 1984; Blaxter 1986). However, experimental investigations combining the study of larval sensory system development and vulnerability to predation are limited. Larvae of several species, including the northern anchovy, *Engraulis mordax*, (O'Connell 1981; Webb 1981; Folkvord and Hunter 1986), Atlantic herring, *Clupea harengus harengus*, (Blaxter et al. 1983; Blaxter and Batty 1985; Fuiman 1989), Cape anchovy, *Engraulis capensis*, (Brownell 1985), bloater, *Coregonus hoyi*, (Rice et al. 1987), and white perch, *Morone americana*, (Margulies in press) have been studied to examine either sensory system development or predator-avoidance behaviors. Similar studies have been conducted on larvae of flatfish (Neave 1984, 1986) and several gadoids (Fridgeirsson 1978; Bailey 1984). These types of investigations, however, have not been combined during one study using a single cohort of experimental fishes.

The purpose of this study was to examine, experimentally, the size-specific vulnerability of white seabass, *Atractoscion nobilis*, larvae to different types of fish predators, and to determine if there was a developmental or neurological basis for any observed changes in larval vulnerability or behaviors. The developmental studies of larval white seabass centered on the ontogeny of two sensory systems, vision and

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mechanoreception, which are presumed to be important components of predator detection and larval escape responses (Blaxter 1986). The ontogeny of avoidance/escape responses and other larval behaviors of white seabass were then analyzed in relation to the structural and functional development of their sensory systems.

Very little is known of the early life history of the white seabass, even though it is the largest sciaenid occurring in coastal waters of California and Baja California and has historically been a favored sport and commercial species (Feder et al. 1974; Vojkovich and Reed 1983). White seabass spawn in spring and early summer in near-shore coastal waters of southern California, and produce pelagic eggs. Abundance and distribution of young-of-the-year in southern California waters have been reported by Allen and Franklin (1988). Larval morphological development has been described by Moser et al. (1983), but larval ecology, predator-avoidance behaviors, and sensory system development have not been described.

METHODS

Larval Rearing

White seabass larvae used in the experiments were hatched from eggs obtained from broodstock adults maintained at the Hubbs Marine Research Center at Sea World in San Diego. Eggs were transported to the aquarium at the Southwest Fisheries Center La Jolla Laboratory and stocked in 76 L aquaria at stocking densities of 6 L^{-1} . During the culture experiments water temperature ranged from 17° to 19°C , and a constant photoperiod of 13 h light: 11 h dark was maintained.

First-feeding white seabass larvae were fed rotifers, *Brachionus plicatilis*, cultured on the green alga *Tetraselmis*. Older larvae were sequentially fed diets of *Artemia* nauplii, a mixture of *Artemia* nauplii and wild copepods, and adult *Artemia*. The developmental size range of white seabass tested ranged from hatching (2.6 mm SL, 0 day after hatch) to juvenile metamorphosis (15.0 mm SL, 42 days after hatch) (Fig. 1).

Experimental Predators

Adult northern anchovy and juvenile white seabass were used as predators. Both of these predator groups occur in nearshore waters of

southern California and are potential natural predators of white seabass larvae. These two predator groups represent different types of raptorial predatory behavior (Table 1). Adult northern anchovy are pelagic, cruising predators that attack prey at relatively high speeds and often from oblique angles. Juvenile white seabass attack at much slower speeds and have a somewhat discontinuous mode of attack that involves an approach, glide, and then engulfing of prey. Northern anchovy also initiate attacks from much greater distances.

Predators were held in laboratory holding tanks and fed adult *Artemia*, minced euphausiids and occasionally white seabass larvae. To minimize predator learning behavior, after completion of predation trials on a given date, predators were transferred to separate holding tanks; this ensured that no predator was used more than twice during the 6 wk experimental period.

Experimental Methods

The predation experiments were conducted following the methods of Folkvord and Hunter (1986), with several modifications. Predation trials were carried out in rectangular fiberglass tanks, 1.4 m^3 in volume, with a clear glass win-

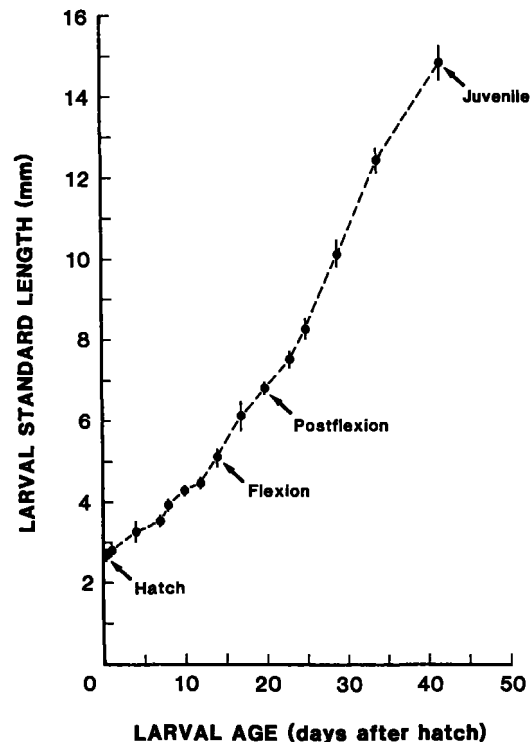


FIGURE 1.—Sizes, ages, and developmental stages of larval white seabass prey used in predation trials.

TABLE 1.—Modes of predation exhibited by adult *Engraulis mordax* and juvenile *Atractoscion nobilis*.

Predator	Size (mm)		Attack distance (dm)		Attack speed range (m/s)	Mode of attack
	Range	Mean	Range	Mean		
<i>Engraulis mordax</i> (Adults)	85–107	96.4	20–70	36.6	0.50–1.50	Fast speed; approach and attack continuous; often from oblique angle
<i>Atractoscion nobilis</i> (Juveniles)	62–86	72.2	5–30	14.7	0.05–0.20	Slow to moderate speed; attacks often discontinuous, with approach, glide, then ingestion; angle of attack horizontal or oblique

dow on one side for observation. Fluorescent lamps produced 2,000–3,000 mc at the surface of each tank. A black plastic tent enclosed the window, providing a darkened compartment for observations. Metric rules placed on the tank window allowed estimation of predator attack distances. The tanks were supplied with flow-through ambient seawater (17°–19°C), except during an experiment when the water was static. Since adult northern anchovy often occur in large schools and juvenile white seabass are solitary or found in loose aggregations, it was decided that northern anchovy predators in groups of five individuals and white seabass in groups of three should be used. This simulated the predators' natural condition yet prevented predator "swamping" of larval prey.

Feeding motivation of predators was standardized by presenting constant numbers of adult *Artemia* to predators prior to predation trials with larvae. (*Artemia* are a good standard prey because they do not avoid predatory attacks by fishes.) Preliminary experiments had indicated that feeding behavior of adult northern anchovy was more variable than that of juvenile white seabass; thus, five groups of five *Artemia* each were presented to each anchovy predator group and three groups of five *Artemia* each were presented to white seabass. After the *Artemia* additions, white seabass larvae were introduced into the predation tanks in groups of five (each larval group added = trial). Trial duration was 10 minutes or until all prey were eaten. Larvae and *Artemia* were added to the tanks in clear beakers that were gently submerged at the water surface. After the initial *Artemia* trials, each predator group was tested with 6–8 larval trials, followed by a final *Artemia* trial to test for predator satiation.

