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SIZE-SPECIFIC VULNERABILITY OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE TO PREDATION BY FISHES

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ABSTRACT

Vulnerability of larval northern anchovy (6-33 mm SL) to predation by adult northern anchovy and juvenile chub mackerel, *Scomber japonicus*, was estimated by measuring the response and escape probabilities of larvae. The proportion of larvae responding to the attacks of either predator increased with larval length and differed little between predator species. About 20% of 6 mm larvae responded to attacks of predators while 85-100% of 33 mm larvae responded. The proportion of larvae escaping attacks also increased with larval length, but more larvae of all sizes escaped the attacks of adult northern anchovy than those of juvenile chub mackerel. The rate of consumption of northern anchovy larvae by adult northern anchovy was highest when the larvae were 8.5-15 mm long, indicating that greater avoidance success of larvae in this size range relative to smaller ones may not completely compensate for their greater visibility to predators.

The events that cause variation in year-class strength in marine fish stocks occur during the first year of life, but no single life stage or period has been identified as being uniquely influential in the establishment of year classes. Mortality rates are size specific over this period with rates being the highest during the egg and yolk-sac stages and declining thereafter (Hunter 1984; Smith 1985). Variation in the relatively low mortality rates of older larval and juvenile stages may be more influential in year-class formation than the variation of the high mortality rates of eggs and first feeding larvae (Smith 1985). Thus all early life stages from egg through juvenile must be considered and knowledge of the size- or age-specific vulnerability of larvae to predation and starvation is central in any attempt at modeling the recruitment process.

Starvation is probably a direct source of larval mortality for only a few weeks after the onset of feeding, and most losses in the first year of life may be attributed to predation. Predation is believed to be the major cause of mortality during the egg and yolk-sac stages (Hunter 1984), and incidence of starving jack mackerel, *Trachurus symmetricus*, and northern anchovy, *Engraulis mordax*, in the sea indicate that significant starvation mortality is restricted to the first 1-2 wk of feeding or about 10-20% of the larval period (O'Connell 1980; Hewitt et al. 1985; Theilacker 1986). The vulnerability of larvae to predation has been studied over limited size ranges; laboratory data indicate that yolk-sac larvae seem to be vulnerable to small invertebrate predators (copepods, amphipods, and euphausiids [Hunter 1984]). In addition, some egg and larval predators have been identified in field studies and in several cases loss rates due to predation have been estimated (Möller 1984; Frank and Leggett 1984; Van der Veer 1985; Purcell 1985; older literature summarized by Hunter 1984).

The objective of this paper was to determine the size-specific vulnerability of northern anchovy larvae to predation by pelagic fishes. The size-specific vulnerability of larval Cape anchovy, *E. capensis*, to cannibalism has been investigated by Brownell (1985) and vulnerability of larval *E. mordax* to predation by the aquarium fish *Amphiprion percula* was studied by Webb (1981). The results of the current study will be compared to these papers in the discussion.

Our approach was to observe the avoidance behavior of northern anchovy larvae in response to predatory attacks by adult northern anchovy and juvenile chub mackerel, *Scomber japonicus*. Adult northern anchovy were selected as a predator because it is the most abundant fish stock in the California Current region and because it has a planktivorous diet which includes fish eggs and larvae (Baxter 1967; Hunter and Kimbrell 1980). Chub

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mackerel is also a major fish stock in the region and is both planktivorous and piscivorous, with juvenile and adult northern anchovy being a dominant item in the diet of larger individuals (Schaefer 1980; Hunter and Lynn, unpubl. data, Southwest Fisheries Center, La Jolla, CA).

MATERIALS AND METHODS

Experimental Fishes

The northern anchovy larvae used in the experiments were reared from the egg; 2,000-7,000 eggs, from a laboratory brood stock (Leong 1971), were stocked in 400 L black circular fiberglass tanks containing about 150 L of filtered seawater. The culture methods of Hunter (1976) were used to rear the larvae, with extra additions of wild zooplankton when the larvae were 10-25 mm SL. Temperature in the rearing tanks was maintained at about 18°C (range, 17.2°-19.2°C).

Three groups of 5 adult northern anchovy (range of mean standard length [SL] = 8.3-8.9 cm) and a single group of 3 juvenile chub mackerel (mean SL = 19.1 cm) were used as predators. They were fed mainly adult brine shrimp and occasionally northern anchovy larvae. The predators were not fed for 10 h before an experiment.

Apparatus

Predators were kept in two rectangular fiberglass tanks (0.75 m × 2.15 m × 0.83 m = 1.35 m^3) with a clear glass window on one side for observation. Two 100 W tungsten household lamps produced 2,000-3,000 mc at the surface of each tank and a black plastic tent enclosed the window, providing a darkened compartment for an observer. Larvae were released into the tank by gently submerging a beaker at the water surface. Horizontal and vertical metric scales on the tank window aided estimation of predator attack distances. The tanks were continuously supplied with ambient seawater ranging from 20.5° to 23.8°C, except during an experiment when the water was static.

