

BURST SWIMMING PERFORMANCE OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE

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ABSTRACT

Burst swimming performance was measured for northern anchovy larvae from 0.23 to 1.33 cm total length at a temperature of 17° C. Fast starts and burst swimming were initiated using a 3 V/cm direct current electric shock. Performance was measured from movie film recorded at 250 frames/s. Percentages of larvae responding to the stimulus increased from 9% 40 hours after eggs were spawned to a maximum of 95 ± 4% after 125 hours. Distances traveled in a given time period increased linearly with length so that maximum speed (U_{\max}) and mean speed (\bar{U}) similarly increased linearly with total length (L) according to $U_{\max} = 20.8L + 1.95$; $\bar{U} = 8.18L + 4.89$. The maximum distance traveled per burst (S_{\max}) was used as a measure of endurance and increased with length according to $S_{\max} = 3.79L + 0.08$. These swimming speeds and endurance relationships can explain a large portion of size-dependent selectivity of towed plankton nets.

Larval swimming performance has been the focus of several studies (Blaxter 1969; Rosenthal and Hempel 1970; Hunter 1972). These have emphasized sustained swimming speeds which are considered an important factor affecting the volume of water searched by a larva, and hence food density requirements or the encounter frequency with food items. These low levels of activity apparently affect ration and at the same time are major contributors to routine energy expenditures (Vlymen 1974).

In contrast, very high activity levels (fast starts and steady burst swimming) are rare. While they are unlikely to constitute a large metabolic load, high speeds are essential to the act of capturing food items (Hunter 1972) and in escaping from predators. This aspect of larval performance has not been evaluated. Therefore, the purpose of this work was to determine the effect of size on burst swimming performance (acceleration and sprints) for northern anchovy, *Engraulis mordax*, larvae, and to evaluate the importance of such high levels of activity in prey capture and escape from predators, including nets.

METHODS

Northern anchovy larvae were reared from eggs as described by Hunter (1976). Eggs were spawned from five groups of parents taken from laboratory stocks on five separate occasions during the fall of 1979 (Table 1). Eggs were transferred to noncirculated filtered seawater in 400 l black fiber glass tanks. Food for the larvae was the dinoflagellate *Gymnodinium splendens* for 2- to 5-d-old larvae, and thereafter the rotifer *Brachionus plicatilis*. Water temperature was maintained at 17° C. Larvae were held under constant illumination from standard room fluorescent lights.

Experiments were performed on larvae of 11 different total lengths, ranging from 0.23 to 1.33 cm. Observations were concentrated on larvae in the first few days after hatching (Table 1) when greatest larval development occurs (O'Connell in press).

Groups of 5-50 larvae were observed using Schlieren optics. Details of this system are given in 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 attached to the ceiling. A second mirror on the floor focused the light on a black spot on a glass plate. The focal length of the mirrors was 140 cm.

A cylindrical tank, 17 cm in diameter and 5 cm deep, with parallel plate glass top and bottom, was introduced into the light beam. Discontinuities in

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TABLE 1.—Summary of spawning batches and dates of anchovy larvae of various total lengths used in experiments on burst swimming performance. Data for total length are $\bar{X} \pm 2$ SE.

Total length (cm)	Batch of eggs ¹	Date spawned (1979)	Number of larvae sampled
0.23±0.03	E	2 Dec.	10
0.27±0.03	B	1 Nov.	10
0.29±0.02	B	1 Nov.	10
0.34±0.05	E	2 Dec.	10
0.46±0.03	C	8 Nov.	10
0.51±0.05	C	8 Nov.	10
0.55±0.06	A	31 Oct.	10
0.65±0.06	A	31 Oct.	10
0.72±0.04	C	8 Nov.	5
1.14±0.08	C	8 Nov.	5
1.33±0.27	A	31 Oct.	5

¹Batch D was infected by bacteria and therefore rejected.

the refractive index (e.g., larvae in water) deflected the light from the focus spot on the glass plate and were seen as bright spots against a dark background.

The stimulus initiating a maximum fast start and swimming burst was a 10 ms, 3 V/cm square wave electric shock delivered via two grids in the water bath. Responses were recorded on Kodak³ Plus-X 16 mm movie film at a framing rate of 250 Hz. Experiments were performed at 17° C.