On the same day as predation experiments, subsets of 10–12 larvae were removed from cul-

ture tanks and fixed in 5% formalin for calculation of mean larval sizes; additional subsets of larvae were removed for examination of sensory system ontogeny (discussed below). The total number of predator-prey interactions observed for each larval size class and predator type is presented in Table 2.

TABLE 2.—The total number of predator-prey interactions observed for each larval size and age class and predator type.

\bar{x} larval size (mm)	Larval age (d)	Observations per predator type	
		Northern anchovy	White seabass
3.1	4	36	39
4.5	12	35	32
6.1	17	33	38
7.4	23	30	37
9.1	27	40	38
12.5	34	38	40
14.8	42	42	50

Classification of behaviors followed Folkvord and Hunter (1986). Four measures of predator-prey interactions were calculated: mean and maximum attack distances; percentage of larval avoidance responses; percentage of larval escapes; and predation rate (percentage of larvae captured during each 10 min trial). Approximate predator attack speeds also were estimated. A predator attack was a directed movement toward a prey with the mouth open. Predator attack distance was the distance in decimeters (dm) from a prey to the point of origin of attack. An avoidance response was a change in speed or direction of a larva occurring before a predator could complete an attack. An escape occurred when a predator failed to capture a larva during a single attack. Repeated attacks were scored as separate events.

Two potential biases to the predator-prey

interactions were addressed. Variation in predator performance was examined by calculating the percentage of predator error occurring in five groups of both types of predator feeding on adult *Artemia*. Since *Artemia* show no avoidance responses, a predator error was recorded when a predator simply missed the prey. Percentage of predator error was calculated for each predator group and among groups. In addition, potential stress or mortality of larvae due to handling was examined. For each larval size class, four replicates (trials) of five larvae each were transferred into 76 L tanks containing no predators. Mortality observed in control tanks was used to adjust for handling-induced mortality or increased vulnerability of larvae in predation trials.

Analysis of Larval Sensory System Development

Subsets of larvae from each size class were removed from culture tanks for analyses of larval visual and mechanoreceptive systems. Groups of 6–8 larvae from each size class were fixed in 5% phosphate-buffered formalin for histological analysis of organogenesis. Larvae were dehydrated, cleared, embedded in paraplast, and serially sectioned at 5 μm transversely and sagittally. Sections were stained with Harris' haematoxylin, counterstained with eosin, and viewed under light microscopy at 80–1250 magnification. Ontogenetic development of the lens, retina, and optic tectum were examined and swimbladder inflation was noted. Size-specific visual acuity was calculated from retinal sections using the formula: $\sin \alpha = c/f$, where α is the minimum separable angle, c is the distance between the centers of adjacent cones, and f is the focal length of the lens (Neave 1984). Cones were measured as numbers per 100 μm length of retina (d), thus the reciprocal $10 d$ gives cone separation in mm. The expression was multiplied by 1.11 to adjust for approximate 10% shrinkage during processing, and the focal length of the lens was calculated by multiplying its radius (r) by 2.55 (Matthiessen's ratio; Matthiessen 1880), giving: $\sin \alpha = 0.0435/dr$.

Separate groups of 6–8 larvae from each size class were examined for development of free neuromast organs. These larvae were anaesthetized with MS-222 and immersed in a bath of the vital stain Janus Green (0.05% Janus Green made up with 50% seawater) (Blaxter et al. 1983). Larvae were immersed for 20–30 minutes

and then removed for examination of number and location of free neuromasts under light microscopy.

Histological sections also were examined to determine the timing of swimbladder inflation in larvae.

Data Analysis

For each predation trial, predation rate (percent killed in 10 minutes) was calculated from the equation: $A = m + n - mn$, where A = total mortality rate, m = control mortality rate, n = experimental predation rate, and mn = the interaction effect which estimates the proportion of larvae consumed but which would have died anyway from handling stress or other causes (Ricker 1975). Percentage of larvae responding and escaping were considered total survival rates (S) and were calculated by first estimating total conditional mortality (A) (proportion "not responding" or "not escaping") and then calculating the difference as $S = 1 - A$ (Ricker 1975).

Lens diameter, visual acuity, and thickness of the optic tectum were calculated for each larval size class and developmental stage. Developmental ontogeny of the retina, optic tectum, and swimbladder were described. The mean number of neuromast organs also was calculated, and composite maps were developed of the patterns of neuromast organ formation.

Statistical analyses of data were performed using SAS (SAS 1982) statistical programs.

RESULTS

Predator/Prey Interactions

Potential Biases

Preliminary determinations of predator error by both predator types indicated that predator performance would not bias results. Mean predator error per trial for northern anchovy adults feeding on *Artemia* was 3.3% (range 2.1–5.1%) while error rate for juvenile white seabass was 2.7% (range 0.8–6.1%). There were no significant differences in mean error rate among predator groups, within trials, or between species (ANOVA, $P > 0.10$).

Larval mortality in control tanks (no predators) was low, ranging from 0.0 to 12.5% mean values for any larval size group. Experimental predation and escape rates were adjusted by the control rates.

Larval Responses

The probability of a white seabass larva responding to or escaping a predatory attack generally increased with larval size, although major differences in these responses were apparent depending upon type of fish predator. The mean percentage of larvae escaping attacks by northern anchovy ranged from 3% in yolk-sac larvae (3 mm SL) to 43% in metamorphosing fishes (15 mm SL) (Fig. 2A), while the percentage responding to anchovy attacks ranged from 14% (yolk-sac stage) to 56% (at metamorphosis) (Fig. 2B). Mean predation rate (percentage of larvae eaten in 10 minutes) by anchovy predators decreased from 95% on yolk-sac larvae to 56% on early juveniles (Fig. 2A). The predator/prey interactions were best described by exponential regressions (Fig. 2).

White seabass larvae were better able to respond to or escape attacks of juvenile white seabass than those of northern anchovy. Mean percentage of larvae escaping white seabass attacks ranged from 8% for yolk-sac larvae to 74% for metamorphosing fishes (Fig. 3A), while the percentage responding to attacks increased from 18% (yolk-sac stage) to 84% (at metamorphosis)

(Fig. 3B). Responses and escapes from juvenile white seabass improved significantly in larger larvae, particularly between the larval sizes of 7.5 versus 9.0 mm SL (t -test, $P < 0.01$). Response and escape success nearly doubled during this developmental stage. Mean predation rate by juvenile white seabass predators decreased from 80% on yolk-sac larvae to 65% on 6 mm larvae, increased to 87% on 7.5 mm larvae, and then steadily decreased to 30% on early juveniles (Fig. 3A). These predation functions also were fit to exponential regressions (Fig. 3).

The success of avoidance movements by responding larvae (numbers escaping/numbers responding) generally increased with larval size (Table 3). Approximately 21% of responding larvae in the 3.1 mm size category successfully escaped northern anchovy attacks; this percentage increased to 50% in 4.5 mm larvae and 75% at metamorphosis. Avoidance success from juvenile white seabass attacks ranged from 39% for 3.1 mm larvae to 75% for 7.0 mm individuals and improved to nearly 90% in early juveniles.