Experimental Procedure

It was necessary to measure the feeding performance of predators fed a standard prey because 1) adult northern anchovy are easily frightened and fright behavior reduces feeding motivation; 2) feeding could be affected by satiation during an experiment; and 3) feeding could be affected by the fish learning and responding to cues associated with the introduction of food. We used live adult brine shrimp (*Artemia* sp., 6.4 mm mean total length, standard deviation [SD] 1.2 mm, n = 25) as a standard prey. Variation in feeding performance of the predators could be more easily detected when *Artemia* were used because unlike the larvae the *Artemia* did not vary in size among experiments nor did they avoid attack by the predators.

Northern anchovy larvae and the adult *Artemia* were added to the tank in groups of three. An addition of three of either prey constituted a trial. A trial ended after 5 min or when all prey were taken. During a trial we used a computer compatible event recorder to record observations of the interactions between predator and prey. All the experiments using northern anchovy as predators started with 5 consecutive trials in which 3 *Artemia* were offered per trial. This was done to insure that northern anchovy predator groups had a similar level of feeding motivation. Preliminary experiments indicated that it normally took a few feeding trials before adult northern anchovy fed consistently. After the 5 initial trials, predators were offered fish larvae and adult *Artemia* alternately for 4-10 trials. Adult *Artemia* were always used in the last trial to determine if satiation had occurred. A less rigorous schedule was used for the chub mackerel predators because their feeding behavior was less variable than that of the northern anchovy. After 3 initial *Artemia* trials, the chub mackerel were given 5 larval trials followed by an *Artemia* trial. In most cases, a second set of 5 larval trials were also given and these were followed by a final *Artemia* trial to check if satiation had occurred.

The number of observations for each larval size class was the total number of predator-prey interactions observed among larvae in that size class. This number exceeded the number of larvae tested in many cases because, if a larva escaped the first encounter with a predator, the subsequent encounter was also recorded as an event. The total number of observations (predatory events) per larval size class (mean SL), when northern anchovy were the predators, was 5.9 mm, 24; 8.5 mm, 55; 11 mm, 48; 15 mm, 53; 21 mm, 82; and 33 mm, 62. Those for the chub mackerel experiments were 6.7 mm, 19; 10 mm, 75; 16 mm, 54; 21 mm, 27; 31 mm, 47; and 50 mm, 39.

Classification of Behavior

Prey behavior was recorded only when the predator attacked a prey. An attack was defined as a movement directed toward the prey with the mouth open. During an attack the northern anchovy predator usually increased its swimming speed, but the chub mackerel increased speed only when attacking larvae larger than 10 mm SL.

Four measures of predator-prey interactions were calculated: mean and maximum attack distance; frequency of avoidance responses; frequency of escapes; and predation rate (percentage of larvae captured during the 5-min trials). The attack distance was the distance in decimeters (dm) from the prey to the point where the predator started the attack. An avoidance response was a change in speed or direction of a larva occurring before the predator had completed the attack by closing its mouth.

An escape was defined as a larval response in which the predator failed to capture the larva during a single attack. Repeated attacks were scored as separate events. By definition, adult *Artemia* could not be credited with an escape since they did not respond to an attack. Cases where attacked *Artemia* were not captured were considered predator errors. Predator error could only be assessed for *Artemia*. All interactions between predators and larvae in which the larvae were not captured were recorded as an escape.

Predator Performance

The feeding success and variation in feeding rates of predator groups fed live adult *Artemia* were analyzed to estimate predator error and to determine if differences existed in feeding performance among predator groups, or among or within experiments. An experiment was 2-5 larval trials conducted on a single size class of larvae on one day using a single predator group.

Predator errors were obvious when *Artemia* were the prey because *Artemia* did not avoid the attack. In such cases the trajectory of the attack was inaccurate and the predator simply missed the prey. Such errors occurred in 3.4% of the attacks on *Artemia*; this estimate is similar to error rates estimated for other predators (Curio 1976). We could not measure the predator error when larvae were the prey because we attributed any failure to capture a larva to larval avoidance success. Presumably our estimates of larval escape probabilities include an unknown number of cases where failure to capture a larva was the direct result of inaccuracies in the predator's attack rather than being the result of larval avoidance.

Considering all northern anchovy predator groups, predator error in capturing *Artemia* was higher in the first 5 trials than in the subsequent trials of the experiments where *Artemia* trials were alternated with larval trials (Fig. 1A). Predator error averaged 3.4% for all *Artemia* trials, whereas it was 2.1% during the period of alternating larval and *Artemia* trials. Similarly, adult northern anchovy took more time to capture all the *Artemia* in the first trial than in subsequent ones (Fig. 1B). No decline in feeding performance on *Artemia* existed at the end of the experiments, indicating that satiation did not constitute a bias in the experiments. The initial decline in the time required for northern anchovy predators to capture *Artemia* may have been caused by an increase in feeding motivation, learning, or a decrease in fright behavior. As the decline occurred during only the initial 5 *Artemia* trials, the larval data were probably unaffected.