Movie film was analyzed frame by frame. The progression of the head was traced from frame to frame and the mean distance travelled was calculated as described by Hunter (1972) avoiding artifacts due to lateral oscillations of the head associated with propulsive movements. Speeds were calculated from the distances travelled and the elapsed time between measurements. Elapsed time was calculated from the product of number of frames between measurements divided by the framing rate.

RESULTS

The percentage of larvae responding to the nonspecific electric shock stimulus increased with age to a maximum of 88-100% (mean $95 \pm 4\%$; $n = 7$) after 125 h measured from the time of spawning (Figure 1). This corresponds to the age at which larvae raised under the same conditions begin intermittent swimming, i.e., periods of low speed swimming alternating with periods of rest (Hunter 1972).

The response to the stimulus was a fast start followed by a period of continuous high speed (sprint) swimming. Fast starts and sprint speeds

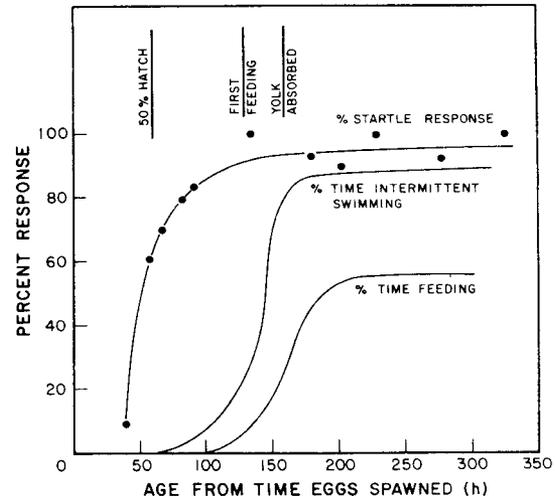


FIGURE 1.—Percentage responses ($n = 20-50$) to a 3 V/cm d.c. electric shock by northern anchovy larvae as a function of age, calculated from the time the eggs were spawned. The curve was fitted by eye. The curves for the time spent in intermittent swimming and in feeding are from Hunter (1972).

are defined as burst activities (see Webb 1975; Hoar and Randall 1978 for definitions). Therefore the response can be described as a burst of swimming activity.

Kinematics of larval fast starts and sprint swimming have been described in detail for zebrafish, *Brachydanio rerio*, (Eaton et al. 1977) and for northern anchovy (Hunter 1972). No differences were seen in the present experiments and therefore details are not repeated.

The most direct, and hence most accurate, measure of performance during a burst of swimming is the distance traveled in a known elapsed time for larvae accelerating from rest. The form of this relationship for the distance traveled by larvae of various total lengths is shown in Figure 2 for three representative time periods. Data were described by best fit linear regression equations without data transformation (Table 2). Similar linear relationships have been shown for larval cruising performance of plaice, *Pleuronectes platessa*, (Ryland 1963); herring, *Clupea harengus*, (Rosenthal 1968); walleye, *Stizostedion vitreum vitreum*, and yellow perch, *Perca flavescens* (Houde 1969). The total distance traveled per burst of swimming (S) also increased linearly with total length (L) according to

$$S = 0.08 + 3.79 \pm 0.76 L \quad (r^2 = 0.57; n = 85).$$

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

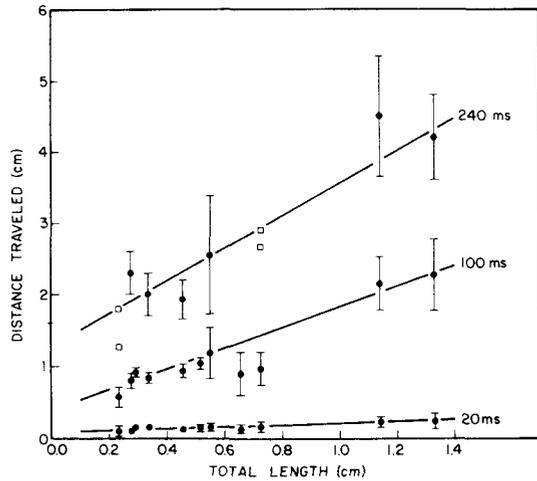


FIGURE 2.—Exemplary relationships between the distance traveled and total length of northern anchovy larvae after 20, 100, and 240 ms of burst swimming initiated by an electric shock stimulus. Vertical bars show ± 2 SE. Open squares show individual data points for individuals of groups of larvae when few swam for 240 ms.