Statistical comparison of the responses and escapes from northern anchovy versus white seabass predators indicated that a significantly higher percentage of larvae >6.0 mm SL

FIGURE 2.—Vulnerability of white seabass larvae to adult northern anchovy predators as a function of larval length. A. Solid circles are percentage of larvae escaping an attack, error bars are $2 \times SE$, regression equation is $\text{Arcsine } Y = 5.078 e^{0.144SL}$ ($n = 44$, $r^2 = 0.73$), where Y = proportion of larvae escaping and SL = larval standard length (mm); open circles are percentage of larvae eaten in 10 min trials, error bars are $2 \times SE$, regression equation is $\text{Arcsine } Y = 81.326 e^{-0.035SL}$ ($n = 44$, $r^2 = 0.96$), where Y = proportion of larvae eaten in 10 minutes and SL = larval standard length (mm). B. Percentage of larvae responding to an attack, error bars are $2 \times SE$, regression equation is $\text{Arcsine } Y = 15.293 e^{0.081SL}$ ($n = 44$, $r^2 = 0.89$), where Y = proportion of larvae responding and SL = larval standard length (mm).

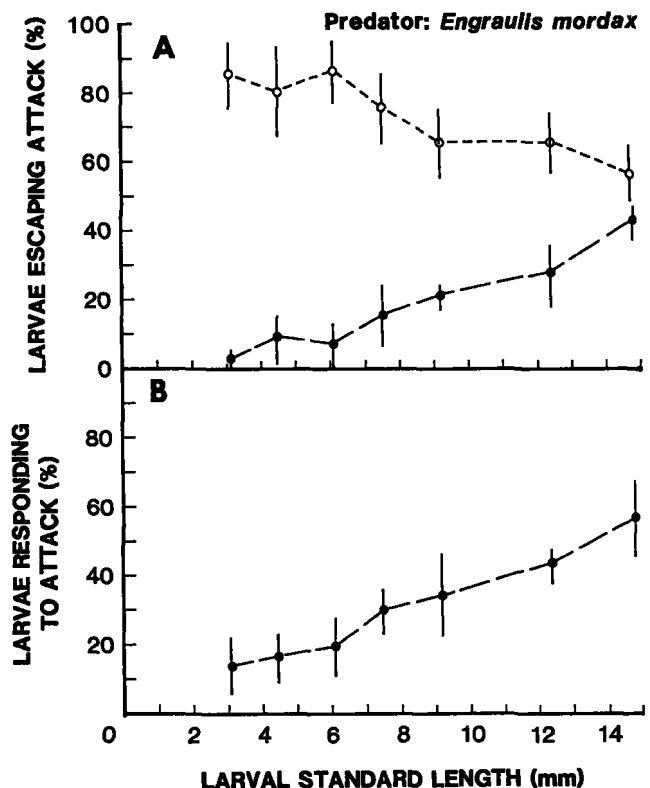


FIGURE 3.—Vulnerability of white seabass larvae to juvenile white seabass predators as a function of larval length. A. Solid circles are percentage of larvae escaping an attack, error bars are $2 \times$ SE, regression equation is $\text{Arcsine } Y = 10.976 e^{0.120SL}$ ($n = 44$, $r^2 = 0.89$), where Y = proportion of larvae escaping and SL = larval standard length (mm); open circles are percentage of larvae eaten in 10 min trials, error bars are $2 \times$ SE, regression equation is $\text{Arcsine } Y = 81.210 e^{-0.0488SL}$ ($n = 44$, $r^2 = 0.92$), where Y = proportion of larvae eaten in 10 minutes and SL = larval standard length (mm). B. Percentage of larvae responding to an attack, error bars are $2 \times$ SE, regression equation is $\text{Arcsine } Y = 16.822 e^{0.096SL}$ ($n = 44$, $r^2 = 0.94$), where Y = proportion of larvae responding and SL = larval standard length (mm).

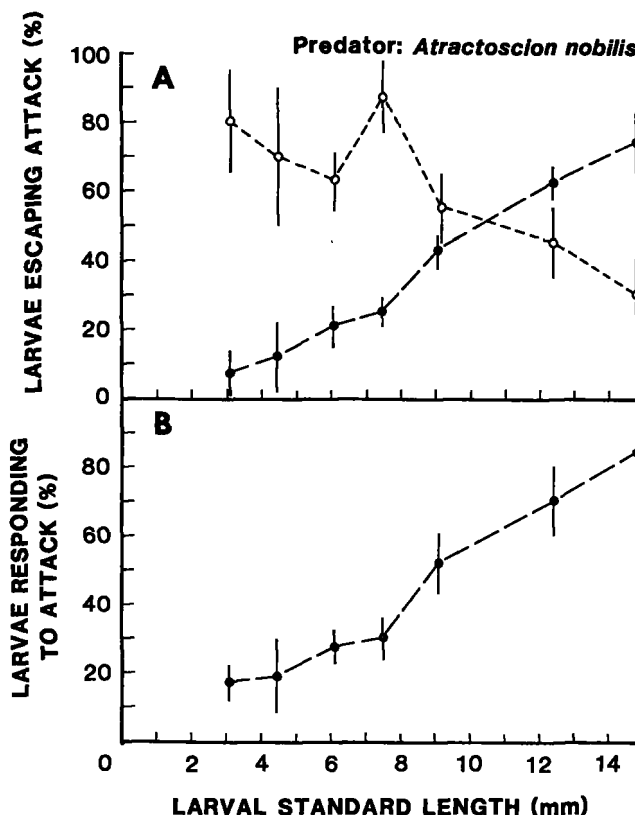


TABLE 3.—Avoidance success of responding larvae (numbers escaping/numbers responding).

Larval SL (mm)	Predator type			
	Northern anchovy		White seabass	
	\bar{x} escape success	SE	\bar{x} escape success	SE
3.2	21.4	4.9	38.8	7.1
4.3	47.0	11.5	57.9	9.1
6.8	63.0	13.2	70.0	7.0
7.4	51.7	6.7	80.0	7.5
9.2	58.8	7.3	81.1	6.6
12.4	64.3	5.3	90.0	5.1
14.8	75.0	6.0	88.0	4.5

escaped white seabass attacks, while a significantly higher percentage of larvae >7.5 mm SL responded to white seabass attacks (ANCOVA with Least Squares Means, $P < 0.05$). This increased responsiveness to white seabass predators (compared to northern anchovy) translated into significantly reduced consumption rates by white seabass predators on larvae >8.5 mm SL (ANCOVA with Least Squares Means, $P < 0.05$).

Larval Visual Ontogeny

The Retina and Visual Acuity

Histological examination of the white seabass visual system revealed numerous developmental changes from hatch to juvenile metamorphosis. In yolk-sac larvae, the lens was present, but the retina was unpigmented and undifferentiated. At time of yolk absorption (ca. 3.2 mm SL), the retina became differentiated into distinct layers, the photoreceptive layer contained visual cells and the epithelial (basal) layer became pigmented. Presumably, at this stage the eye was functional.

In young larvae (3.5–7.0 mm SL), the retina appeared to be composed of only cone cells and no retinomotor (light-dark) responses were noted by either the photoreceptor cells or the epithelial masking pigment. In larvae >4 mm SL, the posteroventral area of the retina (~ 15 – 20° below the horizontal plane) was characterized by densely packed cone cells, constituting an *area temporalis*. A lens retractor muscle first appeared histologically at a standard length of 4.5 mm (Fig. 4). Seen in sagittal section, the lens retractor articulated posteriad with the ventral

floor of the retina and anterior to the lens by means of an extremely thin ligament. In older larvae and juveniles, the lens retractor became bipartite, presumably aiding in movements of the lens posterior and/or ventrad.

