RESPONSES OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE TO PREDATION BY A BITING PLANKTIVORE, *AMPHIPRION PERCULA*

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ABSTRACT

Responses of northern anchovy larvae, ranging from 0.29 to 1.2 cm total length, to attacks by a biting planktivore, the clown fish, were recorded on video tape. Schlieren optics were used to simultaneously view an opaque predator and transparent prey. All fish were reared, and experiments performed, at 20° C. The percentage of larvae responding to attacks increased from about 9% for 0.29 cm larvae to 80% for 1.2 cm larvae. Of these larvae responding to attack, 26 ± 10% attempted to escape too late and were caught. This proportion was not related to larval size. The direction of larval escape paths to the initial orientation of the body was not related to larval size, but escape distances traveled and mean escape speeds increased with size from 1.0 cm and 4.0 cm/s respectively for larvae 0.29 cm total length to 3.5 cm and 8.2 cm/s in larvae 1.2 cm total length. Larval performance was not maximal except during rare chases which occurred in 7% of attacks by the predator.

Escape maneuvers in vertebrates are initiated by the magnifying retinal image of an approaching object, called the looming effect, and calculated as the rate of change of the angle subtended by the predator as seen by the prey. In the present study, apparent looming thresholds for larval avoidance responses were calculated at the start of the response, and differ from the true response because there must be a finite time difference between the stimulus exceeding the response threshold and the motor response itself (response latency). Maximum likelihood mean apparent looming thresholds were calculated for log-transformed data, assuming nonresponding prey had apparent looming thresholds greater than the maximum actually observed. These mean apparent looming thresholds decreased with larval length from approximately 32 rads/s at 0.29 cm to 1.7 rads/s at 1.2 cm. The most important feature of the larval avoidance response was that an escape attempt should be made appropriately timed to an attack.

The method could be used to examine larval fish responses in other interactions where predation events take place over a small distance. Examples are attacks by biting juvenile and adult fish, and other planktonic invertebrate predators. Effects of larval density and alternate prey species could also be evaluated.

Predation and starvation are believed to be the dominant factors contributing to the extensive mortality of fish eggs and larvae (Blaxter 1969; Hunter 1977, in press; Hunter and Kimbrell 1981). Following Hjort's critical period concept concerned with the importance of first-feeding success to larval survival (Hjort 1914), most attention has concentrated on feeding behavior and food consumption (e.g., Hunter 1972, in press; Arthur 1976; Lasker 1978). Fish eggs and larvae are also extremely vulnerable to a wide variety of fish and invertebrate predators. A few experimental studies have determined feeding rates for invertebrate predators on eggs and larvae in the laboratory (Lillelund and Lasker 1971; Theilacker and Lasker 1974; von Westernhagen and Rosenthal 1976) and rates of egg cannibalism by fish in the field (Hunter and Kimbrell 1981). I know of no studies that have examined responses of larvae to a fish predator.

Northern anchovy, *Engraulis mordax*, larvae are exposed to a wide range of juveniles and adults of fish and consequently to a range of feeding habits on a continuum from filter-feeding to biting (e.g., Leong and O'Connell 1969). The purpose of the experiment described here was to develop a method to study responses of northern anchovy larvae to attacks by fish, and to determine how avoidance responses and larval vulnerability to capture change during early development. A biting fish planktivore was used as a predator in an attempt to complement studies relating to filter-feeding predators, often crudely simulated by towed plankton nets (e.g., Webb and Corolla 1981).

METHODS

Northern anchovy larvae were reared from eggs

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as described by Hunter (1976). Eggs were spawned from five groups of adults taken from laboratory stocks on five occasions during spring 1980 (Table 1.) Eggs were transferred to noncirculated filtered sea water in 400 l black fiber glass tanks. Food for larvae was the dinoflagellate *Gymnodinium splendens* for 2- to 5-d-old larvae, and the rotifer *Brachionus plicatilis* for older larvae. Water temperature was maintained at 20° C. Larvae were held under constant illumination of 2,000 lx at the water surface, provided by standard room fluorescent lights.

Observations were made on predation of eggs and 10 groups of larvae of different total lengths, ranging from 0.29 to 1.2 cm (Table 1). Lengths were based on measurements of a subsample from each group at the time they were used for experiments. Observations were concentrated on early larvae because this is the period of greatest morphogenesis (O'Connell 1981) and maturation of response systems (Kimmel 1972; Webb and Corolla 1981).