TABLE 2.—Summary of relationships between distance traveled (*S* in centimeters) in various elapsed times as functions of total length (*TL* in centimeters) of northern anchovy larvae stimulated to maximum performance by an electric shock. 95% confidence intervals about the slope are shown.

Elapsed time from start of swimming (ms)	Best-fit equation relating distance traveled with total length	r^2	<i>n</i>
20	$S = 0.09 + 0.10 \pm 0.04 TL$	0.31	95
40	$S = 0.15 + 0.37 \pm 0.08 TL$	0.65	95
60	$S = 0.17 + 0.80 \pm 0.15 TL$	0.67	87
80	$S = 0.21 + 1.17 \pm 0.22 TL$	0.68	83
100	$S = 0.28 + 1.46 \pm 0.27 TL$	0.71	81
140	$S = 0.54 + 1.75 \pm 0.37 TL$	0.69	65
180	$S = 0.82 + 2.06 \pm 0.44 TL$	0.75	48
220	$S = 1.07 + 2.25 \pm 0.60 TL$	0.73	36
260	$S = 1.26 + 2.52 \pm 0.53 TL$	0.66	23

These distances were traveled by continuous swimming because gliding is limited for organisms the size of the larvae moving at low speeds (see Weihs 1980).

Although the relationships between distances traveled and total length were best described by linear regression equations, the coefficients of determination indicated that the relationship usually described only 65 to 75% of the variability. A major contributor to the variability was the apparent low performance of larvae with mean total lengths of 0.65 and 0.72 cm. For example, r^2 for the relationship between distance traveled in 100 ms and total length increased from 0.71 to 0.83

on deletion of the observations for larvae in these two groups. However, the larvae appeared healthy and there were no apparent reasons to assume these data were anomalous. The reason for their lower performance is unclear. Another factor contributing to variability in the data may have been the use of larvae from several spawnings at different times from different small sets of only 25-50 parents from laboratory stock. The very low r^2 for the distance-total length relationships at small elapsed times can also be attributed in part to greater measurement error. Larvae traveled small distances, of the order of 1 mm in 20 ms for small fish, and even with magnification of $2 \times$ these small distances were obviously subject to greater measurement error than larger distances.

Swimming speeds were not constant. Speed increased with time to reach the maximum burst speed after 80-100 ms and then speed declined for the remainder of the burst (Figure 3). The time to reach maximum burst speed was not affected by total length, but the decrease in speed from the maximum was greater for larger larvae, and extended over a longer period of time. The maximum burst speed increased linearly with total length (Figure 4), and since time to maximum speed was independent of length, mean acceleration rates will also be proportional to total length. Mean speeds during a burst of swimming (\bar{U}) also increased linearly with length (Figure 5), but at a lower rate than maximum burst speeds (U_{max}) where

$$\bar{U} = 4.89 + 8.18 \pm 1.1 L \quad (r^2 = 0.861; n = 85)$$

$$U_{max} = 1.95 + 20.8 \pm 2.5 L \quad (r^2 = 0.891; n = 85).$$

The difference between maximum and mean speeds increased with total length because variations in speed in a burst increased with total length (Figure 3). Maximum and mean speeds during a burst were consequently similar for the smallest larvae.

Figure 5 also shows other relationships between swimming speed and length reported in the literature for comparison. The mean speeds measured for anchovy larvae were greater than those measured for other larvae, exceeding the "... theoretical 10 body lengths/sec ..." (Blaxter 1969) maximum. Intermittent swimming speeds (Hunter 1972), the normal voluntary swimming pattern of larvae, and voluntary bursts were lower than the burst speeds measured here, presumably because of the absence of threatening stimuli.