Minor differences in feeding performance also existed among predator groups. In two experiments northern anchovy predatory groups fed markedly less on both *Artemia* and larvae (30% fewer prey taken in 5 min; *t*-test, $P < 0.05$). The effect of omitting these two experiments is indicated in the results. Overall, comparisons of feeding performance among groups, within trials, and among experiments indicated that variation in predator performance as measured by predation rates on *Artemia* was not significantly biased (additional details are given by Folkvord 1985) (see also Figure 1).

RESULTS

Probability of a Response to Predators

The most striking feature of the vulnerability of the youngest larval stages of northern anchovy to predators was the low frequency of escape attempts. Only 16% of the 6 mm larvae responded to the attacks of northern anchovy predators (Fig. 2B) and only 26% of 6.7 mm larvae responded to chub mackerel predators (Fig. 3B). The probability of smaller larvae (SL <20 mm) responding to either chub mackerel or northern anchovy predators was about the same (Fig. 4), although size, feeding behavior, and body form of these two fishes were distinctly different. The tendency to respond to attacking predators steadily increased with larval size until by the time northern anchovy larvae were 30 mm all attempted to avoid attacking northern anchovy and over 80% responded to chub mackerel attacks.

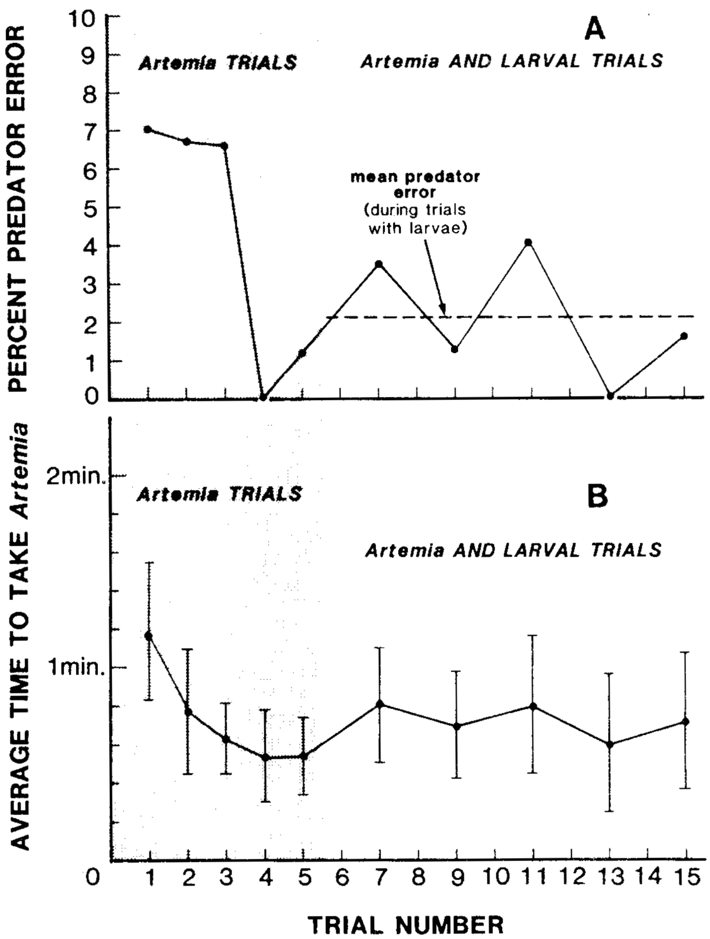

FIGURE 1.—Variation in feeding performance of northern anchovy predators fed live *Artemia* as a function of trial number (equivalent to elapsed time of experiment); shaded area indicates trials in which northern anchovy were fed only *Artemia*; unshaded areas, *Artemia* trials alternated with larval trials. A, percent predator error in capturing adult *Artemia* (percentage of attacks in which a northern anchovy missed the prey); dashed line indicates mean. B, mean time required for predator group to capture 3 adult *Artemia*; bars are 2 × SE of the mean. (N = 21.)

Success of Avoidance Movements

Larval vulnerability depended not only on the responsiveness but also on the success of avoidance movements. The proportion of larvae escaping northern anchovy predators increased from 8% for 6 mm larvae to 92% for 33 mm larvae with an estimated 50% of the 17 mm larvae escaping. The percentage of larvae escaping the attacks of chub mackerel was lower than for adult northern anchovy, but the curves given in Figures 2 and 3 had a similar form. Weibull curves were fit to the data to provide trend lines (equations and parameters given in Figure legends). The fraction of larvae that escaped increased from 6% of 6.7 mm larvae to an estimated 50% of the 30 mm larvae. Of the 50 mm juvenile northern anchovy used as prey only 64% escaped the attacks of the chub mackerel.