The outer nuclear layer (ONL) of the retina, containing the photoreceptive cell nuclei, was single-tiered until larvae reached a length of 7.0–7.5 mm SL. At this stage, compact and darkly staining mitotic bodies began to appear in the ONL (Figs. 5, 6A); these mitotic bodies appeared to be rod precursors. At a larval length of 10.5 mm SL, double cones were present in the photoreceptive layer and the ONL was multi-tiered. At 12.5 mm SL the ONL nuclei were multilayered and a clear retinomotor response was evident, indicating the presence of rods (Figs. 6A, 7).

During ontogeny the density of cone cells in the photoreceptive layer decreased linearly, while lens diameter increased linearly (Fig. 6B).

Visual acuity improved nonlinearly with larval size, changing from 91 minutes of arc in first-feeding larvae to 26 minutes in metamorphosing fishes (Fig. 6A). The period of most rapid improvement in acuity occurred from approximately 4–9 mm larval length.

Development of the Optic Tectum

In yolk-sac larvae, the optic tectum of the mesencephalon (midbrain) was composed of undifferentiated matrix cells. During early feeding stages, the tectum differentiated into an inner, neuronal *stratum periventriculare* (SPV) and an outer, fibrous *stratum zonale* (SZ) (Fig. 8). This bilayered configuration persisted throughout the larval stages, with the entire tectum and the outer SZ thickening during ontogeny (Fig. 9A, B). The period of most rapid tectal differentiation during the early life stages occurred from approximately 3 to 9 mm larval

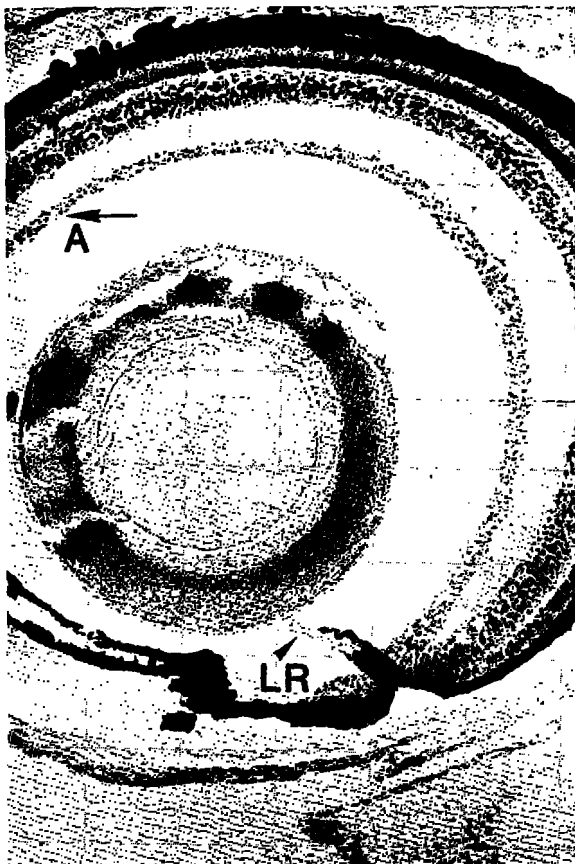


FIGURE 4.—Sagittal section of the eye of a 4.8 mm SL white seabass larva showing the position of the lens retractor muscle (LR). (A) indicates the anterior direction. $\times 100$.

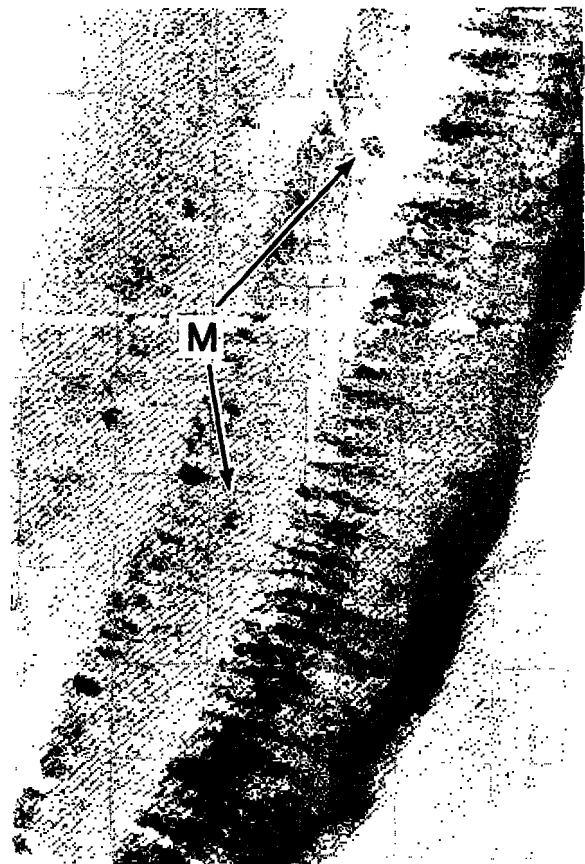


FIGURE 5.—Cross-section of the retina of an 8.0 mm SL white seabass larva showing several dark mitotic bodies (M) in the outer nuclear layer. $\times 250$.