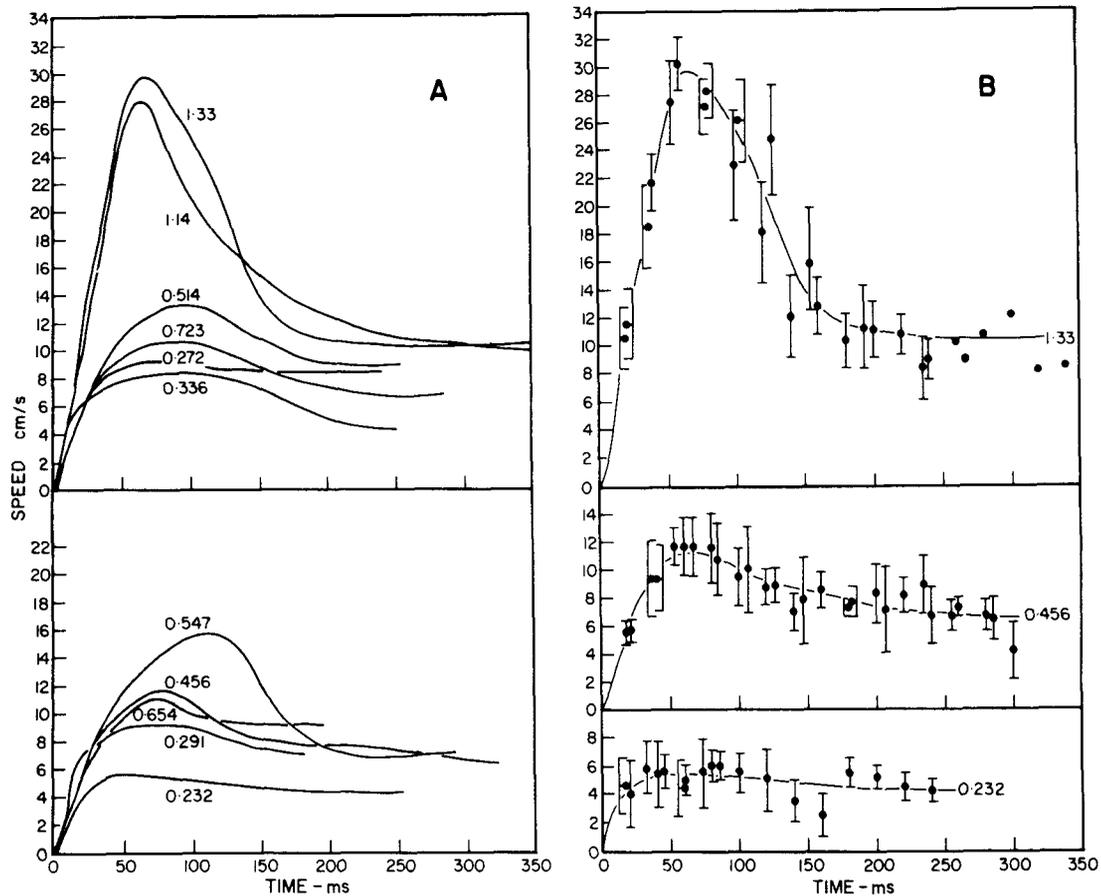


FIGURE 3.—Relationships between swimming speed and time during a burst for 11 groups of northern anchovy larvae ranging in mean total length from 0.23 to 1.33 cm. Panel A shows mean curves, separated into two groups for clarity. Panel B indicates the nature of the data from which the curves were constructed. Curves were fitted by eye. Vertical bars show ± 2 SE.

DISCUSSION

Northern anchovy larvae are important planktonic predators as well as being prey items for other organisms. Burst swimming speeds and burst swimming response ability will be important in this predator-prey role because the ability to rapidly strike prey and to escape strikes by predators will make major contributions to survival.

Response ability was assayed following an electric shock stimulus. While this is not a normal stimulus, observations on adult fish suggest responses to electric shock and more typical stimuli are comparable (Eaton et al. 1977; Webb 1978, 1979). For the larval northern anchovy, response

patterns to electric shock correlated with expectations based on the onset of intermittent swimming and feeding (Figure 1). Similar patterns of maturation of the nervous system, especially the eyes (O'Connell in press), and reduced vulnerability to predators (Lillelund and Lasker 1971) suggest the stimulus is a suitable assay for maturation of locomotor coordination systems.

Following maturation of response capabilities, the effectiveness of a larva as a predator and in avoiding predation will depend to a large extent on locomotor performance (Lillelund and Lasker 1971). A model by Howland (1974) showed speed and maneuver were major factors in catch and avoidance behavior that contribute to success in predator-prey encounters. Larvae may be pursued

