# Developmental changes in escape response performance of five species of marine larval fish

P.J. Williams, J.A. Brown, V. Gotceitas, and P. Pepin

**Abstract**: We measured the escape response performance by four species of larval fish: Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus harengus*), radiated shanny (*Ulvaria subbifurcata*), and capelin (*Mallotus villosus*). The resultant data were combined with information from larval winter flounder (*Pleuronectes americanus*) to produce general models relating escape response performance to larval size. Three components of the escape response produced models with reasonable predictive ability, including mean and maximum speed during the response, and the distance travelled by larvae during the first 100 ms of the response (the latter representing the contribution of the C-shaped fast start that initiates the response). The logarithm of mean and maximum escape speed increased linearly with increasing larval length. The distance after 100 ms was linearly related to larval length. Our general model for mean escape speed produced significantly higher length-specific speed values than did the general model proposed by Miller et al. (T.J. Miller, L.B. Crowder, J.A. Rice, and E.A. Marschall. 1988. Can. J. Fish. Aquat. Sci. 45: 1657–1670).

**Résumé** : Nous avons mesuré l'efficacité de la réaction de fuite chez les larves de quatre poissons : la morue (*Gadus morhua*), le hareng (*Clupea harengus harengus*), l'ulvaire deux-lignes (*Ulvaria subbifurcata*) et le capelan (*Mallotus villosus*). Les données résultantes ont été combinées aux renseignements sur la plie rouge (*Pleuronectes americanus*) pour produire des modèles généraux de l'efficacité de la réaction de fuite en fonction de la taille des larves. Trois éléments de la réaction de fuite ont permis de constituer des modèles qui ont une valeur prédictive raisonnable; ce sont la vitesse moyenne et la vitesse maximale atteintes pendant la fuite, et la distance franchie par les larves durant les 100 premières ms de la réaction (celle-ci correspond au départ rapide selon une trajectoire en C qui amorce la réaction de fuite). Le logarithme de la vitesse moyenne et de la vitesse maximale de fuite s'accroît linéairement en fonction de la grandeur de la larve. La distance franchie dans les 100 premières ms est en rapport linéaire avec la longueur des larves. Notre modèle général pour représenter la vitesse moyenne de fuite en fonction de la longueur donnait des prévisions qui étaient significativement supérieures à celles du modèle général proposé par Miller et al. (T.J. Miller, L.B. Crowder, J.A. Rice et E.A. Marschall. 1988. J. can. sci. halieut. aquat. 45: 1657–1670).
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## Introduction

Predation is an important cause of mortality in larval fish (Bailey and Yen 1983; Batty 1989; Blaxter and Fuiman 1990), probably resulting in strong selection for antipredator defences. One antipredator defence that has been demonstrated in many species of larval fish is some form of escape response, consisting of a period of rapid acceleration followed by burst swimming (Webb and Corolla 1981). Studies have shown that this sequence (or some component thereof) is effective in allowing larval fish to escape attacks by both vertebrate (Webb 1981) and invertebrate (Bailey and Batty 1984; McGovern and Olney 1988; Seale and Binkowski 1988; Turner et al. 1985) predators.

In recent years, researchers have attempted to describe general relationships between early life-history parameters of larval fish, such as escape response performance, and larval size (e.g., Bailey and Houde 1989; Blaxter 1986; Miller et al. 1988; Pepin 1991). Earlier studies (Bailey and Batty 1984; Blaxter 1986; Yin and Blaxter 1987) proposed a linear relationship between larval length and burst swimming speed, an important component of the escape response. Miller et al. (1988) compiled published values of burst swimming speed from nine species of larval fish and generated a model of burst swimming speed based on larval length. However, Miller et al. (1988) also pointed out the limitations of their approach, mainly that the different methodologies used in the various source studies sometimes result in different performance by the same species of larval fish. An additional problem is that approximately half of the information contributing to Miller et al.'s (1988) general model (i.e., 37 of 76 data points) originated from two species of clupeoid fishes: northern anchovy (*Engraulis mordax*) and Atlantic herring (*Clupea harengus*). Body flexibility and morphology have been shown to affect fast-start acceleration rate (Webb 1986; Harper and Blake 1990) and general fast-start performance (Domenici and Blake 1991) in adult fish. Therefore, data from a greater diversity of larval fish morphologies would be helpful in evaluating the universal applicability of Miller et al.'s (1988) model.

A first step in evaluating Miller et al.'s (1988) model is reported in Williams and Brown (1992). The escape response performance of larval winter flounder (*Pleuronectes ameri-*

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*canus*) was measured from hatch through metamorphosis. The resulting mean escape speed – larval length relationship for winter flounder was compared with Miller et al.'s (1988) model, and the two regressions were found to be significantly different. Specifically, larval winter flounder exhibited higher length-specific mean escape speeds than were predicted by Miller et al. (1988). Miller et al. (1988) state that their proposed framework is not intended to be predictive for any particular species; however, it would be useful to know if winter flounder have unusually high length-specific escape speeds or if, instead, the model proposed by Miller et al. (1988) tends to underestimate larval escape speeds.