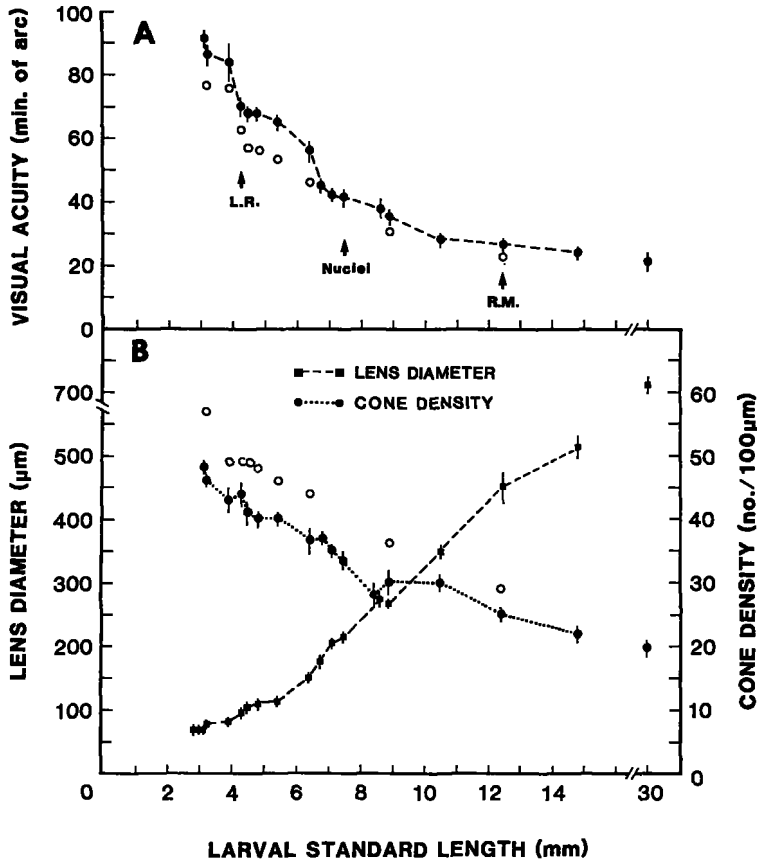


FIGURE 6.—Visual development of larval white seabass as a function of larval length. A. Visual acuity, error bars are $2 \times SE$, regression equation is $Y = 138 - 18.2 SL + 0.726 SL^2$ ($n = 66$, $r^2 = 0.96$), where Y = visual acuity (min of arc) and SL = larval standard length (mm). L.R. is the first appearance of the lens retractor muscle; Nuclei is the first appearance of mitotic bodies in the outer nuclear layer; and R.M. is retinomotor response. B. Squares are changes in lens diameter, error bars are $2 \times SE$, regression equation is $Y = -58.7 + 37.8 SL$ ($n = 78$, $r^2 = 0.97$), where Y = lens diameter (μm) and SL = larval standard length (mm); circles are changes in cone cell density, error bars are $2 \times SE$, regression equation is $Y = 52.6 - 2.3 SL$ ($n = 66$, $r^2 = 0.89$), where Y = cone cell density (no./100 μm) and SL = larval standard length (mm). Open circles are measurements taken in the *area temporalis*. Values for a 30 mm SL juvenile are given for comparison to larvae.

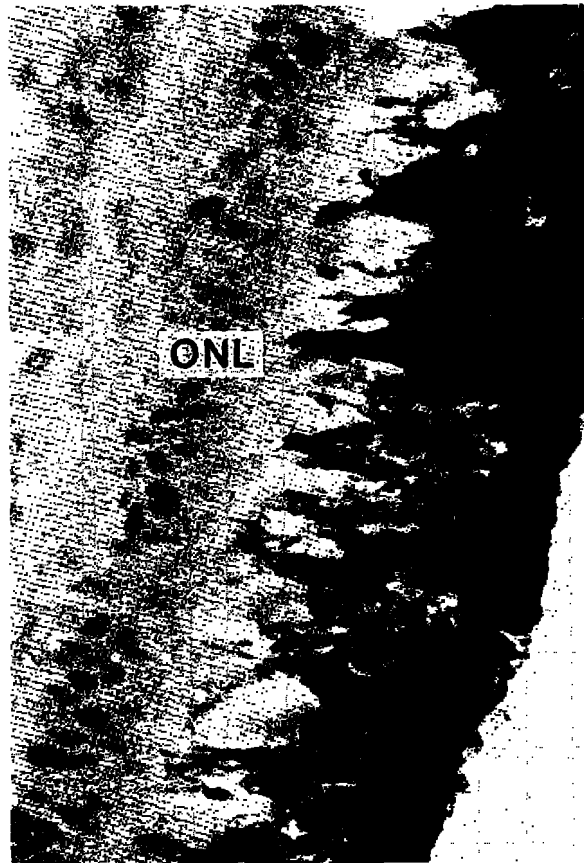


FIGURE 7.—Retinomotor response of a 12.5 mm SL, light-adapted white seabass larva, showing migration of the epithelial masking pigment. ONL is the outer nuclear layer. $\times 400$.



FIGURE 8.—Cross-section through the optic tectum of a 9.2 mm SL white seabass larva. The tectum is bilayered at this stage, with an inner *stratum periventriculare* (SPV) and an outer *stratum zonale* (SZ). The SZ is thickening and exhibits increasing numbers of neurons migrating from the inner layer. The *torus longitudinalis* (T) is quite prominent by this stage. $\times 100$.

length (Fig. 9B). Growth and differentiation of the SZ appeared to involve cell migrations from the inner SPV with a progressive increase in the SZ:SPV ratio (Fig. 9A). This ratio increased rapidly at first feeding (~ 3 –4 mm SL), stayed constant at lengths of 4.0–7.5 mm SL, and then increased again from 7.5 mm to early juvenile stages.

Another important event in the ontogeny of the optic tectum involved the development of the *torus longitudinalis* (TL). This structure first appeared histologically at a larval length of 6.8–7.0 mm SL (Fig. 9A). Seen in transverse section, the TL developed as a teardrop-shaped structure with a wide area of contact dorsad with the optic tectum and ventrad with the epithalamus (Fig. 8). The TL continued to grow with ontogeny, and in older larvae and early juveniles the TL exhibited an increasing number of neuronal projections to the cerebellum.

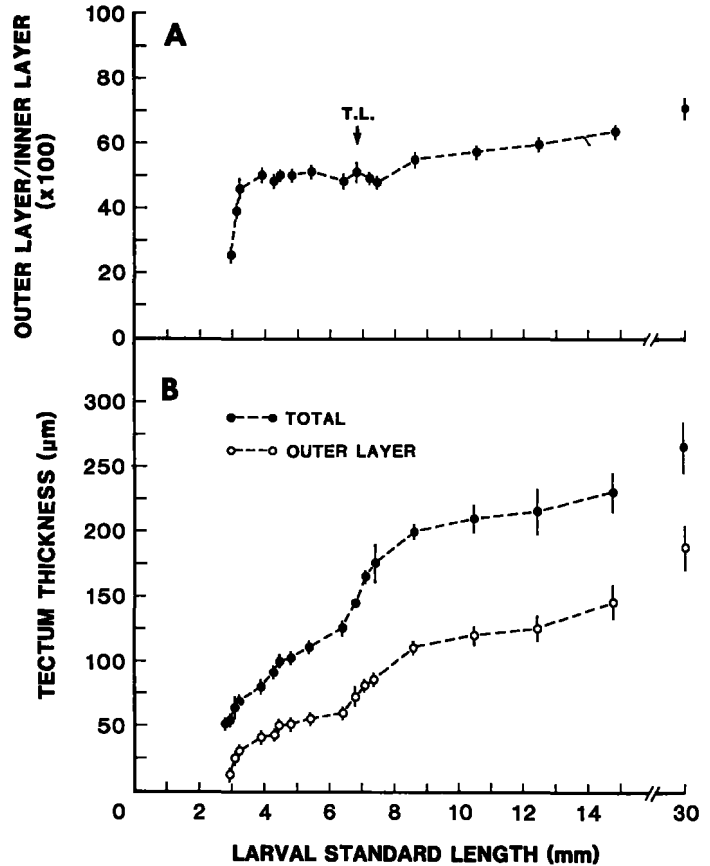


FIGURE 9.—Development of the optic tectum of larval white seabass as a function of larval length. A. Change in the ratio of the outer layer/inner layer, T.L. is the first appearance of the *torus longitudinalis*. B. Solid circles represent total thickness of tectum, error bars are $2 \times SE$, regression equation is $Y = -48.6 + 38.8 SL - 1.35 SL^2$ ($n = 64$, $r^2 = 0.97$), where Y = total width of tectum (μm) and SL = larval standard length (mm); open circles represent thickness of outer layer, error bars are $2 \times SE$, regression equation is $Y = -33.8 + 20.3 SL - 0.56 SL^2$ ($n = 60$, $r^2 = 0.97$), where Y = width of outer layer (μm) and SL = larval standard length (mm). Values for a 30 mm SL juvenile are given for comparison to larvae.