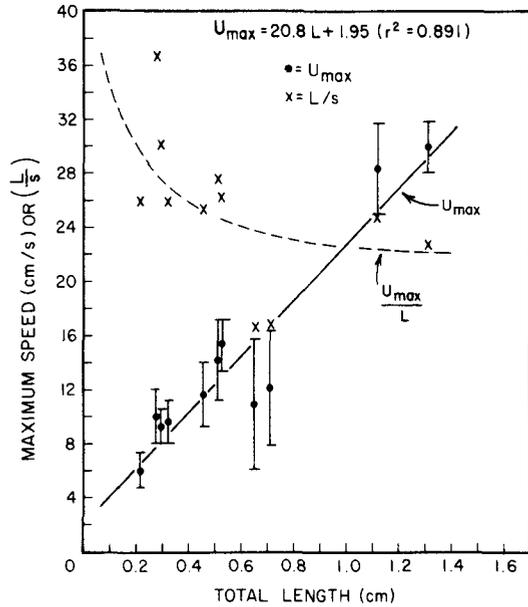


FIGURE 4.—Maximum burst speeds (U_{max}) as a function of total length (L) for northern anchovy larvae. Solid circles are absolute speeds (cm/s). Crosses show specific speeds in body lengths (L/s) calculated as U_{max}/L . Vertical bars show ± 2 SE.

by predators so that endurance must be added to these components of predator-prey behavior. Of these three factors the physical ability to turn seems least important. Fish can turn in extremely small radius circles (Webb 1976; Eaton et al. 1977; Kimmel et al. in press) so that the optimal escape strategy of turning inside a predator's turning radius, forcing the predator to stop and reorient (Howland 1974), is probably impractical. For artificial predators, nets, the scale of the net makes turning ability unimportant. Therefore, speed is expected to be the major performance component of larval behavior contributing to the outcome of encounters with their prey, while both speed and endurance will affect interactions with predators and nets.

Hunter (1972) found that northern anchovy larvae accelerated over 8-16 ms to reach their prey. He found that a 0.8 cm larva would travel about 0.04 cm in that time, and a 1.3 cm larva about 0.09 cm. In the present experiments, the distance traveled was 0.03 and 0.09 cm in 12 ms for larvae of 0.8 and 1.3 cm TL, respectively. This shows that northern anchovy larvae use their maximum burst performance in attacking their prey.

Northern anchovy larvae are also prey items for

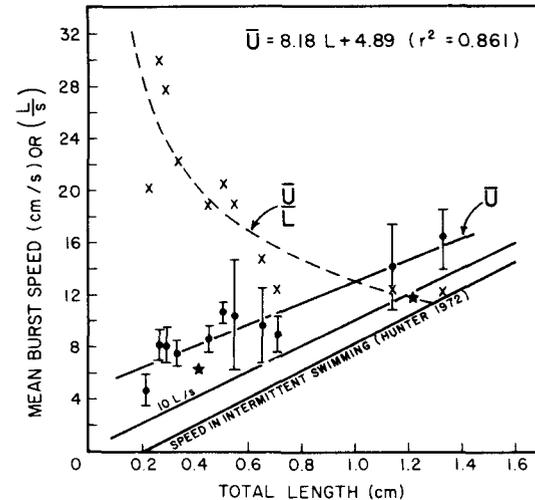


FIGURE 5.—Mean burst speeds (\bar{U}) as a function of total length (L) for northern anchovy larvae. Solid circles are absolute speeds (cm/s) and crosses show specific speeds (\bar{U}/L). Vertical bars show ± 2 SE. The 10 body length/s relationship is based on Blaxter (1969). The intermittent swimming speed relationship is taken from Hunter (1972). Stars show mean voluntary burst speeds, from Hunter (1972).

a variety of fish and invertebrates (Hunter 1977, in press) so that the larvae would require a variety of response patterns to attempt to escape from predation. For example, lunging predators typically overshoot the prey location (Hoogland et al. 1956; Hunter 1972) when the rapid acceleration in a fast start would facilitate escape by quickly removing the potential prey from the predator's strike path. The rapid improvement in maximum burst speed with size (Figure 4) should reduce the vulnerability of larger northern anchovy to such predators. Chasing predators, for example, juvenile fish and larvae of more active species such as scombrids, are at the opposite extreme to lunging predators. Northern anchovy larvae should have reduced vulnerability to such predators as they grow because of improved mean swimming speed during a burst (Figure 5). In addition, the distance traveled per burst increases with size, implying improved stamina with increasing total length which should further facilitate escape of larger larvae from chasing predators.

The effect of size on the ability of northern anchovy larvae to escape natural predators and the mechanisms involved in escape behavior have received little attention. Decreased vulnerability of larger larvae to predation by copepods and

euphausiids has been documented (Lillelund and Lasker 1971; Theilacker and Lasker 1974), but since experiments were performed in the dark, the factors leading to reduced vulnerability are not known. An alternative approach to assessing the importance of changing swimming performance with larval size is to consider an artificial "predator," a net, which simulates some actions of certain natural predators, such as filter feeders. The problem of sampling bias by nets has provided a variety of observations and models suitable to evaluate size-performance effects on vulnerability.

