

Development changes in the escape response of larval winter flounder *Pleuronectes americanus* from hatch through metamorphosis

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ABSTRACT: A predatory amphipod (*Calliopius laeviusculus*) was used to elicit escape responses in larval winter flounder *Pleuronectes americanus* ranging in age from time of hatch to metamorphosis. The escape response observed consisted of fast c-start type acceleration followed by a period of burst swimming. Mean and maximum speed over the duration of the response increased linearly with larval total length. Total distance travelled by the larvae during the response was also positively linearly related to larval total length. Despite the extensive morphological reorganization that larval flounder undergo during metamorphosis, we did not find any decrease in escape response parameters of larvae during metamorphosis. Larval winter flounder displayed lower mean escape speeds than many other organisms found in the plankton. Size-specific mean escape speeds of larval flounder are lower than those reported for other species of larval fish.

INTRODUCTION

Many marine fish are egg-scattering pelagic spawners that produce larvae which drift in the plankton (Balon 1990). These larvae spend from days to weeks in the pelagic zone, where they are exposed to a variety of vertebrate and invertebrate predators (Hunter 1984). Mortality during this larval stage is typically very high (Pepin 1991), and much of this mortality has been attributed to predation (Miller et al. 1988). High predation pressure should strongly select for anti-predator defences in larval fish. One anti-predator defence that has been demonstrated in several species of larval fish is an escape response.

In larval fish, the escape response typically begins with a series of rapid contractions of the musculature on alternate sides of the body. This series of movements, variously termed a c-start or quick-start, rapidly displaces a larva several body lengths from the initiation point (Eaton & Didomenico 1986, Webb 1986). The c-start is generally followed by a period of burst swimming (Webb & Corolla 1981), possibly serving to remove the larva from the perceptual field of the predator. With respect to larval fish, the term 'escape response' has sometimes been used in the past

to describe only the c-start at the beginning of the response (Eaton & Didomenico 1986). Here, we use the term to encompass the entire response (i.e. both the c-start and the period of burst swimming). Our definition is consistent with that used by researchers studying other taxonomic groups (Gilbert 1985, Browman et al. 1989).

The escape response acts late in the predation cycle, and is the only defence most larval fish may employ once an attack has been initiated by a predator. The effectiveness of this type of response in escaping any particular predator is mediated by several factors. First, particularly in the case of lunging or contact predators, the timing of the response must be exact (Webb 1976, Webb 1981). Second, the response must generate the necessary acceleration and speed to enable the larva to escape the attack. Thorough knowledge of these aspects of the larval escape response should aid in interpretation of existing and future data concerning larval vulnerability to predation.

Study of the escape response in larval fish is somewhat complicated by the dynamic nature of larval fish development during the first weeks of life. In order to identify 'windows' of vulnerability to predators, it is necessary to determine the quantitative and qualita-

tive changes in anti-predator defences that occur as the larvae develop. If one is studying the escape response, it is important to know when the escape response becomes operative, and to know the relationship between the escape response and larval size. Webb (1981) and Webb & Corolla (1981) reported positive linear increases in escape response speed parameters of northern anchovy *Engraulis mordax* larvae as they grew larger. Miller et al. (1988) summarized data from 9 species of larval fish (including northern anchovy) and reported that burst swimming speed increased with increasing larval size; however the fit to a linear relationship was poor in this interspecific comparison. Additional data, particularly from non-clupeoid fish, is needed to develop a general relationship between larval size and escape response performance, if indeed one relationship is sufficient.

In addition to documenting improvements in the escape response, it is necessary to determine if there are any intervals where a decrease in performance occurs. For example, one logical point in larval development where we may expect such a reduction in performance to occur is when larvae approach metamorphosis. This transition from the larval to the juvenile stage is accompanied by marked changes in body systems, including rearrangement and redistribution of red and white muscle fibres, which are used for aerobic sustained vs anaerobic burst swimming (Batty 1984). It is possible that the performance of larval fish will decrease during the period when they are undergoing metamorphosis, as has been demonstrated by increased vulnerability to predation in amphibian climax tadpoles (Huey 1980, Richards & Bull 1990). As such, if feasible, testing of the escape response of larval fish should extend to include metamorphosis.