TABLE 1.—Total length of subsample ($\overline{X} \pm 2$ SE; N = 10) of northern anchovy larvae populations used in predation experiments with a model predator, the clown fish. Data are also given on spawnings.

Total length at test (cm)	Group	Date spawned (1980)	Date tested
Eggs[1]	C	13 Mar.	13 Mar.
Larvae 0.287 ± 0.015	C	13 Mar.	14 Mar.
.322 ± 0.008	E	4 Apr.	5 Apr.
.391 ± 0.020	E	4 Apr.	6 Apr.
.399 ± 0.010	E	4 Apr.	7 Apr.
.417 ± 0.011	E	4 Apr.	8 Apr.
.421 ± 0.011	B	28 Feb.	4 Mar.
.626 ± 0.050	B	28 Feb.	12 Mar.
.867 ± 0.053	D	27 Mar.	14 Apr.
.953 ± 0.090	A	7 Feb.	29 Feb.
1.166 ± 0.095	A	7 Feb.	18 Mar.

[1] Eggs were 0.135 ± 0.005 cm long × 0.069 ± 0.003 cm wide.

Attempts to obtain natural predators of uniform and suitable size were not successful. Therefore a mimic for biting predators was used. This model was the clown fish, *Amphiprion percula*, cultured from eggs. The fish were held in 40 l polypropylene tanks at 20° C and under constant illumination. The fish were fed daily on a diet of Tetramin[2] and northern anchovy eggs and larvae. The predator was readily available at uniform sizes throughout the duration of the experiment. The clown fish were 4.4 ± 0.2 cm total length (TL) and mass was 1.58 ± 0.17 g. The maximum depth was 1.8 ± 0.2 cm, and maximum width 0.6 ± 0.1 cm, both located 1.3 ± 0.1 cm from the nose (data are $\overline{X} \pm 2$ SE; N = 10).

Interactions between the model predator and northern anchovy eggs and larvae were observed using schlieren optics (Holder and North 1963). Briefly, a vertical collimated light beam was produced by a high intensity monochromatic point source at the focus of a concave mirror (focal length 140 cm) attached to the ceiling. A second mirror, with the same focal length, was located at the floor and focused the light on a black spot on a glass plate.

The observation arena was a cylindrical tank, located in the light beam. It was 35 cm in diameter and 10 cm deep and had a plate-glass bottom. The tank contained a central cylinder, 26.5 cm in diameter and 5 cm deep, which supported a circular plate-glass lid. The lid and the bottom were parallel to each other and normal to the light beam. Discontinuities in refractive index (i.e., larvae in the water) deflected the light from the focus spot on the glass plate, and were seen as bright objects against a dark background. Opaque objects (i.e., the predator) were seen as black silhouettes.

The clown fish were starved for 5 d to ensure uniform high motivation. This was necessary because northern anchovy larvae grow rapidly and loss of a day required starting new batches, particularly for young larvae. Individual clown fish were placed in the observation arena and left for 24 h. After this period, up to 100 northern anchovy eggs and larvae were introduced through a side port in the central cylinder. After 10 to 30 min, the predator began feeding on the prey distributed through the tank. The reason for the delay in the onset of feeding is not known. Behavior was recorded on video tape. Experiments were performed at 20° C.

The video tape was manually advanced to analyze images frame by frame (framing rate = 60 Hz). The following observations were made: the number of attacks by clown fish, escape attempts by prey, escape success of the prey, catch success of the predator, and the number of predator errors. The prey escape angle, distance traveled, and mean speed during an escape attempt were measured.

Animals from a wide range of taxa, including fish, show avoidance responses to approaching, presumably threatening objects (see Gibson 1980). The image of such an object on the retina expands rapidly and this magnification in time is called the "looming effect." It is measured as the rate of

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

change of the angle, α, subtended by the approaching object measured at the prey's eye (Dill 1974a, b). The looming effect is greater as the speed of an approaching object increases, as the object gets closer, and for larger objects. The threshold was calculated at the start of an escape attempt by the larvae, after Dill (1974a),

$$\frac{d\alpha}{dt} = \frac{4\,U\,S_h}{4(D+d)^2 + {S_h}^2} \tag{1}$$

where U = predator speed at the time of the prey response,
S_h = predator shape; mean of maximum depth and width of the clown fish,
D = distance between the predator's nose and the prey when the prey responded,
d = posterior distance of the predator's maximum depth and width from its nose.