Most studies of net avoidance start with, or parallel, Barkley's (1964) model on selectivity of towed nets. This model identified three factors determining escape (and catch) probabilities: reaction distance, speed, and orientation of the escape path. Endurance must be added. In the absence of adequate data on the relevant parameters for fish larvae, results of sensitivity analyses have been fitted to catch data (Barkley 1964, 1972). The present data can be used to compare scaling relationships between escape probability and burst swimming performance to evaluate the importance of the latter in determining vulnerability of northern anchovy larvae to net "predators." Such a scaling approach allows some simplification because it is reasonable to assume that probability distributions for orientation of escape paths do not scale with size.

Escape probabilities, as a function of length, can be estimated from a comparison between day and night catches using towed nets. The ratio of night/day catches as a function of larval northern anchovy length is well known to be linear (Ahlinstrom 1954; Zweifel and Smith in press) which means that the relationship between escape probability and size is curved, rapidly approaching an asymptote (Figure 6). The data shown in Figure 6 were obtained with a 1 m diameter ring net towed obliquely at about 125 cm/s (Zweifel and Smith in press). Ninety percent avoidance is reached by 1.0 cm larvae, with rather small improvements in escape probability at greater lengths. The decline in escape probability cannot be attributed to the capture of starving or sick larvae (Isaacs 1965) because O'Connell (1980) found no emaciated larvae >1 cm TL in net-caught samples.

In order to compare performance data with the catch probabilities, mean speeds and distances traveled in a burst were normalized about the performance measured for 1 cm larvae (Figure 6). The

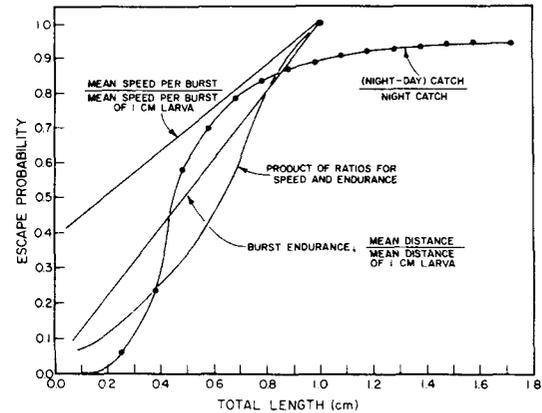


FIGURE 6.—Escape probabilities, estimated from day-night plankton net hauls, and those possible on the basis of burst swimming speed, burst endurance, and their product as a function of total length of northern anchovy larvae. Performance data are normalized with respect to a larval length of 1 cm, where the escape probability reaches 90%. Data for day-night catches were taken from Zweifel and Smith (in press).

scaling relationship for mean speeds in a burst, assuming bursts are repeated until a larva escapes, obviously do not parallel escape probabilities (Figure 6). Endurance in a burst shows a greater length effect, which is further accentuated by the interaction (product) of speed and endurance. This latter curve has the steepest slope, most closely paralleling escape probability, such that it is apparent that speed and endurance are major determinants of avoidance ability.

However, the shape of the curves suggests avoidance is underestimated for larger larvae between about 0.4-1.0 cm long. Length dependent maturation of sensory systems and motor control (O'Connell 1980) may contribute to increased escape probability of larger larvae. A behavioral factor may also contribute. Dill (1974) has shown that experienced juvenile zebra danio respond earlier to a predator than do inexperienced fish. Since the predation rate is high for northern anchovy larvae, then larger larvae are likely to be much more experienced with diverse attacks than are smaller larvae. Response thresholds decreased linearly with contacts up to 10 encounters in Dill's experiments, but this effect would undoubtedly decline with larger numbers of encounters, when a minimum threshold would presumably be obtained. Therefore, an age (experience) dependent decrease in reaction distance may contribute to net avoidance and the declining rate of catch probability at larger sizes.

Finally, it should be noted that improvements in plankton nets and catch techniques would shift the position of the curves in Figure 6. This would require different normalization points in evaluating effects of performance on escape probability, taking into account the new point at which larvae out-swim the net. However, such changes would not alter the nature of the arguments nor the conclusions concerning the importance of swimming performance in determining escape probability.

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