The present study measures the size-dependent escape response performance of an additional four species of larval fish: radiated shanny (*Ulvaria subbifurcata*), Atlantic herring (*Clupea harengus harengus*), capelin (*Mallotus villosus*), and Atlantic cod (*Gadus morhua*). Combined with the data from winter flounder, these five species of larvae represent a range of body morphologies and flexibility. The herring and capelin have long, slender eel-like bodies, similar to the northern anchovy. Although of similar size to the herring and capelin, the shanny larvae have deeper bodies and are more developed at hatch. Finally, cod and flounder are shorter, deeper, more tadpole-like larvae and display less flexibility. The approach taken was to test the additional four species using the same methodology as that used to test the flounder larvae. The study had the following objectives: (*i*) to develop models describing the relationship between escape response performance and larval length and (*ii*) to compare the model for length-specific mean escape speed with that proposed by Miller et al. (1988).

## Materials and methods

The term escape response has been used to refer only to the period of rapid acceleration that initiates the response (e.g., Batty 1989; Domenici and Blake 1991; Harper and Blake 1990). In the present study, an escape response is defined as consisting of the three kinematic stages described by Weihs (1973). In the first stage, the musculature on one side of the body contracts, and the larva assumes a C or reverse-C shape. The second stage consists of a strong propulsive stroke of the tail in the direction opposite to that of the initial contraction, often bending the larva in the opposite C shape. Stage three is characterized by a period of continuous high speed swimming, also called burst swimming.

### Experimental animals

Fertilized eggs from Atlantic cod (from NAFO division 3L) were collected from broodstock tanks in the spring of 1991. The eggs were incubated in mesh-sided baskets in a running ambient seawater wet bench. Upon hatch, the larvae were transferred to 40-L aquaria containing static filtered seawater. The aquaria were partially immersed in a running ambient seawater wet bench that maintained temperature between 5 and 11°C. Larvae were fed cultured rotifers (*Branchionus plicatilus*) at an approximate density of 10 prey/mL for the first 30 days post-hatch. From day 30 onward, newly hatched brine shrimp nauplii (*Artemia salina*) were added instead at a density of approximately 1/mL. The flounder larvae were reared similarly to cod (see Williams and Brown (1992) for details).

Fertilized eggs of the other three species tested were collected from the wild. Separate masses of radiated shanny eggs were collected by divers at Tappers Cove, Newfoundland, in June 1991. The egg masses were incubated and the resultant larvae reared in a fashion similar to that used for cod, with the exception that shanny larvae were fed *A. salina* from hatch onwards. Batches of beach substrate containing fertilized capelin eggs were collected at low tide at Middle Cove, Newfoundland, and vegetation with attached herring eggs was collected by divers at Bellevue Beach, Newfoundland, in June–July 1991. Eggs and larvae were reared in a similar manner as were flounder and cod.

*Calliopius laeviusculus*, a common free-swimming epibenthic amphipod, was used to elicit the escape responses in the larvae. *Calliopius laeviusculus* are omnivorous, consuming algae, detritus, and live zooplankton (Hudon 1983). They are contact predators, grasping and biting prey they come in contact with, and have been shown to prey upon larval fish (Bailey and Yen 1983; Bailey and Stehr 1986). Preliminary trials indicated that, provided there were no crevices or edges for them to cling to, the amphipods swam almost continuously in small test chambers, thereby facilitating contact with larvae in an experimental situation. The amphipods were used only as a predatory stimulus, and most amphipod–larva interactions did not result in the capture of the larva. The experiments were designed to examine the escape responses of the larvae, rather than evaluate capture rates of amphipods on the various larvae.

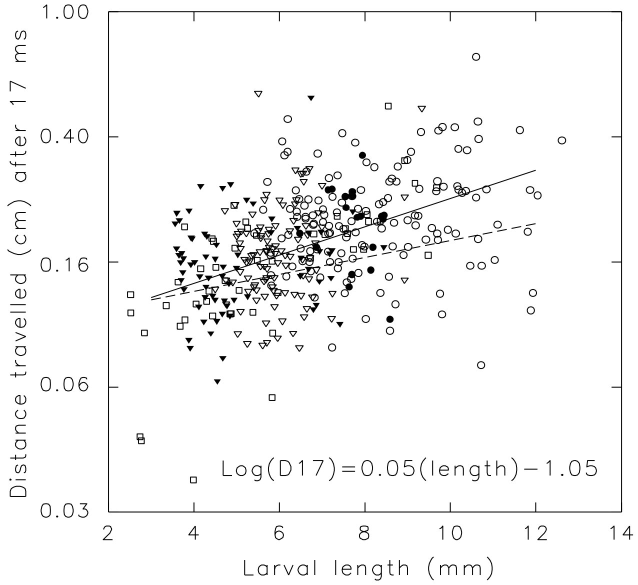
All experimental trials were carried out in a 20 cm diameter glass dish (the experimental chamber) containing seawater to a depth of 1.5 cm. This dish was floated in a circular 80 cm diameter, flat-bottomed Plexiglas water bath, supplied with running seawater at a depth of 10 cm. The temperature of the seawater was maintained at 8 ± 1°C. All trials were videotaped using a silhouette system (Arnold and Nuttall-Smith 1974), wherein a biconvex lens is used to collimate light, which then passes through the experimental chamber to a video camera (Panasonic 5010 digital SVHS video camera). Low light levels (less than 10 lx in this experiment) provided sharp silhouettes of larvae and amphipods. The low light levels are necessary when working with positively phototactic larvae. To facilitate filming, the experimental chamber was fixed directly over the biconvex lens.