The ability to successfully avoid predator attacks was strongly affected by species-specific differences in predator behavior since the fraction of larvae escaping the attacks of northern anchovy increased much more rapidly with larval length than did the fraction escaping the attacks of chub mackerel. In contrast, the fraction of smaller larvae (SL <20 mm) responding to the attacks of these two predators was similar (Fig. 4). This indicates that probability of a larva responding to an attack is less affected

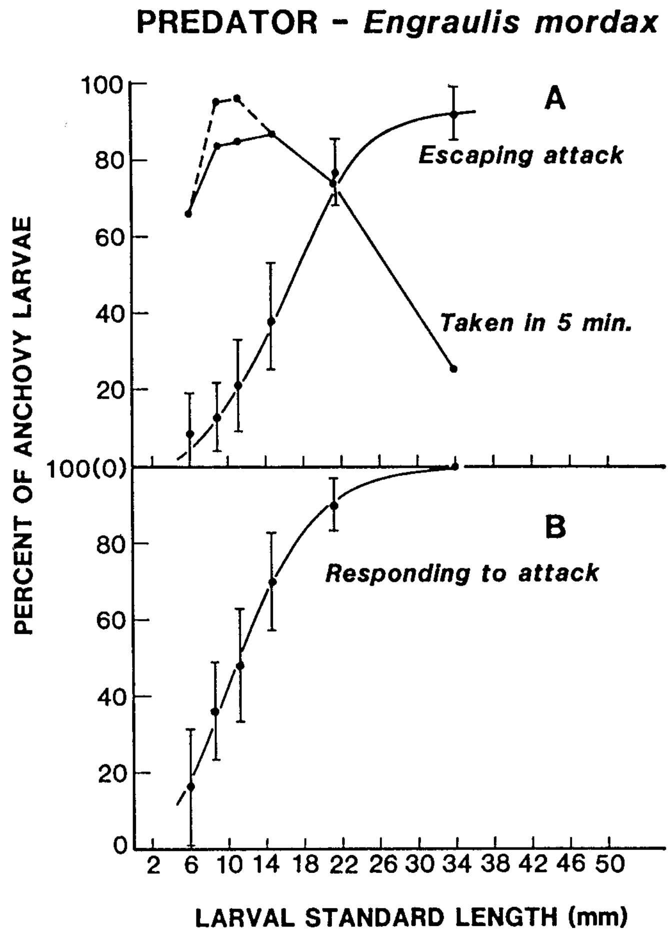

FIGURE 2.—Vulnerability of northern anchovy larvae to adult northern anchovy predators as a function of larval length. A, Percentage of northern anchovy larvae escaping attack; bars are 2 × SE; line is Weibull curve fit to six points using Marquardt's least squares method (Pielou 1981); equation is $N = K(1 - \exp(1 - (L/b) - \lambda))$ where $K = 0.93$, $b = 17.85$, $\lambda = 2.85$, N is the percentage of larvae and L = larval length; and predation rate of the northern anchovy predators (percentage eaten in 5 min) where dashed line is data when experiments with biased predator feeding motivation are omitted. B, Percentage of northern anchovy larvae that responded to the attack of an adult northern anchovy; bars are 2 × SE; and Weibull parameters for curve are $K = 1.00$, $b = 13.58$, and $\lambda = 1.94$.

by differences in predator behavior than is its success in avoiding the attack.

The success of avoidance movements can be separated from larval responsiveness by calculating the avoidance success of responding larvae (numbers escaping/numbers responding). Webb (1981) found no change in this fraction over the larval size range he examined (3-12 mm SL), indicating that changes in responsiveness alone were responsible for the decline in the vulnerability of northern anchovy larvae to *Amphiprion* with increasing larval length. In the present study, no significant trend existed in the success of avoidance movements over the size range of larvae studied by Webb (1981) but success of avoidance movements greatly increased in larger larvae (Fig. 5). The figure also indicates that northern anchovy larvae were much more successful in avoiding *Amphiprion* than in avoiding adult northern anchovy and that the larvae had the least success in avoiding chub mackerel.