Winter flounder *Pleuronectes americanus* larvae spend approximately 40 to 70 d in the pelagic zone (Chambers & Leggett 1987) where they undoubtedly encounter a variety of predators. At the end of this pelagic phase, winter flounder undergo an extreme metamorphosis in that the larva changes for demersal life, rotating 90 degrees so that what was the larval right side becomes the dorsal surface and the left side becomes the ventral surface. This change, accompanied by a migration of the left eye to the right side of the body, takes approximately 1 wk to complete (Chambers & Leggett 1987). Considering the extensive reorganization during this transition phase, some reduction in the efficiency of the escape response might be expected. Therefore, the objectives of this study were to measure and describe the escape response of larval winter flounder from hatch through metamorphosis, and compare their per-

formance with examples from other phylogenetic groups including fish.

MATERIALS AND METHODS

Experimental animals. Winter flounder eggs were fertilized and incubated in plastic petri dishes (Harmin & Crim 1992). Hatched larvae were maintained in 40 l aquaria containing static, filtered seawater. The aquaria were partially immersed in a running ambient seawater wet bench to maintain temperature between 5 and 11 °C. Because rearing and testing temperatures were slightly higher than flounder larvae would be exposed to in nature, it is possible that the results obtained in this study represent slight overestimates of performance in the field. Larvae were fed cultured rotifers (*Branchionus plicatilis*) at an approximate density of 10 prey ml⁻¹ for the first 30 d post-hatch. From 30 d onward, newly hatched brine shrimp nauplii *Artemia salina* were added at a density of approximately 1 prey ml⁻¹. Larvae from different female-male pairings fertilized on different dates were used in the experiments.

We used *Calliopius laeviusculus*, a common free-swimming epibenthic amphipod (DeBlois & Leggett 1991), to elicit the escape responses in the larval flounder. *Calliopius* spp. are omnivorous, consuming algae, detritus, and live zooplankton (Hudon 1983). They are contact predators, grasping and biting prey they come in contact with. *Calliopius* spp. have been shown to prey upon larval fish (Bailey & Yen 1983, Bailey & Stehr 1986). Preliminary trials indicated that the amphipods swam almost continuously in small test chambers, provided there were no crevices or edges for them to cling to, thus facilitating contact with larvae in an experimental situation. It should be emphasized that the amphipods were used in this experiment as a predatory stimulus, and most amphipod-larva interactions did not result in the capture of the larva. The experiments were not intended to evaluate capture rates of amphipods on flounder larvae, but rather to examine the escape responses of the larvae.

Test chamber. All experimental trials were carried out in a circular 80 cm diameter, flat-bottomed plexi-glass water bath, supplied with running ambient seawater at a depth of 10 cm. All trials were videotaped using a silhouette system (Arnold & Nuttall-Smith 1974), where a biconvex lens is used to collimate light which then passes through the experimental chamber to a video camera. Low light levels (less than 10 lux in this experiment) provided sharp silhouettes of larval flounder and amphipods. The low light levels are necessary when working with positively phototactic larvae such as flounder.

Experimental protocol. Larvae were placed in a 20 cm glass dish containing 1.5 cm seawater. This dish was floated in the water bath, restrained directly over the biconvex lens. After 1 min, 2 amphipods were pipetted into the dish, and the video recording initiated. Video recording continued for 20 min, after which the larvae were pipetted from the dish, anaesthetized and preserved in 10 % formalin. The larvae were later examined to determine whether or not they had metamorphosed, defined as the point in development at which the iris of the migrating eye becomes visible from the right side of the body (Chambers & Leggett 1987).

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. All escape responses were recorded as starting from the first contraction of the larva after being contacted by 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 (1/30 s = 33 ms) intervals on an acetate overlay of the monitor. These tracings were then digitized, and for each amphipod-larva interaction we recorded the distance larvae travelled (mm) during each 1/30 s interval of the response. From these data, we calculated mean and maximum larval speed, and total distance travelled by each larva. We also noted total length of the larvae, total duration of the response, and the point in the response where the maximum speed occurred.