### Experimental protocol

Between 10 and 15 larvae (sample sizes were smaller with some of the oldest larvae because of reduced availability) were placed in the experimental chamber for 1 min, after which two amphipods were transferred using a pipette into the dish and the video recording was initiated. Video recording continued for 20 min. All video recording and playback were carried out on a Panasonic AG-1960 SVHS videocassette recorder.

Only encounters in which the larvae did not come in contact with the sides of the dish during the escape response were used in subsequent analyses, resulting in 384 responses suitable for analysis. All escape responses were recorded as starting from the first contraction by the larva after contact with the amphipod. The response was considered to have ended when the larva stopped moving. Data from each suitable amphipod–larva interaction were extracted during playback of the video recording, by tracing the movements of the larvae at single-frame (1/60 s, 17 ms) intervals on an acetate overlay of the video monitor. The slow framing rates used in this study, although inaccurate for measuring instantaneous acceleration, have been shown to be suitable for speed and distance measurements (Harper and Blake 1990). The location of the end of the snout of each larva was digitized to measure the distance larvae travelled (millimetres) during each 17-ms interval of the response. When oscillation or yaw of the head was observed, points were digitized on a midline fitted by eye as in Hunter (1972). From these data, the following measurements were calculated: (*i*) the distance travelled after 17 ms (one video field), which represents displacement resulting from the first C-shaped contraction of the larva; (*ii*) the distance travelled after 100 ms (six video fields), which represents the contribution of the fast-start portion of the response; (*iii*) the mean speed for the entire response, which is indicative of the larva's ability to escape a chasing predator, such as juvenile fish (Webb and Corolla 1981) and some invertebrates; (*iv*) the maximum speed during the response, which may be important in swimming out of the flow field of a suctorial

**Fig. 1.** Distance travelled (cm) during the first 17 ms of larval escape responses versus total larval length (mm). The five species of larvae tested were Atlantic herring (*Clupea harengus harengus*, solid circles), Atlantic cod (*Gadus morhua*, solid triangles), radiated shanny (*Ulvaria subbifurcata*, open circles), capelin (*Mallotus villosus*, open triangles), and winter flounder (*Pleuronectes americanus*, squares). The solid line is the least squares regression line ($r^2 = 0.22$, $n = 384$). The broken line is the regression line of a similar relationship from Webb and Corolla (1981). Note that the *y* axis is $\log_{10}$ scaled.



predator (Drost and van den Boogaart 1986); and (*v*) the total distance travelled during the response, which is important in the event of a prolonged chase by a predator. This variable also describes the extent to which the larva may move itself out of the perceptual field of a predator after an unsuccessful initial strike.

To determine the general relationships between escape response parameters and larval length, linear regressions were calculated for all performance variables, with larval length as the independant variable, using the general linear models procedure (SAS Institute Inc. 1988). The observations for each species were weighted depending on sample size. Sample sizes and length ranges (total length) of larvae tested were as follows: cod, $n = 71$, 3.2–8.4 mm; capelin, $n = 105$, 4.5–9.3 mm; flounder, $n = 50$, 3.5–9.7 mm; herring, $n = 19$, 6.5–8.6 mm; shanny, $n = 139$, 5.4–12.6 mm. The residuals from the regressions were tested for normality using the Shapiro–Wilk statistic, and plots of residuals versus the predicted values were examined to detect violations of the assumptions of independence and constant variance. If the residuals for any model were not normal, the dependent variable was $\log_{10}$ transformed. This transformation restored normality.

Four comparisons using analysis of covariance (Zar 1984) were made between our mean escape speed – length model and that of Miller et al. (1988). The first two of these analyses included all 384 data points from the present study. Of these first two comparisons, one analysis included all values from Miller et al. (1988). The other analysis excluded measurements from Miller et al. (1988) that originated from larvae greater than 13 mm in length, thereby comparing equivalent size ranges of larvae from each data set. Reviews of an earlier version of the present article suggested that because many of the data points in Miller et al.'s (1988) model were actually mean values, an appropriate comparison with our data would use means for each experimental trial (i.e., mean speed for 24-day-old shanny larvae) rather than individual data points. Consequently, we performed two further comparisons using this approach, one of all larvae and one excluding larvae greater than 13 mm in length.