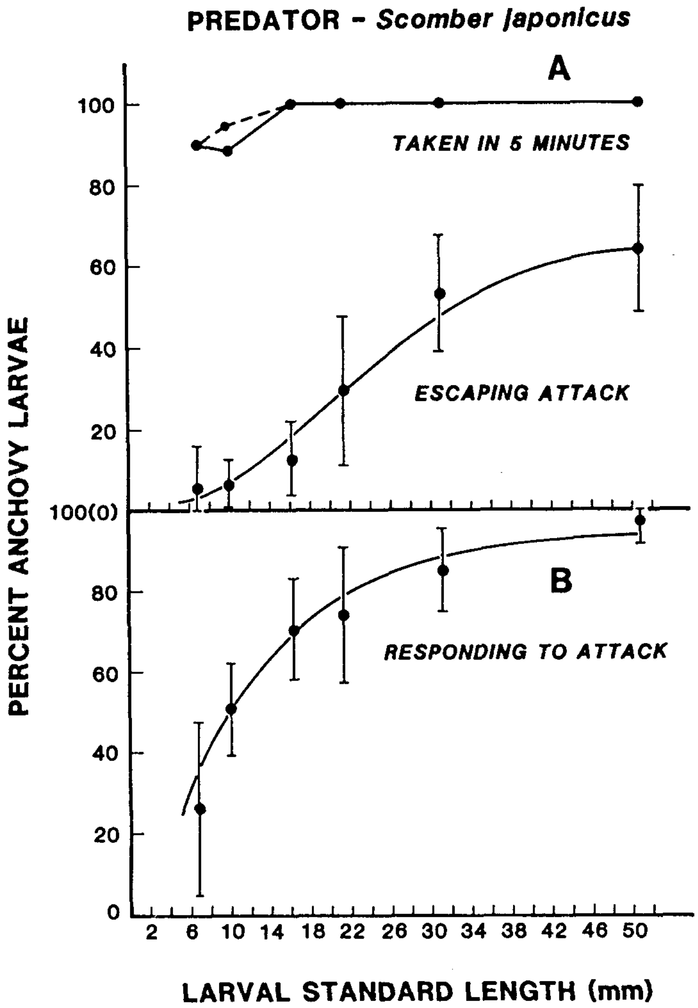

FIGURE 3.—Vulnerability of northern anchovy larvae and juveniles to juvenile chub mackerel predators as a function of anchovy length. A, percentage of northern anchovy larvae escaping attack; bars are 2 × SE; line is Weibull curve fit to six points using Marquardt's least squares method (Pielou 1981); equation is $N = K(1 - \exp(1 - (L/b) - \lambda))$ where $K = 0.66$, $b = 27.41$, N = percentage of larvae, L = larval length, and $\lambda = 2.12$; and predation rate of chub mackerel predators (percentage eaten in 5 min) where dashed line is data when experiments with biased predator feeding motivation are omitted. B, percentage of northern anchovy larvae that responded to the attack of a chub mackerel, bars are 2 × SE; and Weibull parameters for curve are $K = 0.93$, $b = 12.61$, and $\lambda = 1.24$.

Predation Rates

The predation rate of northern anchovy (proportion of larvae consumed by northern anchovy predators in 5 min) reached a maximum somewhere between larval lengths of 8.5 and 15 mm when all data were used, but it occurred between larval lengths of 8.5 and 11 mm when we deleted the experiment where northern anchovy predator performance was lower than average (dashed line in Figure 2A). Statistical comparisons of the fraction of larvae consumed in the various size classes indicated that 6.8 mm larvae were taken less often than larvae in 8.5, 11, and 15 mm size classes despite the fact that these larvae had a low escape ability ($P < 0.05$; normal approximation to the binomial mean; n = 35, 48, 40, and 60, for 5.9, 8.5, 11, and 15 mm size classes). Owing to their small size and

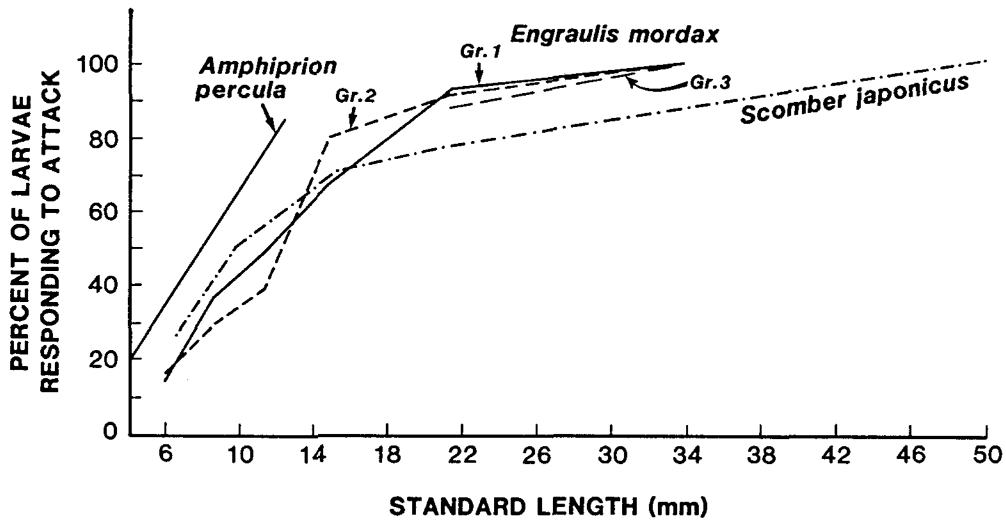

FIGURE 4.—Percentage of northern anchovy larvae that responded to attacks by adult northern anchovy (lines for the three different predator groups shown separately), chub mackerel and the aquarium fish *Amphiprion percula* (from Webb 1981).