Scatterplots of mean speed, maximum speed, and total distance travelled vs larval length appeared to describe linear relationships, with no violations of the assumptions of linear regressions. Linear regressions were performed on these 3 variables using the GLM procedure in SAS (SAS Institute Inc. 1988). The resid-

uals were tested for normality using the Shapiro-Wilk statistic, and plots of residuals vs the predicted values were examined to detect violations of the assumptions of independence and constant variance. The residuals generated by maximum speed were not normally distributed, therefore a \log_{10} transformation was performed, which restored normality.

RESULTS

Prior to the introduction of the predator, the behaviour of the larval flounder in the 20 cm dish did not appear qualitatively different than their behaviour in the rearing tanks. A total of 50 larval-amphipod interactions were used in the analyses (Table 1). Examination of the preserved larvae after the experiments showed that only the 50-d-old larvae had metamorphosed. Up to metamorphosis, the larvae spent nearly all of their time at the surface of the water, while after metamorphosis they were usually resting on the bottom.

The escape response of larval flounder consisted of a series of contractions which caused the larvae to alternately bend in a shape that resembled a 'c' or reverse 'c', when viewed from above. The extent of bending was usually most pronounced at the beginning of the response; contractions gradually reduced over the course of the response. These contractions rapidly propelled larvae and metamorphosed flounder through the water. The contractions of the metamorphosed flounder during their escape responses were no longer from side to side, but rather alternated dorsally and ventrally.

Plots of the average speed (cm s^{-1}) during each 1/30 s interval vs time elapsed since contact with the predator exhibited considerable variation (Fig. 1A). Part of this variability can be attributed to the framing rate of the video system, which at 1/30 s intervals has been shown to be too slow to record details of the

Table 1. *Pleuronectes americanus*. Summary of ages and lengths of larval winter flounder tested. n: no. of amphipod-larva interactions used in the analysis. Larvae tested originated from several batches

Age (d)	n	Mean length (mm)	SE	Temp.	Date tested
1	5	3.38	0.060	9.0	Jul 4
7	4	5.23	0.140	12.0	Jul 28
8	6	4.05	0.216	12.5	Jul 31
10	4	5.24	0.300	12.5	Jul 31
12	4	3.84	0.113	13.0	Aug 9
20	5	4.80	0.137	14.0	Aug 12
24	4	5.17	0.419	14.0	Aug 16
30	1	4.51	—	10.0	Jul 15
30	2	8.77	0.716	12.5	Aug 4
43	5	6.80	0.281	12.5	Jul 28
50	5	7.75	0.131	12.0	Aug 3
50	5	8.94	0.234	14.0	Aug 6