Ontogeny of Mechanoreceptors

Neuromast Development

Staining with Janus Green provided somewhat variable results, in that not all white seabass larvae took up the stain equally well. Some neuromast organs stained better than others, but the use of 6–8 fish per larval size class seemed to provide good composite patterns of neuromast formation.

At hatching, larvae had 5 or 6 pairs of neuromasts on the head and 5 or 6 pairs extending along the trunk (Fig. 10A, B). All of these organs appeared to be free neuromasts (not enclosed by canals). Each free neuromast consisted of a basal, naked neuromast organ attached apically to a cylindrical, gelatinous cupula. The

only other stained structures were the nasal pits.

The total number and patterned formations of free neuromasts increased with ontogenetic development (Figs. 10, 11). At first feeding, larvae had 6–8 neuromasts on the head and 6 or 7 on the trunk. During development, new head neuromasts appeared first in the supraorbital and infraorbital areas, while on the trunk they recruited midlaterally (Fig. 11). The period of most rapid addition of free neuromasts was in the larval size range of 4–9 mm SL. During the early postflexion stage (~7–10 mm SL), free neuromasts began to form in distinct supraorbital, infraorbital, and preopercular (hyomandibular) rows on the head and in a single midlateral row on the trunk (Figs. 10, 11). By 12.5 mm SL,

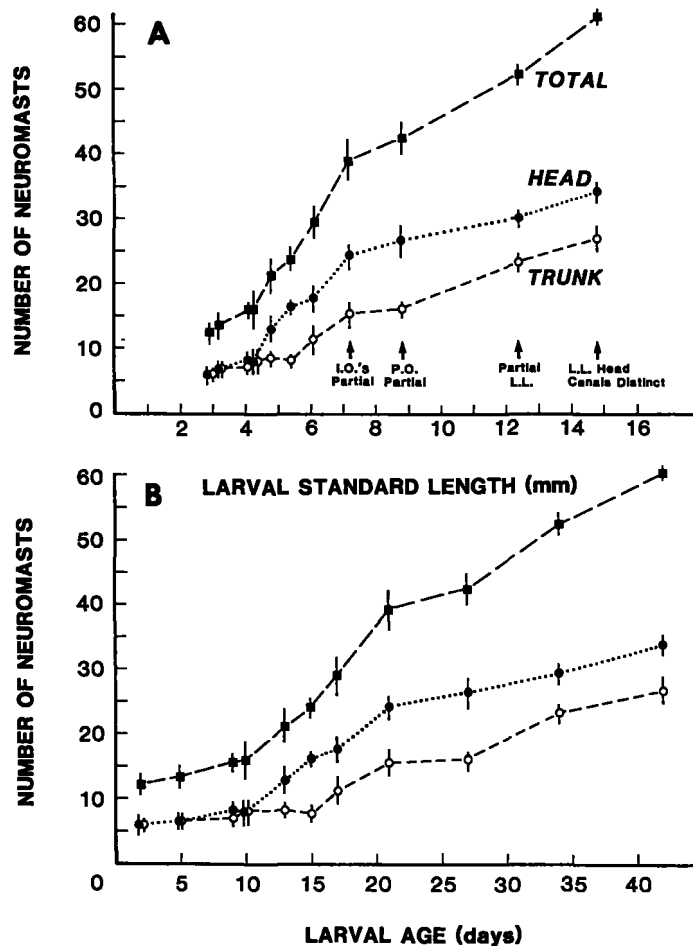


FIGURE 10.—Numbers of free neuromasts developing on larval white seabass as a function of larval length (A) and age (B). Error bars are $2 \times SE$. I.O.'s are infraorbital and supraorbital rows on the head; P.O. is the preopercular or hyomandibular row on the head; and L.L. is the lateral line. Values are based on staining and should be considered approximate only.

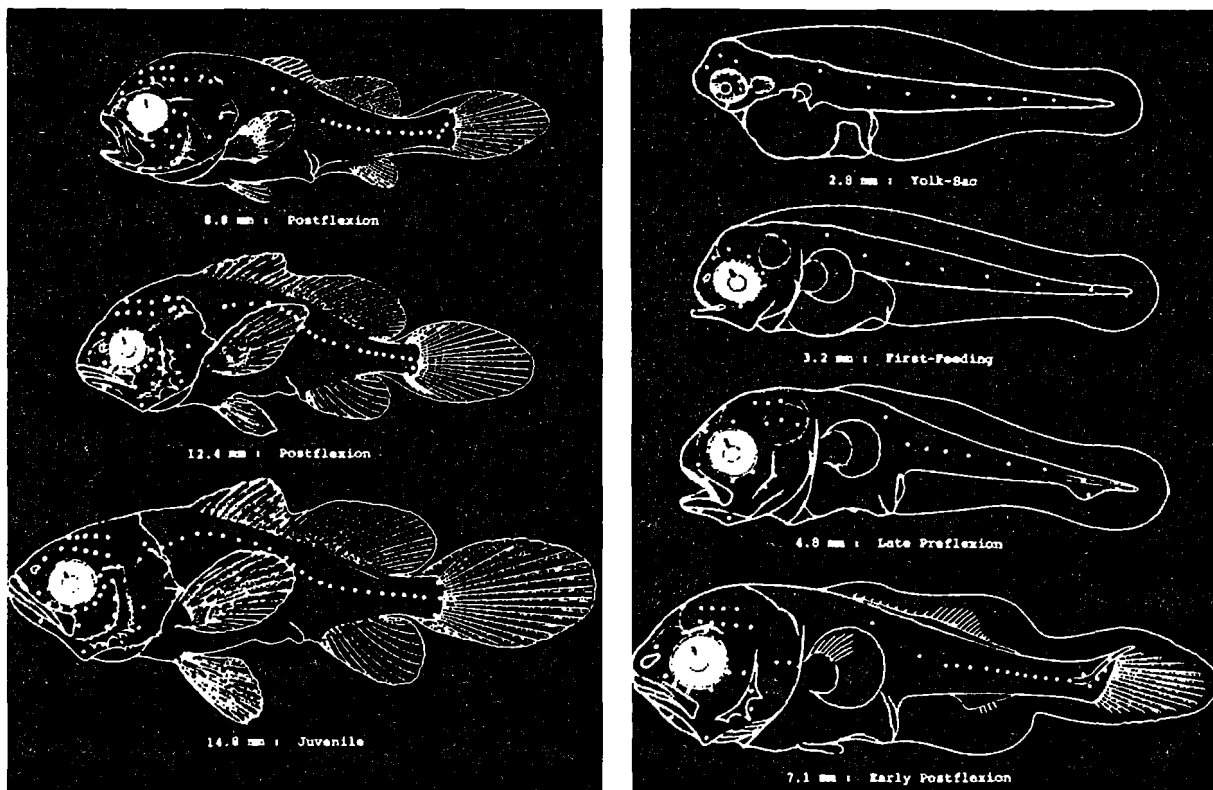


FIGURE 11.—Composite maps showing the location of free neuromast organs during development of white seabass larvae. Larval outlines were modified from those of Moser et al. (1983).

some of the recruiting neuromasts were being enclosed by canals on the head and trunk; some existing free neuromasts were being incorporated in canals as well. At juvenile metamorphosis, the three major branches of the head canals, as well as the lateral line on the trunk, were fairly distinct (Figs. 10A, 11), forming the precursor to the juvenile and adult lateral line system.