Here, $d\alpha/dt$ at the start of the response by the larvae is called the apparent looming threshold (ALT). This is because the true threshold must occur prior to the observed motor response because there is a finite delay in the nervous system between receipt of the stimulus and the start of the motor response. The value of this response latency, or reaction time, is unknown for northern anchovy larvae.

RESULTS

Clown fish fed discontinuously on eggs and larvae, feeding intensely on prey in one location and then swimming around the tank before feeding again. Thus the clown fish did not attack prey as encountered, and often ignored nearest prey between feeding bouts. The clown fish were continuously active, swimming mainly by paddling movements of the pectoral fins supplemented with caudal fin beats. The mean speed was 3.2 ± 0.5 cm/s ($\overline{X} \pm 2$ SE; $N = 100$; range 0.5 to 9.1 cm/s).

Attacks were made on individual larva. Orientation by the clown fish prior to a strike could not be distinguished with confidence from normal swimming. Prey that did not attempt to escape were always caught, with the exception of eggs and the smallest larvae tested. Thus 12% of strikes on eggs and 3% of strikes on nonresponding 0.29 cm larvae were not successful. Predator failures are presumed due to predator error, which has been reported as 8% for largemouth bass, *Micropterus salmoides*, (Nyberg 1971) and 34% for chain pickerel, *Esox niger* (Rand and Lauder 1981). Larvae that made an avoidance response to an attack by clown fish were rarely pursued because clown fish usually attacked another larva. Eight chases were observed in 113 escape attempts by northern anchovy larvae. One escape each was observed for larvae in the 0.626 and 1.166 cm TL groups and two in each of the 0.399, 0.867, and 0.953 cm groups.

Larval responses to attacks by clown fish were characteristic startle responses, followed by a short period of sprint swimming. The startle response consisted of a C-start form of a fast start and a turn (Eaton et al. 1977). The sprint was a period of swimming at constant speed for <1 s (see Hoar and Randall (1978) for definitions). Together, these two components constitute a swimming burst (Webb and Corolla 1981).

The proportion of larvae responding to attacks increased with size, from approximately 9% for 0.29 cm larvae to 80% for 1.2 cm larvae (Figure 1A). The proportion of larvae escaping an attack similarly increased with size, but at a lower rate than the proportion making an escape attempt (Figure 1B). This was because $26 \pm 10\%$ ($N = 10$ groups of larvae) of larvae showing an escape response were eaten anyway, before a chase began. These larvae were defined as attempting to escape too late. This proportion of escaping larvae caught

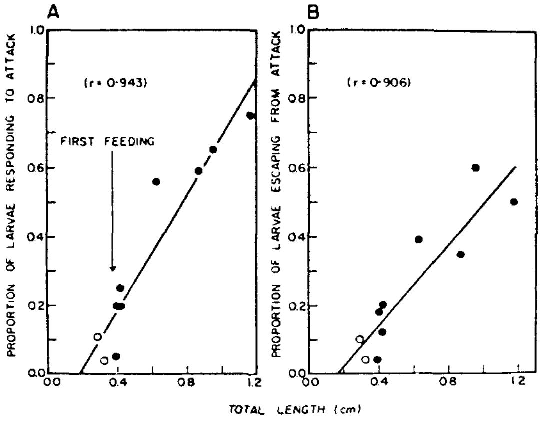

FIGURE 1.—Relationships between (A) the proportion of northern anchovy larvae responding to an attack by clown fish and (B) the proportion escaping an attack, both as functions of the total length. Circles are for prefeeding yolk-sac larvae.

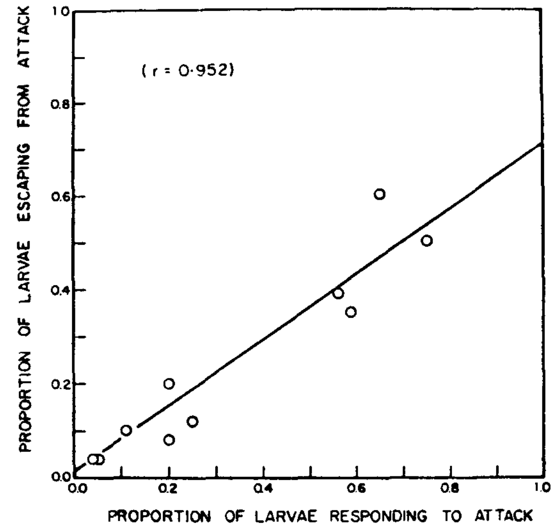

FIGURE 2.—The relationship between the proportion of northern anchovy larvae responding to an attack and the proportion escaping an attack by clown fish.