**Table 1.** Results of the regression analyses of measurements of larval escape performance versus total larval length (mm) ($n = 384$ for all analyses).

| Source | df | SS | MS | *F* | *p* | $r^2$ |
|---|---|---|---|---|---|---|
| **Distance travelled during first 17 ms of response** | | | | | | |
| Length | 1 | 13.4557 | 13.4557 | 109.54 | 0.0001 | 0.22 |
| Error | 382 | 46.9236 | 0.1228 | | | |
| **Distance travelled during first 100 ms of response** | | | | | | |
| Length | 1 | 130.3366 | 130.3366 | 498.00 | 0.0001 | 0.57 |
| Error | 382 | 99.9770 | 0.2617 | | | |
| **Mean escape speed during entire response** | | | | | | |
| Length | 1 | 23.1106 | 23.1106 | 509.27 | 0.0001 | 0.57 |
| Error | 382 | 17.3349 | 0.0454 | | | |
| **Maximum escape speed during entire response** | | | | | | |
| Length | 1 | 19.1304 | 19.1304 | 342.56 | 0.0001 | 0.47 |
| Error | 382 | 21.3329 | 0.0558 | | | |
| **Total distance travelled during entire response** | | | | | | |
| Length | 1 | 16.7655 | 16.7655 | 84.26 | 0.0001 | 0.18 |
| Error | 382 | 76.0057 | 0.1990 | | | |

## Results

The distance travelled during the first 17 ms of the escape response, representing displacement from the first C-shaped contraction of the larva, resulted in a model with considerable variation (Fig. 1) and a regression that is of little predictive value ($r^2 = 0.22$; Table 1). However, the regression is significant, and examination of the plotted data indicated that this performance measurement improved with increasing larval length. The formula for the best-fit regression model is $\log_{10}$(distance after 17 ms) = 0.0451(length) - 1.0485, with distance in centimetres and total length in millimetres.

Measurements of the distance travelled during the first 100 ms of the response, representing the fast-start portion of the response, did not require $\log_{10}$ transformation to produce normal residuals. Variation for this measurement was considerably less than that observed for displacement after 17 ms (Fig. 2, Table 1). Distances larvae travelled in such a short time were impressive, ranging from 0.5 cm for the smallest larvae to 2.5 cm for the largest. The formula for the best-fit regression model is as follows: distance after 100 ms = 0.1405(length) + 0.1133, with distance in centimetres and total length in millimetres.

The mean speed during the entire response increased with larval length (Fig. 3, Table 1). Examination of the plot in which different symbols indicate different species (Fig. 3) supports the fact that the general relationship adequately describes each species. The formula for the best-fit regression model is $\log_{10}$(mean speed) = 0.0591(length) + 0.5624, with speed in centimetres per second and total length in millimetres.

The analysis of the mean escape speed data combined with the data from Miller et al. (1988) found that the slopes of the two relationships were significantly different ($F = 42.93$, $p < 0.0001$, $n = 460$). Examination of a plot of both relationships with accompanying data points (Fig. 4) showed that our model generally predicts greater mean escape speeds than does

**Fig. 2.** Distance travelled (cm) during the first 100 ms of larval escape responses versus total larval length (mm). The five species are as in Fig. 1. The solid line is the least squares regression line ($r^2 = 0.57$, $n = 384$). The broken line is the regression line of a similar relationship from Webb and Corolla (1981).

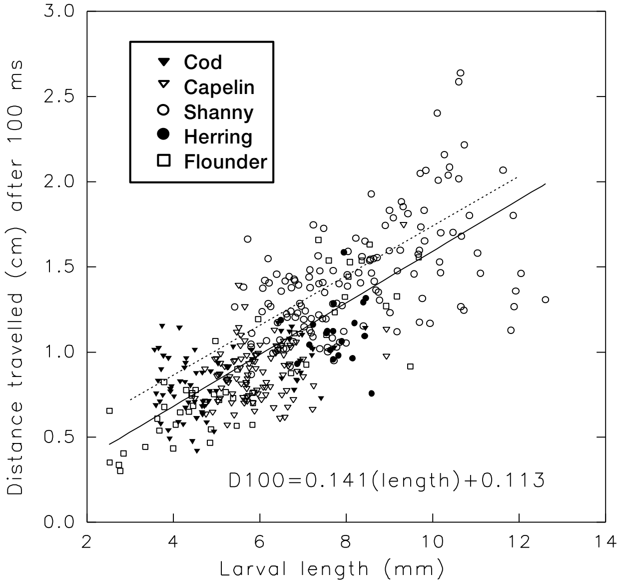


**Fig. 3.** Mean escape speed (cm/s) during the entire larval escape response versus total larval length (mm). The five species are as in Fig. 1. The solid line is the least squares regression line ($r^2 = 0.56$, $n = 384$). The broken line is the regression line of a similar relationship calculated from Bailey (1984). Note that the $y$ axis is $\log_{10}$ scaled.