Swimbladder Development

In yolk-sac larvae, the swimbladder appeared as a collapsed sac dorsad to the yolk sac, while in first-feeding larvae it was still partially flattened and situated dorsad to the anterior digestive tract. Timing of complete swimbladder inflation was variable; most larvae exhibited full inflation at lengths of 4.5–5.5 mm SL. In larvae >4 mm, a pneumatic duct was present in the anterodorsal area of the swimbladder. It was not clear whether swimbladder inflation occurred by way of air-gulping at the surface or by gas secretion internally.

DISCUSSION

Neurosensory Basis For Avoidance Responses

The overall probability of white seabass larvae escaping predatory attacks seems highly dependent on the size of the larvae, the type and quality of sensory input being integrated by the larvae, and the type of predator encountered (Fig. 12). Yolk-sac larvae have nonfunctional eyes, a small number of free neuromast organs on the head and trunk, and a noninflated swimbladder. At first feeding (~3.2 mm SL), the eye becomes functional, but visual acuity is poor; the pure-cone retina limits peripheral vision and motion detection, and no accommodation is possible (since there is no lens retractor muscle). There is strong correlative evidence that increases in numbers of free neuromasts and improvements in the visual system are responsible for the improved avoidance responses observed in predation trials. In larvae <4.5 mm SL, predator detection is most likely a function of mechanoreception by free neuromasts, since visual

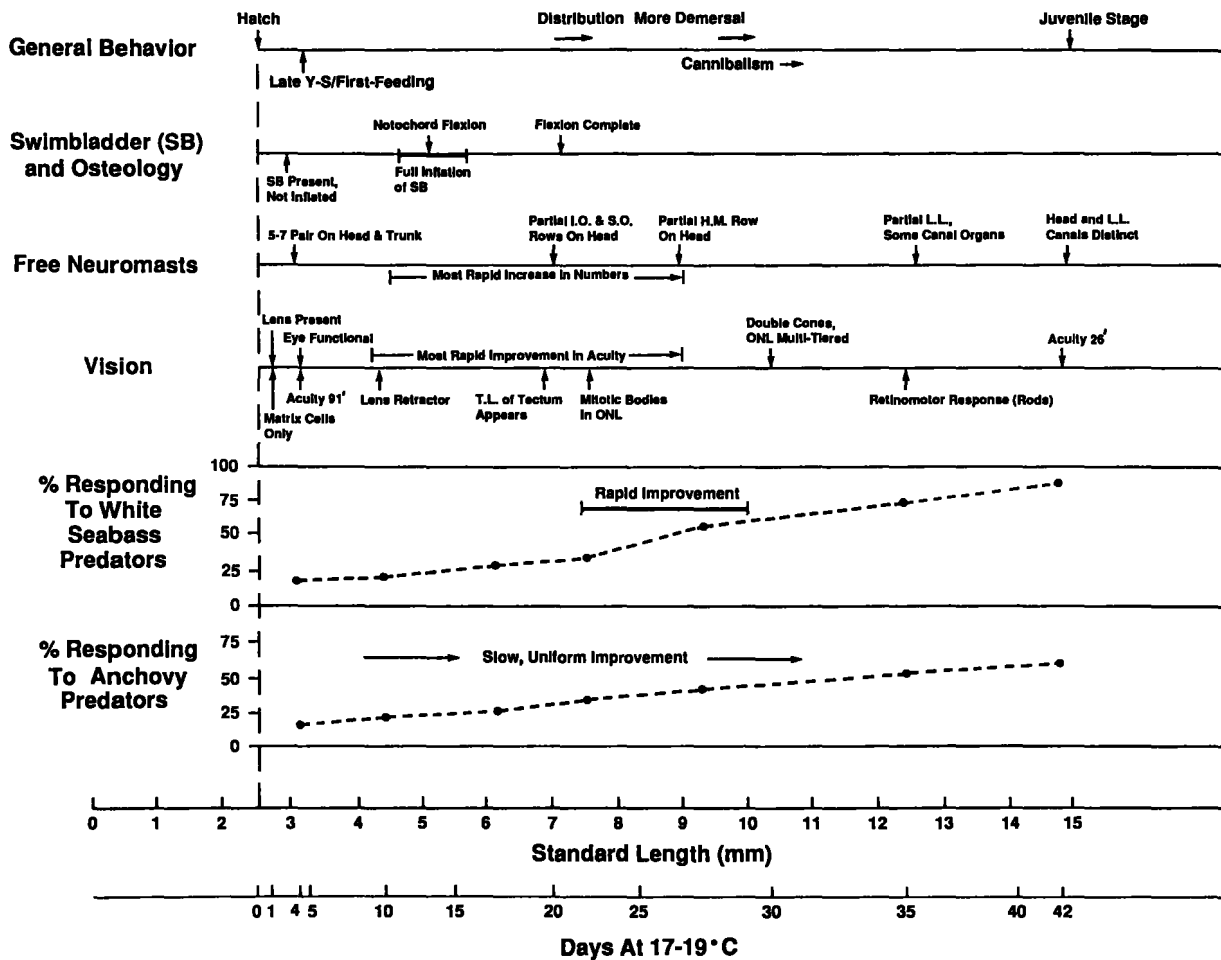


FIGURE 12.—Developmental events and sensory system development during the early life history of the white seabass. Format is based on Hunter and Coyne (1982). Developmental data are from my study, except some behavioral data from Orhun (unpubl. data) and osteological data from Moser et al. (1983). Y-S = yolk-sac stage, I.O. = infraorbital, S.O. = supraorbital, H.M. = hyomandibular, L.L. = lateral line, T.L. = *torus longitudinalis*, ONL = outer nuclear layer of retina.

acuity is poor and no acoustic inputs are likely through the swimbladder. During notochord flexion (~5–7 mm SL), visual accommodation is developed with the lens retractor muscle, the swimbladder is inflated (potentially providing acoustic stimuli), and there begins a major recruitment of free neuromasts on the head and trunk. Up to this point in development, it would appear that vision plays a limited role in predator detection.

During the early postflexion stage (~7 mm), the visual system begins to undergo numerous changes (Fig. 12). Acuity continues to improve, early rod precursors develop in the retina, the optic tectum increases markedly in size and stratification, and the *torus longitudinalis* begins to develop in the midbrain. At 10.5–12.5 mm SL, double cones and early rod cells are present in the retina. These changes are essential to

visual improvement and integration. Visual acuity calculated for most adult marine fishes is 2–10 minutes of arc (Tamura 1957); values for adult white seabass are unknown but probably fall in this range. Thus, approximately 75–80% of the improvement in acuity seen from hatch to adult stage in white seabass has occurred by the late larval stage. However, for vision to play a major role in predator detection, improvement in acuity must be accompanied by development of rod cells, by accommodation to distant objects (lens retractor muscle), and by growth and development of the optic tectum. The development of rod vision helps to improve peripheral vision (O'Connell 1981) and motion detection (Blaxter 1986), both crucial aspects of predator detection. Rods also aid in improved visual performance in dimmer light (O'Connell 1981), which would improve foraging skills and predator-detection

as white seabass become more demersal. Growth and stratification of the optic tectum allow for more complex interconnections with other brain centers in teleosts and are essential for the development of progressively more sophisticated behavioral responses (Munro 1984). The *torus longitudinalis* functions in midbrain integration of proprioceptive information (Groman 1982) and is involved in the control of visual motor patterns (Munro 1984).