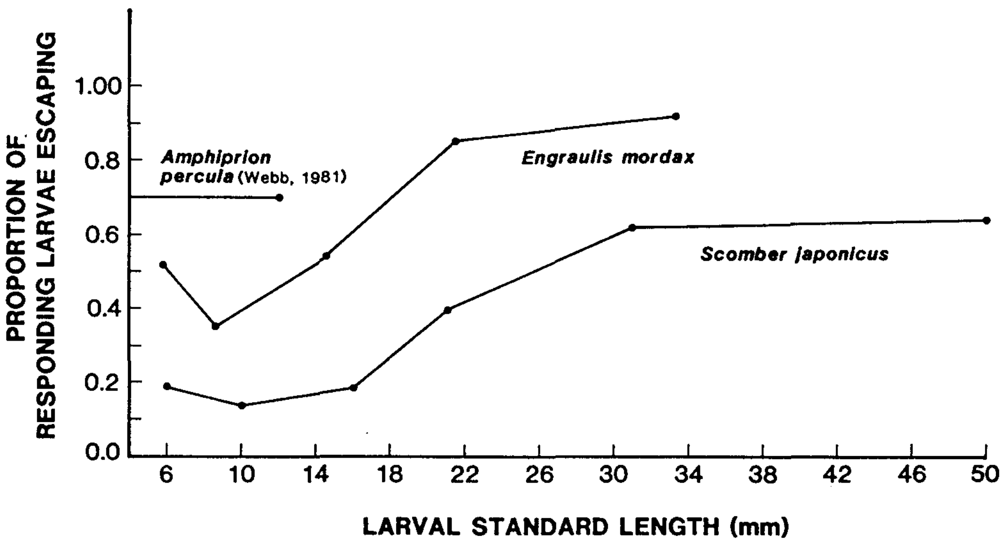

FIGURE 5.—The percentage of responding northern anchovy larvae in various length classes that escaped the predator. Species names identify the predator species.

lack of pigmentation, 6 mm larvae may have been less visible to the predators than larger larvae and consequently were detected less frequently. The decline in predation rates in larvae longer than 15 mm was the result of their greater escape ability.

The number of larvae consumed in 5 min was an insensitive measure of predation rates of chub mackerel, because they usually ate all larvae in the tank within 5 min regardless of their size. Only in the two smallest larval size groups (6-10 mm SL) were some larvae left after a 5-min elapsed time; the deletion of one experiment because of low chub mackerel predator performance changed the predation rate on 10 mm larvae from 87 to 95% (dashed line in Figure 3A). These adjusted data indicate that the feeding rate of chub mackerel was lowest when the smallest larval size group (6.7 mm) were the prey.

Predator Behavior

Sighting distances, persistence of the attack, attack speed, and other characteristics of predator behavior were not well documented in our experiments because our focus was on the larvae. Such information could be quite useful if one were to develop a predation model for northern anchovy larvae, using northern anchovy or chub mackerel predators. We provide some general observations on the behavior of the predators.

Chub mackerel attacked 6.7 mm larvae from a shorter distance than larger larvae (t-test, $P = 0.05$), but no statistically significant trend was evident when northern anchovy were predators. Mean attack distances were a poor measure of sighting range as they included repeated, short-range attacks on the larger larvae. We observed both predator species swimming within 2-3 dm of the smallest larvae without attacking them, whereas larger larvae were always attacked from this distance indicating that sighting distances may be shorter for small larvae.

Adult northern anchovy usually attacked a larva only once during a feeding sequence, and if the larva escaped, it was rarely attacked again or pursued. On the other hand, if the chub mackerel did not capture the larva on the first attack, it usually turned and attacked again. Chub mackerel usually chased an escaping larva until it was captured. The attack speeds of adult northern anchovy, although not measured, seemed to be similar over a wide range of larval prey sizes, whereas the attack speeds of chub mackerel clearly were faster when attacking larvae greater than about 10 mm SL than when attacking smaller larvae.

DISCUSSION

Factors Affecting Larval Vulnerability

A low level of responsiveness seems to be the dominant feature of the vulnerability of northern anchovy larvae to fish predators over the smallest larval size classes we tested (6-10 mm SL). Presumably northern anchovy larvae <6 mm would respond even less frequently, as Webb (1981) found that only 9% of 2.9 mm northern anchovy larvae responded to the aquarium fish *Amphiprion percula*, whereas about 30% of 6 mm larvae did so. During this period vulnerability of northern anchovy larvae to fish predators seems to be primarily a function of visual detection by the predator, because when the larvae are detected they have a low probability of escaping. Our data on predation rates and maximum attack distances indicate that predation in the sea on the small, young larval stages might be lower than expected because of the short range at which such larvae may be detected. Thus, factors that affect the distance at which larvae are detected by predators, such as larval size, visual contrast, and water clarity (Vinyard and O'Brien 1976), may be the most important variables during the first 3 wk of life. As larvae grow they more often respond to the attacks of predators and escape them more frequently. Maturation of visual and lateral line systems (O'Connell 1981) may be the principal cause of this general increase in responsiveness with larval length. Although older larvae are more responsive, they are also more readily detected by predators because they are larger and have more pigmentation. Improved avoidance behavior may not completely compensate for the greater visibility of larvae in the 8-12 mm range, as our data on predation rates by northern anchovy indicated that the rates of consumption were highest for larvae in this range.