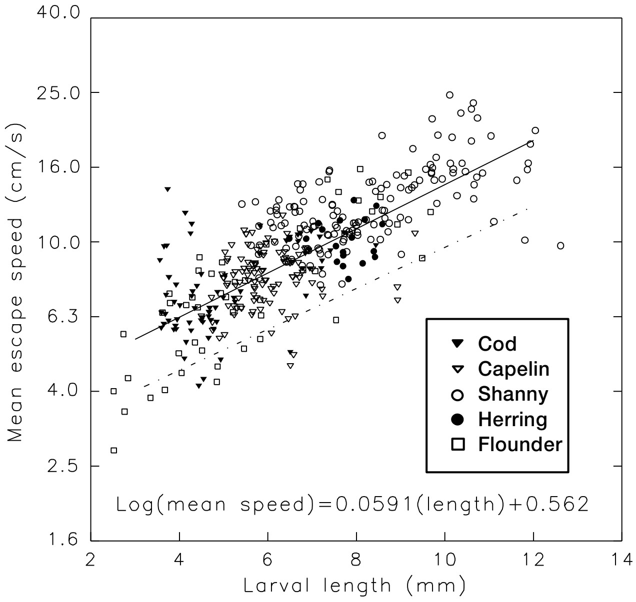
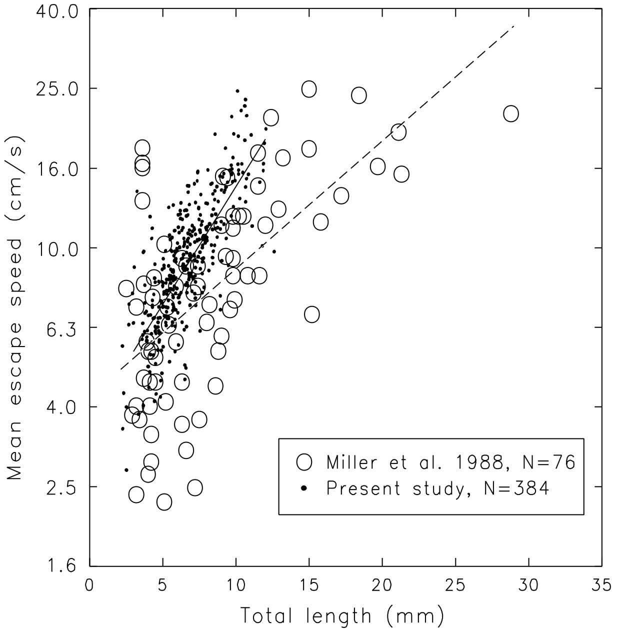


**Fig. 4.** Mean escape speed (cm/s) during the entire larval escape response versus total larval length (mm) for the present study (solid dots, solid regression line) and for Miller et al. (1988) (open circles, broken regression line). Note that the $y$ axis is $\log_{10}$ scaled.



Miller et al.'s (1988) model. The second comparison, in which larvae greater than 13 mm were excluded, also showed a greater slope in the present study ($F = 16.34$, $p < 0.0001$, $n = 449$). When the data was reanalyzed using tank means instead of individual data points, the regression model for our data was essentially the same, with a slope of 0.0605 using tank means versus 0.0591 using individual points and an intercept of 0.5586 versus 0.5624. The slope of our model was still significantly greater than that of Miller et al.'s (1988) model ($F = 4.72$, $p = 0.032$, $n = 114$). When we excluded the speed measurements corresponding to larvae greater than 13 mm in total length, slopes were not significantly different, but the resultant analysis of covariance (ANCOVA) indicated that our model still predicted significantly greater mean escape speeds for a given length of larvae ($F = 12.21$, $p = 0.0007$, $n = 103$).

The regression of maximum speed versus larval length (Fig. 5, Table 1) show somewhat more variability for smaller larvae than for larger ones, although the data satisfy the assumptions of a linear regression. The formula for the best-fit regression model is $\log_{10}$(maximum speed) = 0.0538(length) + 0.8258, with speed in centimetres per second and total length in millimetres.

The data for total distance travelled during the escape response (Fig. 6, Table 1) display considerable variation, and the regression is of little predictive value. Nevertheless, the logarithm of total distance travelled does increase significantly with larval length. The formula for the best-fit regression model is $\log_{10}$(total distance) = 0.0504(length) + 0.1242, with distance in centimetres and total length in millimetres.

A summary table (Table 2) shows the escape response performance measurements of age groups of each species.

## Discussion

There was significant improvement in all escape response performance variables with increasing larval length, although some performance measurements exhibited much more variation than others for a given length class of larvae. For example, the measurement of the distance travelled during the first 17 ms of the response yielded a model that has little predictive

**Fig. 5.** Maximum escape speed (cm/s) during the entire larval escape response versus total larval length (mm). The five species are as in Fig. 1. The solid line is the least squares regression line ($r^2 = 0.47$, $n = 384$). The broken line is the regression line of a similar relationship from Webb and Corolla (1981). Note that the $y$ axis is $\log_{10}$ scaled.