The free neuromasts in fish larvae probably function in detection of differences in velocity between the fish and surrounding water. The incorporation of neuromasts into canals (as occurs in older white seabass larvae and early juveniles) probably aids in schooling or detection of accelerations in water movements caused by other animals, such as predators (Blaxter et al. 1983). The increases in numbers and in patterned formations of neuromasts with white seabass larval size probably improve detection of predator movements and aid in swimming movements and proprioception.

During the early postflexion stage (7.5–10.0 mm SL), these improvements in mechanoreceptive and visual capabilities appear to be directly related to improved detection and escape responses. However, depending upon the type of predator encountered, a significant difference exists in the degree of improvement in avoidance capabilities (Fig. 12). Early postflexion larvae exhibit a modest improvement in evading northern anchovy attacks, but display a dramatic improvement in detecting and escaping the slower, more discontinuous attacks of juvenile white seabass. Since some startle responses are elicited even in yolk-sac larvae, it appears that neural motor pathways such as Mauthner-type neurons (Eaton and DiDomenico 1986) are present and functioning during all developmental stages. Just prior to and during the early postflexion stage, larvae undergo notable additions of neuromast organs and major improvements in the visual system. Since the outcome of a predator-prey interaction is heavily dependent upon reaction velocity and timing (Webb 1976), the slower, close-range attacks of juvenile white seabass probably allow more time for detection of sensory stimuli from several modalities as well as sensory-motor integration needed for response and escape movements.

Improvements in visual and mechanoreceptive systems have been implicated in the evasion behaviors of northern anchovy larvae (Webb 1981; Folkvord and Hunter 1986), while acoustic stim-

uli detected through the gas-filled otic bullae seem important in the development of startle responses of Atlantic herring larvae (Fuiman 1989). The inflation of the otic bullae with gas and the occurrence of a well-developed acoustico-lateralis system, however, seems to be more characteristic of clupeoid larvae (Fuiman 1989). Although acoustic stimuli or Rohon-Beard (mechanoreceptive) input could also be related to improved evasion responses of white seabass larvae, the observed improvements in the neuromast and visual systems seem to be directly related to the improved avoidance capabilities.

Larval Vulnerability to Attacks

Larval size and developmental stage are the most important factors related to larval vulnerability in laboratory trials. The type of predator encountered also influences predation rates. However, although white seabass larvae were better able to respond to juvenile white seabass attacks than those of northern anchovy, this did not result in significantly reduced predation rates (in comparisons between predator types) until larvae were >8.5 mm in length. This suggests that other factors related to predator detection of prey, such as prey morphology, water clarity, and alternative prey abundance, may be as important as predator type in controlling vulnerability of small white seabass larvae. Physical background and morphological conspicuousness of prey can be important factors controlling predation rates of planktivorous fishes (Vinyard and O'Brien 1976), while relative abundance of alternative prey has been shown to have significant effects on fish consumption rates on small white perch larvae (Margulies in press).

One disadvantage of laboratory studies is that realistic encounter rates between larval prey and fish predators are difficult to simulate. Although the main purpose of this study was to delineate the developmental basis for larval avoidance behaviors, it is important to recognize the limitation of predicting total vulnerability of larvae based on laboratory trials only. Total vulnerability to predation is a function of the probability of encounters between predator and prey, the probability of capture of prey and the probability of attacks by a predator (O'Brien 1979). My data provide reliable estimates of probability of prey capture and, to a lesser degree, probability of attacks by the experimental fish predators. Encounter rates, however, are affected by a

number of larval growth-related parameters, including increased larval swimming speeds and search volumes and increased conspicuousness of larger larvae (Hunter 1981). It is possible that increasing encounter rates between a suite of predators and larger white seabass larvae in natural systems would offset the observed steady increase in detection and escape responses observed in larger larvae in laboratory trials. This could occur until larvae became invulnerable to attacks. My laboratory data provide some hint of this pattern in the slightly increased predation rates on larvae in the 4.5–7.5 mm size range (see Figures 2A, 3A). However, white seabass larvae are relatively inactive and become increasingly demersal during ontogeny, thus, they might not be subject to significantly higher encounter rates with predators. This remains speculative, however, and is an area for future investigation.

Implications for White Seabass Early Life History

Compared with white seabass larvae, California sardine, *Sardinops sagax*, and northern anchovy larvae (co-occurring pelagic larvae in nearshore southern California waters) appear better able to detect and avoid attacks by adult northern anchovy predators at comparable stages of larval development (Folkvord and Hunter 1986; Butler and Pickett 1988). These two clupeoid species also exhibit schooling behavior in the later larval stages. Many species exhibit a combination of larval adaptations to minimize fish predation, including long periods of transparency (e.g., dover sole, *Microstomus pacificus*; Hunter¹), rapid development of avoidance capabilities (northern anchovy and sardine) and schooling (clupeoids). During early feeding stages, white seabass larvae develop a robust, highly pigmented body form and exhibit limited mobility. During the early postflexion stage (7–10 mm), white seabass start to abandon a strictly pelagic distribution and become noticeably more demersal. By the late larval and early juvenile stage, they are found almost exclusively associated with submerged cover (often drift algae) or near-bottom habitats (pers. obs.; Allen and Franklin 1988; Orhun²; Kramer³). In nearshore waters of southern California, other

sciaenid larvae show a marked vertical size distribution during daylight hours, with larger larvae (postflexion and larger) occurring in highest densities in suprabenthic habitats and smaller larvae occurring higher in the water column (Love et al. 1984; Jahn and Lavenberg 1986). The suprabenthic distribution of larger larvae has been characterized as a possible adaptation to high concentrations of food, for predator-avoidance or for maintenance of position on the continental shelf. However, recent studies of white croaker, *Genyomenus lineatus*, larvae indicate that the suprabenthic distribution of older sciaenid larvae is probably not related to feeding (Jahn et al. 1988).

My results indicate that this ontogenetic shift deeper into the water column by older white seabass larvae (and other sciaenids) may be related to their predator-avoidance capabilities. The dominant planktivorous species encountered in midwater habitats of nearshore southern California waters are fast-swimming, shoaling pelagics such as northern anchovy, sardine, and Pacific mackerel, *Scomber japonicus*. Potential planktivores in near-bottom habitats include sciaenids, gobiids, embiotocids, clinids, seranids, and various flatfishes (Eschmeyer et al. 1983). All of these demersal species exhibit some type of ambush, hovering, discontinuous, or close-range mode of predatory behavior, similar to the attack behavior of juvenile white seabass, and all attack at slower speeds than the shoaling pelagics. Based on my experimental evidence, it is likely that, as they drop out of the plankton, older white seabass larvae maximize their predator-detection and avoidance capabilities when encountering demersal predators. Remaining in the plankton in later larval stages and being exposed to pelagic, shoaling fish predators would prolong a period of extreme vulnerability, while shifting to a demersal distribution would place white seabass in habitats to which they are better suited developmentally.

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²R. Orhun. Unpubl. data. Hubbs Marine Research Center, Sea World, San Diego, CA 92109.

³S. Kramer. Unpubl. data. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

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