Larvae longer than 20 mm responded more frequently to northern anchovy than to chub mackerel predators, possibly because chub mackerel attacked such large larvae at much higher speeds. At higher attack speeds, less time is available for the larvae to respond; consequently, predators with the most rapid attack speeds evoke the lowest proportion of prey responses (Webb 1982). Thus one might expect a larva to respond to small fish predators more frequently than to larger ones, since attack speed would be expected to increase with predator size. This may explain why northern anchovy larvae (2.9-12 mm SL) responded more frequently to the small *Amphiprion* (44 mm) (Webb 1981) than they did to either northern anchovy or chub mackerel predators (Fig. 4). The pectoral swimming of *Amphiprion* might also provide more cues of an impending attack than did the swimming movements of either northern anchovy or chub mackerel.

In addition to size-specific avoidance capabilities and visibility, many other larval characteristics affect their vulnerability to predators. We briefly consider here three of these: effects of starvation, effects of the onset of schooling, and effects of variations in larval growth rates. Clupeoid larvae undergo degradation of muscle and other tissues during starvation, and a reduced predator avoidance behavior might be anticipated (Ehrlich 1974; O'Connell 1980). In a preliminary experiment Folkvord (1985) reported that only 50% of starved, 33 mm northern anchovy larvae responded to the attacks of adult northern anchovy as compared with 100% for fed larvae. No starved 10 mm larvae escaped attack whereas 15-20% of the fed 10 mm larvae did so. The numbers of observations were insufficient for a statistical comparison, but recent work by Booman (unpubl. data, Southwest Fisheries Center, La Jolla, CA) indicates starvation can have a statistically significant effect on responsiveness of 10 mm northern anchovy larvae to adult northern anchovy predators.

The effect of the onset of larval schooling was not considered in these experiments; however, escape and response probabilities of individual larvae may not be altered greatly by the onset of schooling. The work of Major (1978) indicates that the most important effect of schooling may be to reduce the rate of attack by predators. He also found that the majority of Hawaiian anchovy captured by predators were isolated individuals that had moved away from the school, and predator success on schooled prey was similar to that on isolated prey. The onset of schooling in larval northern anchovy occurs between 11 and 15 mm SL, but the time spent in organized, cohesive schools increases throughout the northern anchovy's larval and juvenile periods (Hunter and Coyne 1982). Thus attack rates of predators might be expected to decline throughout later larval and juvenile life as the northern anchovy spends more time in cohesive schools. The onset of schooling occurs over the size range in which we observed the maximum predation rate (numbers consumed in 5 min) on individual northern anchovy larvae by northern anchovy predators. Thus predation pressure may be an important evolutionary factor in the timing of the onset of schooling during the larval stage.

The interaction between larval growth rate and size-specific vulnerability to predation may be an important source of interannual variation in larval mortality (Shepherd and Cushing 1980; Smith 1985). A simple calculation illustrates this point using the size-specific vulnerability of northern anchovy larvae (10-20 mm SL) to adult northern anchovy predators. We assumed larval escape ability to be an inverse measure of predator vulnerability and normalized it to the average mortality rate over this size interval (Table 1). Thus in our calculation, the rate larval mortality decreased with increasing larval size was inversely proportional to the rate escape ability increased with size (larval escape ability increased linearly with larval length over the 10-20 mm length range). Our calculation indicated that a 50% increase in growth rate from the average rate of growth in the sea resulted in a 58% increase in survival in 30 d compared with average conditions. Decreasing the growth rate by 50% gave a 37% decrease in survival over the same interval. A longer period of reduced or enhanced growth rates will, of course, give a larger deviation from average survival values.

TABLE 1.—Calculation of the effect of growth rate on survival of 10-20 mm northern anchovy larvae when mortality is inversely proportional to length specific escape probabilities.

Terms	Parameter values
Z = mortality rate	Z = 0.05 at 16 mm[a]
S = larval length (mm)	10 mm < S < 20 mm
G = growth rate	G = 0.325 mm/d[b]
T = time	T = 30 d
N = relative numbers of larvae	$N(0)$ = 1

Initial equations

$$Z = 0.15 - (0.00625 \times S)\ ^{a}$$
$$S = 10 + (G \times T)$$
$$dN/dt = -(Z \times N)$$

Final equations after substitution and integration

$$N = 0.0724 \times \exp(2.808 \times G)$$

Estimates of survival after 30 days

Growing conditions	Growth rate (mm/d)	Relative numbers of larvae	Relative survival (%)
Average	0.325	0.1803	—
50% increase	0.488	0.2850	+58
50% decrease	0.162	0.1141	−37

[a]Mortality function generated from larval anchovy escape data with adult northern anchovy as predators. Values are normalized to Z 0.05 at 16 mm (Smith 1985).
[b]From Smith (1985), 0.325 ± 50% also used in calculation.