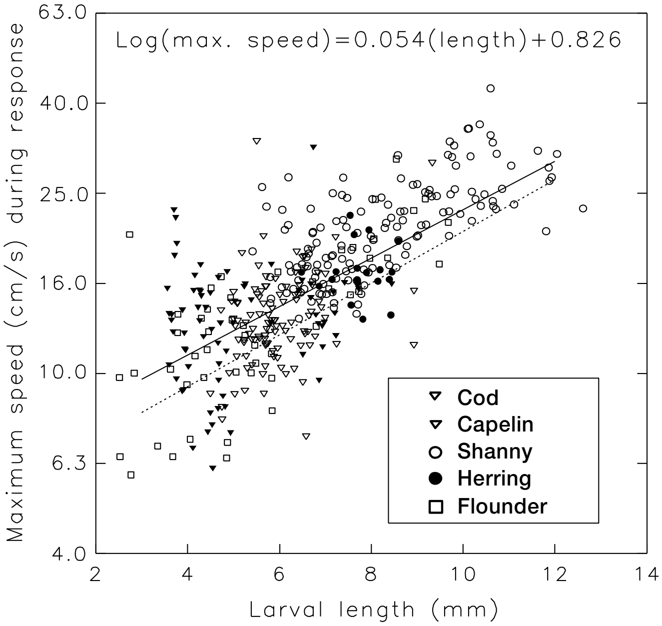
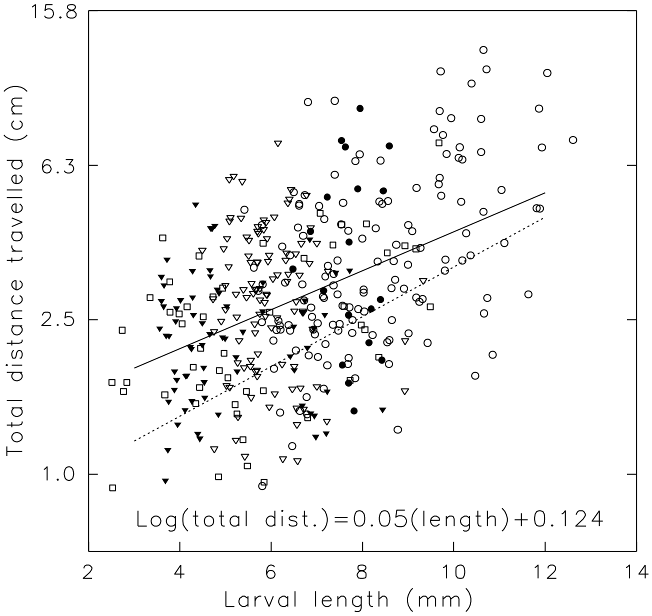


**Fig. 6.** Total distance travelled (in cm) during the entire larval escape response versus total larval length (mm). The five species are as in Fig. 1. The solid line is the least squares regression line ($r^2 = 0.18$, $n = 384$). The broken line is the regression line of a similar relationship from Webb and Corolla (1981). Note that the $y$ axis is $\log_{10}$ scaled.



value, beyond showing that this measurement improves with increasing larval length. Webb and Corolla (1981) also reported a relatively low $r^2$ value (0.31, vs. 0.22 in the present study) for a regression of the distance larval northern anchovy travelled during the first 20 ms of an escape response versus larval length. They cited measurement error associated with the very small distances travelled as a probable cause for this high variability. In the present study the framing rate of the video system (60 Hz, as compared with 250 Hz in Webb and Corolla) probably contributed to the lack of precision in measurement and the resultant low $r^2$ value. Images were recorded every 17 ms, and distance travelled was determined by the movement of larvae from one image to the next. However, an escape response could begin at any point between consecutive images, thereby producing an underestimate of distance travelled and increasing deviation from the expected values generated from the regression. Despite high variability, the resultant regression is similar to that suggested by Webb and Corolla (1981) for the distance northern anchovy travelled in the first 20 ms of escape responses.

The distance travelled during the first 100 ms of the response was measured to assess the displacement achieved by the C-start portion of the response. The fit of the linear model is adequate, and with a $r^2$ value of 0.59 the model has some predictive value. The regression appears to be similar to that reported by Webb and Corolla (1981) for the escape responses of electrically stimulated northern anchovy larvae, albeit with lower length-specific performance in the present study.

Mean speed during the entire response was calculated as a measure of how successful the larvae may be at avoiding chasing predators. Because mean speed is often reported in the literature, it is also useful for comparing experimental results among studies. One additional regression of mean escape speed versus larval length is superimposed on the plot from the present study (Fig. 3). This regression was calculated from data reported by Bailey (1984) for the mean escape speed of five species of larval fish (excluding one speed measurement for 21.1-mm larval herring). Both sets of experiments tested several species using the same protocol. The regression line calculated from Bailey (1984) is clearly at the lower extreme of the distribution of data points from the present study; however, the two slopes appear to be similar. The lower values for the regression calculated from Bailey (1984) may be due to the different method of eliciting the response in the larvae. Possibly the touch from the fine wire probe used in Bailey (1984) was not as strong a stimulus as was the impact of the amphipods used in the present study.

All comparisons of our mean escape speed – larval length relationship with that suggested by Miller et al. (1988) (Fig. 4) showed that for larvae less than 13 mm in length, the model suggested by Miller et al. (1988) tends to underestimate mean escape speeds. This discrepancy is probably due to the differences in experimental methodology used in the source studies summarized by Miller et al. (1988), a problem they acknowledged in their synthesis. Because our study used the same protocol to test all five species, and used contact with a natural predator as the escape stimulus, our resultant model would probably yield more accurate predictions of length-specific mean escape speed than the model proposed by Miller et al. (1988). The examination, revision, and refinement of models is a productive consequence of the formulation of conceptual frameworks such as that presented by Miller et al. (1988).