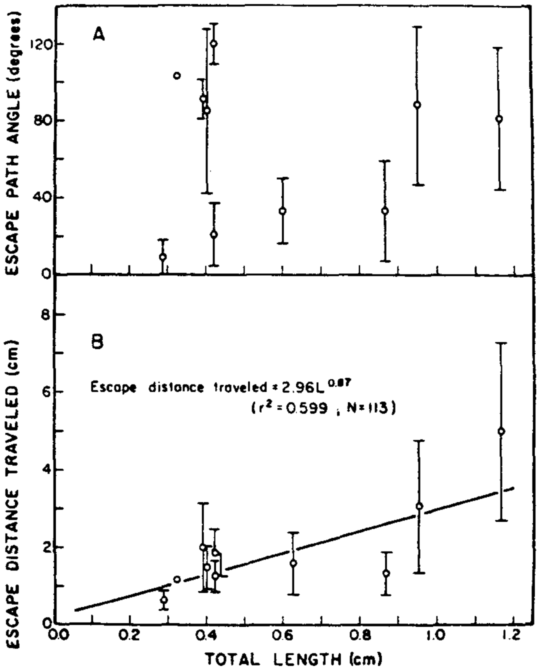

FIGURE 3.—The relationship between (A) the angle of the prey escape path to the predator's strike path and (B) escape distance traveled both as functions of total length of northern anchovy larvae attacked by clown fish. Vertical bars show ±2 SE.

by the clown fish was not correlated with larval size.

The proportion of larvae attempting to escape was therefore related to the proportion escaping (Figure 2). Using functional regression analysis (see Ricker 1979), the relationship was found to be linear, and gave a value of 30% of larvae attempting to escape being captured. This is within the expected range obtained from observations on each group of larvae.

The startle response included a turn. The angle of the prey escape path relative to the predator strike path showed no particular relationship with larval length (Figure 3A), but this was primarily due to the large angles measured for the 0.391, 0.399, and 0.421 cm larvae. Without these data, the escape angle would have increased with larval length, implying larger larvae were better at avoiding the predator's strike path. However, larvae in the three length classes with large angles did not differ from others in any obvious way, and therefore the data cannot be rejected.

However, the distance traveled in an escape swimming burst increased with larval total length (Figure 3B). Using regression analysis (type II) the relationship was best described by a power function, but r^2 values were relatively low. Mean escape speeds in an escape swimming burst also increased with larval size (Figure 4). These speeds were normally about half the mean burst speeds obtained in a forced swimming burst (Webb and Corolla 1981), but escape speeds comparable with the forced maximum were seen during chases.

Analysis of ALT's for larval escape responses is somewhat complex. These ALT's were assumed to be distributed in the population like any other character. However, not all larvae responded. Since nonrespondants were eaten before responding they were assumed to have higher ALT's than larvae showing escape responses. Therefore, the true distribution of ALT's in the population is not known as values above some observed level are missing. Such a population is said to be censored, and since values are missing from one end of the distribution only, it is said to be singly censored. Cohen (1961) has described methods to calculate the maximum likelihood mean and variance of such censored samples. However, before this can be done, the nature of the ALT distribution must be considered.

The nature of the distribution of ALT's in the population was evaluated using probit analysis, developed to examine related problems in toxicology (Sprague 1969). ALT values were ranked and