Effect of Predator Size

We examined the existing literature on predators of larval northern anchovies to determine how the ability to escape a predator varied among different predator species. Regardless of the predator species, larval escape ability always increases with larval size, but the rates vary greatly with predator size. In general the smaller the predator, the faster larval escape abilities improve with increasing larval length (Fig. 6). The results of our work on *E. mordax* were similar to those of Brownell (1985) on *E. capensis*. However, capture success of the 85 mm *E. mordax* predators used in our study was about 20% higher than the 34 mm *E. capensis* predators used by Brownell.

The extent of the predator field for a given size and species of predator can be defined as the larval size range in which larval escape success is <100%. For adult northern anchovy predators (85 mm and

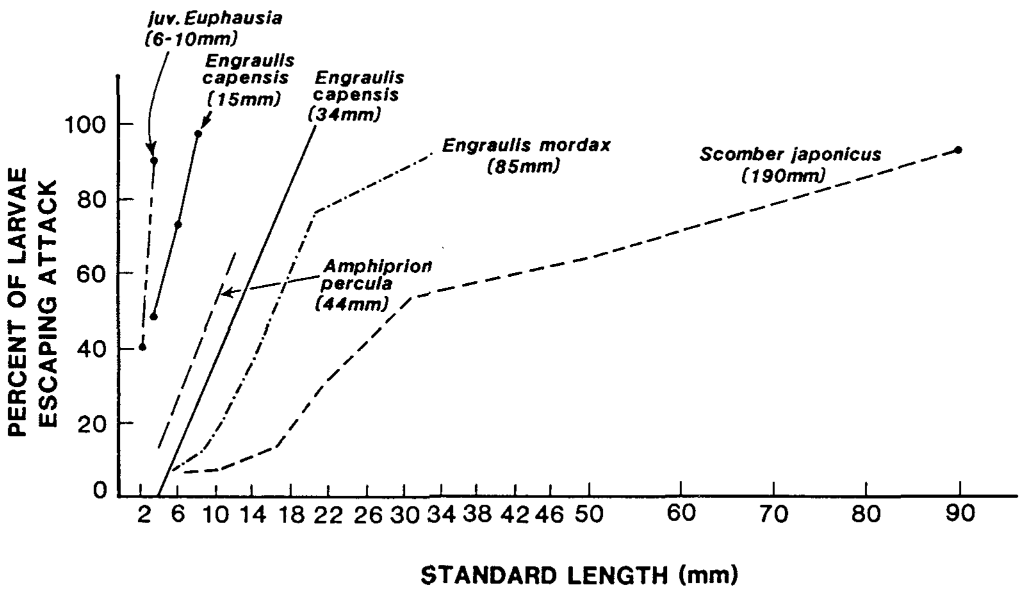

FIGURE 6.—Percentage of larval and juvenile anchovies escaping attacks of various predators as a function of length. Data for *Engraulis capensis* feeding on larval *E. capensis* are from Brownell (1984); juvenile *Euphausia* fed *E. mordax* from Theilacker and Lasker (1974); *Amphiprion percula* fed *E. mordax* from Webb (1981); and others are from this study. Numbers indicate length (mm) of the various predators.

larger), the field extends from the egg (Hunter and Kimbrell 1980) to about 40 mm. The field for juvenile chub mackerel is much wider than that for northern anchovy extending from northern anchovy eggs to adults (120 mm), whereas the predation field for *Euphausia* is restricted to the yolk-sac period (Theilacker and Lasker 1974). The limited data available (Table 2) provide a crude index for the upper limit of the predator field for northern anchovy larvae. When the larval length exceeds about 50% of the predator length little or no predation occurs.

TABLE 2.—Upper limit of some predator fields for larval anchovies, *Engraulis mordax* and *E. capensis*.

Predator: Species	Predator length (mm)	Upper limit of predator field[1]: Larval length (mm)	Upper limit of predator field[1]: Larval length / Predator length
Euphausia juveniles (Theilacker and Lasker 1974)	8	4.5	0.6
Engraulis capensis (Brownell 1984)	15	8.2	0.6
Engraulis capensis (Brownell 1984)	34	20	0.6
Amphiprion percula (Webb 1981)	44	18	0.4
Engraulis mordax (this study)	85	[2]∼40	0.5
Scomber japonicus (this study)	190	[2]∼120	0.6

[1]Upper limit = larval size at which all larvae escape predator.
[2]Extrapolated values.

CONCLUSIONS

Much of the past research on recruitment has focused on early larval stages where mortality rates are the highest (May 1974). Our work supports a growing contention that later larval stages and early juvenile stages may be as important in determining year-class strength (Smith 1985) and that such effects might be mediated through an interaction between larval growth and size-specific vulnerability to predators. Our results and those of others indicate that the ability of northern anchovy larvae to escape pelagic predators increases throughout the larval stage. On the other hand, the susceptibility of larvae to predation may not decrease strictly according to size because large larvae may be more easily detected by visual feeding planktivorous fishes than smaller ones.

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