Maximum speed during the escape response is important in allowing larvae to escape attacks by lunging predators (Webb

**Table 2.** Summary table of escape response performance by age-classes of different species of larval fish.

| Age (days) | *n* | Length (mm) | D17 (cm) | D100 (cm) | Mean speed (cm/s) | Maximum speed (cm/s) | Total distance (cm) |
|---|---|---|---|---|---|---|---|
| **Cod** | | | | | | | |
| 1 | 11 | 4.0 | 0.19 | 0.95 | 9.08 | 15.54 | 2.54 |
| 3–6 | 23 | 4.4 | 0.16 | 0.80 | 6.94 | 14.05 | 2.61 |
| 10 | 18 | 4.5 | 0.13 | 0.66 | 5.80 | 9.68 | 2.14 |
| 28 | 19 | 6.9 | 0.18 | 1.00 | 9.64 | 15.06 | 2.29 |
| **Flounder** | | | | | | | |
| 1 | 5 | 3.7 | 0.08 | 0.41 | 4.04 | 10.53 | 1.67 |
| 7,8 | 10 | 4.5 | 0.12 | 0.60 | 5.26 | 8.67 | 1.78 |
| 10–12 | 8 | 4.5 | 0.16 | 0.70 | 6.67 | 11.27 | 2.54 |
| 20 | 5 | 4.8 | 0.16 | 0.80 | 7.71 | 13.52 | 2.33 |
| 24 | 4 | 5.2 | 0.12 | 0.80 | 8.58 | 13.53 | 2.60 |
| 30 | 3 | 7.3 | 0.18 | 1.05 | 9.02 | 17.63 | 2.55 |
| 43 | 5 | 6.8 | 0.18 | 0.95 | 7.86 | 13.77 | 3.17 |
| 50 | 10 | 8.3 | 0.25 | 1.46 | 12.95 | 21.26 | 3.60 |
| **Herring** | | | | | | | |
| 3 | 19 | 7.8 | 0.22 | 1.11 | 10.17 | 16.93 | 4.13 |
| **Capelin** | | | | | | | |
| 1 | 15 | 6.0 | 0.22 | 0.89 | 7.87 | 14.59 | 2.88 |
| 4 | 16 | 5.2 | 0.16 | 0.79 | 7.29 | 11.64 | 3.41 |
| 6 | 23 | 5.8 | 0.17 | 0.91 | 8.67 | 14.18 | 2.95 |
| 8 | 24 | 6.1 | 0.17 | 0.90 | 8.16 | 13.49 | 3.19 |
| 11 | 16 | 6.4 | 0.15 | 0.84 | 7.68 | 13.14 | 2.28 |
| 13 | 11 | 6.3 | 0.20 | 0.96 | 9.10 | 14.45 | 3.61 |
| **Shanny** | | | | | | | |
| 1 | 15 | 6.6 | 0.23 | 1.20 | 9.76 | 17.75 | 2.70 |
| 3 | 8 | 6.8 | 0.25 | 1.29 | 11.50 | 19.79 | 1.95 |
| 5 | 15 | 6.3 | 0.21 | 1.26 | 11.77 | 18.25 | 3.28 |
| 7 | 6 | 7.1 | 0.22 | 1.16 | 11.26 | 17.19 | 3.15 |
| 11 | 20 | 7.9 | 0.23 | 1.52 | 12.86 | 22.35 | 4.12 |
| 13 | 29 | 7.9 | 0.22 | 1.30 | 10.88 | 18.21 | 3.39 |
| 17 | 9 | 9.5 | 0.23 | 1.62 | 15.45 | 24.49 | 5.50 |
| 22 | 9 | 10.0 | 0.26 | 1.71 | 17.39 | 28.02 | 5.01 |
| 24 | 22 | 10.5 | 0.26 | 1.70 | 15.85 | 27.19 | 5.30 |
| 32 | 3 | 11.5 | 0.29 | 1.38 | 11.85 | 23.10 | 6.25 |
| 45 | 3 | 10.0 | 0.25 | 2.00 | 19.84 | 31.87 | 10.38 |

**Note**: *n*, total number of escape responses included; D17, average distance travelled in centimetres during the first 17 ms of the response; D100, average distance travelled in centimetres during the first 100 ms of the response.

and Corolla 1981). Within the size range tested, maximum speed clearly increases with increasing larval length. Like the distance travelled during the first 17 ms of the response, measurement of maximum speed had the potential to be affected by our relatively slow video framing rate. Suprisingly, the resultant model is very similar to that recorded for northern anchovy by Webb and Corolla (1981), who used a much higher framing rate.

Because it is measured over the entire response, total distance travelled has the least potential for error from measurements of small distances and framing rate. Even so, this measurement displayed considerable variation, and the resultant model, although significant, is of little predictive value.