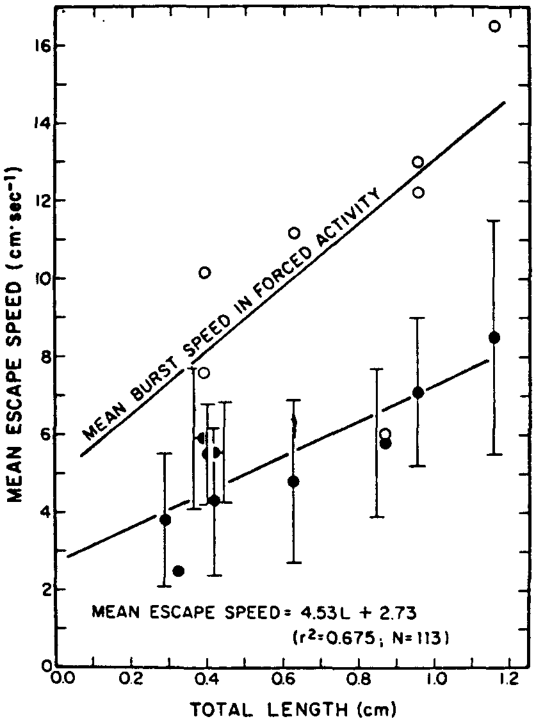

FIGURE 4.—The relationship (dots) between mean escape speed and total length of northern anchovy larvae attacked by clown fish. Vertical bars are ±2 SE. Circles show mean escape speeds during chases. The line for mean burst speeds was taken from Webb and Corolla (1981).

the cumulative percentage of observations was plotted on a probit scale against these values. A logarithmic transformation of ALT values linearized the relationship to the greatest extent (Figure 5) implying ALT's were log-normally distributed in the population. Some curvature remained after this transformation, probably due to decision errors (Treisman 1975) and individual variability in response latencies. Thus ALT values were assumed to be log-normally distributed in the larval populations sampled, and maximum likelihood means and variances were calculated for a type I singly censored sample (Table 2) as described by Cohen (1961). Resulting mean ALT's are shown as a function of total length in Figure 6.

The most important result from this analysis was that ALT's decreased rapidly with increasing size, and hence development, tending towards a plateau for larger larvae and presumably for adults. The relationship was best described by a power function with a negative exponent (see Figure 6) but such a description should be treated with caution. This is because the ALT distributions were severely censored, with a resulting large variance about each mean. In addition, the residual curvature in the transformed data could influence mean ALT values, but this would not alter the general shape of the inverse relationship between ALT's and larval size.

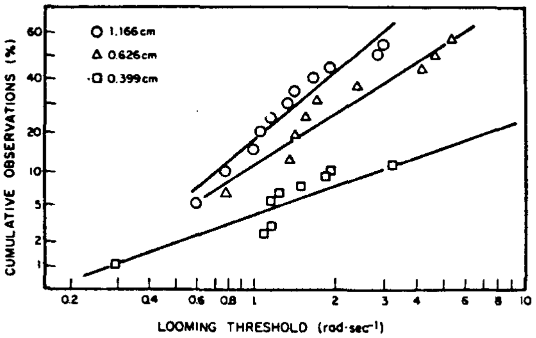

FIGURE 5.—Representative relationships between cumulative number of startle responses, expressed as percentages of total attacks (probit scale) and the logarithm of ALT's for northern anchovy larvae of three different total lengths.

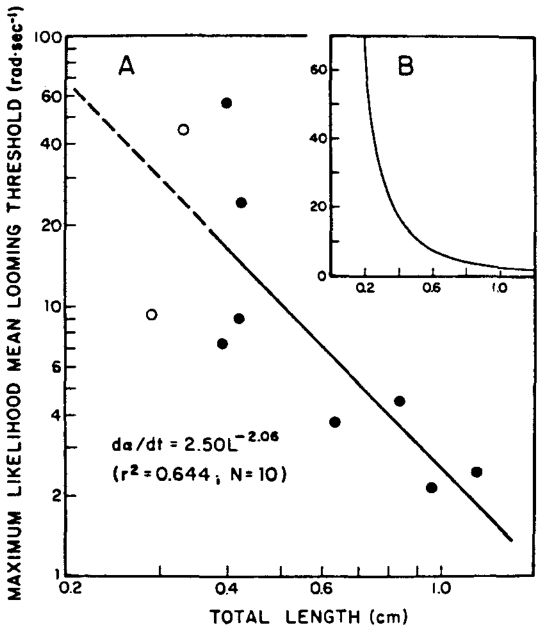

FIGURE 6.—The relationship between the maximum likelihood mean ALT and total length of northern anchovy larvae attacked by clown fish. The relationship is shown for logarithmic coordinates in (A) and for arithmetic coordinates in the inset (B). Circles are for prefeeding yolk-sac larvae.