All of the escape response performance variables measured displayed considerable variability. Several factors may have contributed to this variation. The method of stimulating the response, impact by swimming amphipods, was potentially more variable than methods used in other studies (e.g., electrical stimulation used in Webb and Corolla (1981)). The relatively slow framing rate of the video system also could have introduced error, particularly for distance travelled during the first 17 ms and maximum speed. Some adult fish exhibit three separate types of fast starts, with accompanying variation in mean and maximum velocity (Harper and Blake 1990). Larval fish also might use different types of fast starts. Finally, some of the observed variability is due to differences among species. (Inclusion of species as a class variable in the regression model allows for calculation of the contribution of species differences to total variation, and in the case of our mean escape speed model, species differences account for approximately 15% of the total variation.) Obviously any suggested general relationship will not describe all species equally. Species differences within a general model are to be expected, just as one might expect differences between individuals in single species functions (such as weight–length relationships). What is important is to take steps to ensure that each species has an equal contribution to the eventual model, as we have done by using a weighted regression.

The escape response performance measurement that has been most often measured and reported is mean escape speed, with considerable recent attention given to the nature of the relationship between mean escape speed and larval length. The two regressions developed for northern anchovy (Webb 1981; Webb and Corolla 1981), the compilations by Blaxter (1986) and Miller et al. (1988), and our results with winter flounder larvae (Williams and Brown 1992) all show a positive linear relationship between mean escape speed and fish length. However, the relationship calculated for the five species tested in the present study is clearly nonlinear, with the rate of improvement in performance (slope) increasing with increasing larval length. Is the real relationship linear or nonlinear? A reasonable expectation for a mean escape speed – length relationship for the entire period from hatch to adult may be a sigmoidal curve, as was demonstrated for routine swimming attributes for an age range of zebra danio (*Danio rerio*) (Fuiman and Webb 1988). The curve would have an initial period of gradual linear improvement corresponding to the larval period, followed by a period of greater slope corresponding to the postmetamorphic period, and finally a gradual leveling off in late adulthood through senescence. Under this scenario, a mean speed – length relationship would only be linear within various stanzas of development, i.e., hatch through premetamorphosis, metamorphosis through adulthood, adulthood through senescence. In the present study, the larger larvae tested may have been reaching the period of greater slope corresponding to the postmetamorphic period.

A positive linear relationship was found between the logarithm of most escape response performance measurements and larval length, yet in some cases, vulnerability has been shown to increase with increasing larval length (Litvak and Leggett 1992; Pepin et al. 1992). How may linear improvement in escape response performance be reconciled with an increase in vulnerability? The answer lies in making the distinction between vulnerability and the component probabilities that combine to equal gross vulnerability.

Vulnerability ($V$) may be represented as follows (O'Brien 1979): $V = P(\text{E}) \times P(\text{A}) \times P(\text{C})$, where $P(\text{E})$ is the probability of encounter with a predator, $P(\text{A})$ is the probability of an attack given an encounter, and $P(\text{C})$ is the probability of capture given an attack. In the present study, only one factor, the probability of capture $P(\text{C})$, was examined. Other factors may result in changes in vulnerability with increasing larval length. The $P(\text{A})$ of both invertebrate and vertebrate planktonic prey has been shown to increase with increasing size, linked to greater prey motion and pigmentation (Lillelund and Lasker 1971; Zaret and Kerfoot 1975; Kerfoot 1978; O'Brien 1979; Williamson 1983; Turner et al. 1985; Orr 1989; Bollens and Stearns 1992; Litvak and Leggett 1992; Pepin et al. 1992). In some predator–prey situations, the increased $P(\text{A})$ overshadows the decreased $P(\text{C})$, and the net result is an increase in vulnerability with increasing size.

Similarly, it is overly simplistic to expect that, on the basis of the results of the present study, $P(\text{C})$ will decrease in a linear fashion with increasing larval size. The escape response parameters that were measured are only one component that will determine whether or not a larval fish will successfully evade an attack by a predator. The evidence does show that $P(\text{C})$ decreases with increasing larval length (Lillelund and Lasker 1971; Folkvord and Hunter 1986; Butler and Pickett 1988; Leucke et al. 1990; Litvak and Leggett 1992), and there is evidence that escape velocity is very important in determining the outcome of an attack by a predator (Drenner et al. 1978; Browman et al. 1989; Fuiman 1989). However, most researchers also found that the timing of the response was equally as important as, or more important than, the escape velocity (Webb 1976, 1981; Eaton and Didomenico 1986; Fuiman 1986, 1989). The timing of the response is often tied to events in the development of the sensory system of larvae, and these plateaus in development can lead to nonlinear decreases in $P(\text{C})$ with increasing larval size. This was elegantly demonstrated by Fuiman (1989) and Blaxter and Fuiman (1990), who showed that an abrupt rise in the responsiveness of herring larvae to predator attacks corresponded with discrete developmental events. The results of the present study may be useful in delineating such important plateaus in the development of larval fish. The improvement in escape response speed parameters was found to be a gradual process. If a dramatic decrease in the $P(\text{C})$ of a larval fish is detected, that decrease should not necessarily be attributed to improved swimming ability. Instead, researchers should look to sensory systems or neural pathways for the cause of abrupt improvements.

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