TABLE 2.—Parameters used in the calculation of maximum likelihood values of the population mean $d\alpha/dt$ ($\hat{\mu}$) and variance ($\hat{\sigma}^2$) for northern anchovy larvae responses to clown fish predators, using the method of Cohen (1961). Logarithm-transformed data for $d\alpha/dt$ were used in these calculations. $\hat{\lambda}$ taken from tables in Cohen (1961); $h = (N - n)/N$, $\hat{\gamma} = S^2/(\bar{X} - X_0)^2$, $\hat{\mu} = \bar{X} + \hat{\gamma}(\bar{X} - X_0)$, and $\hat{\sigma}^2 = S^2 + \hat{\gamma}(\bar{X} - X_0)^2$.

Length (cm)	Sample mean $\bar{X}$ (log rad/s)	Sample variance S^2 -	Sample range $(\bar{X} - X_0)$ -	h -	$\hat{\gamma}$ -	$\hat{\lambda}$ -	$\hat{\mu}$ (log rads/s)	$\hat{\sigma}^2$ -	N
0.29	0.12	0.03	0.24	0.91	0.56	3.60	0.97	0.23	63
.32	.34	.19	.31	.96	2.00	4.31	1.65	.59	45
.39	−.64	.41	−.64	.93	.99	4.18	.86	.95	56
.40	.10	.08	.52	.87	.30	3.16	1.75	.93	79
.42	.17	.11	.36	.75	.87	2.23	.96	.39	32
.42	−.05	.07	.41	.91	.42	3.53	1.39	.65	45
.63	.33	.08	.44	.45	.47	.76	.65	.22	36
.83	−.08	.41	.63	.50	.40	.96	.58	.36	34
.95	−.12	.45	.30	.41	.47	.72	.33	.46	40
1.17	.14	.44	.42	.42	.46	.83	.39	.12	32

DISCUSSION

These experiments were performed to examine responses of northern anchovy larvae to attacks by biting (i.e., nonfilter-feeding) fish planktivores such as juvenile fish preying on zooplankters. The nature of the predator is relatively unimportant. Inexperienced larvae are likely to respond to an attack in the same way because in all cases failure to do so is terminal. The other alternative is that prey have specific predator images to which they respond, which seems improbable.

One objective was to evaluate an experimental technique that could be easily repeated and applied further (e.g., to problems of larval vulnerability and starvation interactions, effects of alternate prey species, prey density, and other questions affecting larval predation mortality). For this reason it was considered important initially to use a predator that was readily available at a uniform size. Natural fish predators could not be obtained in good condition and in a reasonable size range for the period of the experiment. Clown fish were found to be an excellent substitute.

However, experiments were performed at 20° C which is at the upper extreme of the temperature range of northern anchovy, but this probably had a small effect on the observations. The energy required for the short periods of high level activity in an escape swimming burst is undoubtedly derived mainly from anaerobic metabolism, which is known to be less dependent on temperature than aerobic metabolism (see, e.g., Bennett 1980). Experimental data on burst swimming performance are only available for rainbow trout and these data confirm the small effect of temperature in the range of 10° to 25° C (Webb 1978).

Two primary measures of response to attack were obtained, the proportion of larvae showing a startle response and the apparent looming threshold for that response. The proportion of larvae responding to attack increased linearly with length (Figure 1). This result is surprising. Kimmel (1972) has shown that several days are required for the Mauthner cell, which initiates the startle response, to extend caudally. The eyes are not functional before first feeding, so they could not initiate a startle response (O'Connell 1981). Neuromasts are present from hatching but if they were involved in stimulating a startle response, very high percentages of early larvae should show responses to attack. These developmental events suggest a rapid increase in percent response to attack would be expected in the yolk-sac stages, approaching maximum response levels at about first feeding, as found for responses to electric shock stimuli (Webb and Corolla 1981).

However, development rates are likely to vary widely in a population of larvae. It is for this reason that food is first added on the second day after hatching in spite of the fact that the mean time to first feeding is about 4 d (Hunter 1976). The percentage of yolk-sac larvae responding to attack was quite small and was probably due to early maturation (most likely of the visual system) of the most rapidly developing individuals.

The ALT changed with larval size, decreasing rapidly as larvae grew in length. This decline could have been due to improved acuity in the visual system and/or maturation of neural pathways processing visual information. This later could include shorter response latencies with age. The changes in ALT may be the basis for the increasing proportion of avoidance responses in larger larvae.

The only other measurement of looming thresholds for fish are those of Dill (1974a, b) for postlarval zebra danio, *Brachydanio rerio*, in response to attacks by largemouth bass and to silhouettes. These data are not fully comparable with those obtained here for several reasons. First, the mean depth plus width was used to characterize the shape of the clown fish. Dill (1974a) used only width, citing reports that fish are more sensitive to horizontal movement than to vertical movement (Cronly-Dillon 1964; Jacobson and Gaze 1964). In contrast, operant conditioning experiments show that fish are particularly sensitive to apices (e.g., Hinde 1970; Baerends 1971) which occur at the dorsal and ventral margins of laterally compressed bodies. In the absence of definitive experiments relating shape to looming response thresholds, the mean value of depth plus width was considered most appropriate. Use of the mean value of depth and width would give larger values of $d\alpha/dt$ than use of depth alone (Equation (1)).

Second, the distance between the nose and the maximum depth and width of the predator was added to the reaction distance separating the predator and prey. This assumes that the prey either has depth vision or sees the equivalent of a silhouette of the predator. The inclusion of this term would reduce values of $d\alpha/dt$ compared with Dill's method.

The ALT values for postlarval zebra danios (2.0 cm long) was 0.43 rad/s. Northern anchovy larvae of the same size would be expected to have a mean value of about 0.6 rad/s from the relationship in Figure 6.

The overall function of the startle response is to avoid predators. How effective is it? The clown fish rarely pursued escaping larvae, although when they did so, the larvae were easily caught. In these experiments, chases may have been rare because larval densities were high. However, observations on adult piscivores attacking single prey show that chases are also rare with pike, *Esox* (Neill and Cullen 1974; Webb and Skadsen 1980), largemouth bass (Nyberg 1971; P. W. Webb unpubl. obs.), and rock bass, *Ambloplites rupestris* (P. W. Webb unpubl. obs.). Presumably the cost of pursuit is large relative to the benefits of capturing small prey particularly where there are alternative prey. In a normal planktonic assemblage, alternate prey could be important in reducing vulnerability of larval northern anchovy, especially in the presence of more opaque forms and those with more strongly pigmented eyes (Zaret and Kerfoot 1975).

Unfortunately, there are no field observations on larval responses to predation, and the likelihood of making the requisite field observations is remote. Nevertheless, the response of a prey to an attack is an obvious indicator of the prey's awareness and the possible difficulty of capture. The reluctance of many predators to attack responding prey, as noted above, together with the behavior of the clown fish observed in these experiments, imply that the startle response is an effective deterrent. Thus, it is most important that the larvae respond, but initially maximum swimming speeds are not required. Indeed the latter would be energetically more costly. Larvae clearly behave appropriately with a submaximal evasion (Figure 4), except when maximum performance becomes desirable in the rare event of a chase. Nevertheless, timing of the escape attempt must be accurate as 24 to 30% of the larvae attempted a response too late to escape capture.

Larval looming response thresholds will not only be important in escaping biting predators, but also other predation threats. Webb and Corolla (1981) discussed relationships between burst swimming performance of northern anchovy larvae and escape probabilities from plankton nets as a crude analogy with filter-feeding predators. While swimming performance could explain a large part of net avoidance, other factors were involved. Webb and Corolla suggested that declining response thresholds with experience would be important so that larger larvae responded earlier to an impending collision. The inverse relation between ALT with larval total length suggests that such changes occur. Presumably, similar thresholds or size relations would apply to larger predators. Then the reaction distance to a net moving, for example, at a given towing speed would be expected to be greater for larger northern anchovy larvae. This would contribute significantly to the size-dependent sampling bias of such nets.

This work has attempted to evaluate a method for quantifying responses of a fish larva to attacks by a predator as one step in studying the neglected aspect of predation on larval mortality. The advantages of the method are the visualization of both opaque and transparent individuals of small size and continuously recording their behavior. The disadvantages are that the space viewed must be small and hence only small predators can be used, and filtering predators are excluded. However, predation could be studied for particular feeders (e.g., biting fish and chaetognaths) arthropods (e.g., copepods and euphausids), and less discriminating feeders such as thaliaceans and cnidarians. These are abundant in the plankton. In addition, effects of 1) larval density, 2) alternate prey in mixed planktonic assemblages, and 3) effects of starvation on larval vulnerability to predation could be studied.

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