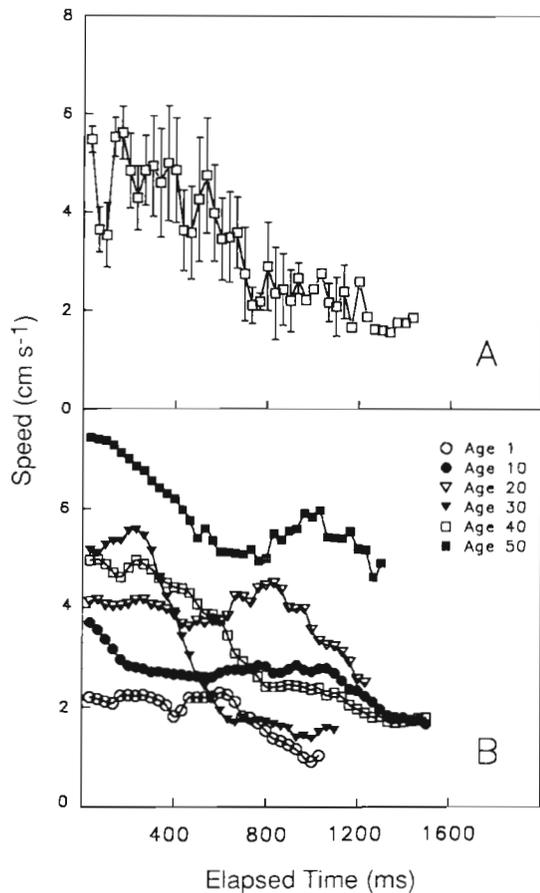


Fig. 1. *Pleuronectes americanus*. Plots of larval winter flounder escape speed vs elapsed time after contact with amphipods. (A) Plot of mean escape speed of 40-d-old flounder larvae presented in order to demonstrate variation present in all 6 age groups plotted in (B). Error bars = SE. (B) Plots of 6 age-groups of flounder, after smoothing with a 6-point running average. Ages in days post-hatch

beginning of the escape response, the c-start (Eaton et al. 1977). In order to see general trends, we smoothed the plots using a 6-point running average, as in Fui-man (1986). General trends from the smoothed plots (Fig. 1B) are that the maximum speeds occur in the first 400 ms, 4 of 6 age groups plots show decreasing speed as elapsed time increases, and there is an increase in speed as age increases.

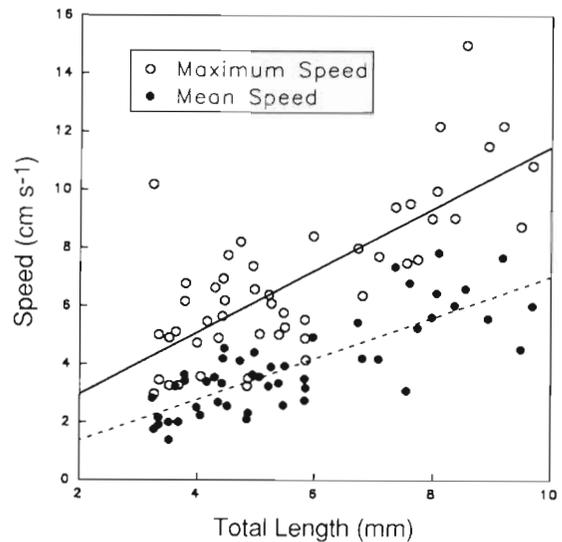


Fig. 2. *Pleuronectes americanus*. Mean and maximum escape speed (cm s^{-1}) during escape responses of larval winter flounder vs total larval length (mm). Each symbol represents the mean or maximum speed during 1 escape response. Open circles and solid regression line represent maximum speed, filled circles and dashed regression line represent mean speed. Equations for regressions are given in Table 2

Mean speed during the escape response was significantly ($p < 0.0001$) positively related to total larval length (Fig. 2, Table 2). Newly hatched larvae attained mean escape speeds of 2 cm s^{-1} (5.7 body lengths per second, bls), while metamorphosed flounder performed at 6 to 7 cm s^{-1} (7.6 bls). Maximum speed was also significantly positively ($p < 0.0001$) linearly related to total larval length (Fig. 2, Table 2). Newly hatched larvae reached maximum speeds of ca 4 cm s^{-1} (11.4 bls), while metamorphosed flounder reached maximums of 10 to 11 cm s^{-1} (12.3 bls). Total distance travelled during the response was quite variable, and was only weakly positively related to length of larva with an r^2 value of 0.23 (Fig. 3, Table 2). There was no clear relationship between larval total length and the point during the response where speed was maximized. Similarly, the duration of the escape response was not linearly related to length of larva, and fitting of various non-linear relationships to the data proved unsatisfactory.

Table 2. *Pleuronectes americanus*. Regression equations for larval winter flounder escape response parameters vs larval length. n = 50 in all analyses

Variable	Relationship	F-value	p > F	r ²
Mean speed (U)	$U = 0.707(L) - 0.043$	91.41	0.0001	0.6557
Maximum speed (M)	$\log(M) = 0.065(L) + 0.434$	53.72	0.0001	0.5281
Total distance (D)	$D = 0.311(L) + 0.796$	14.37	0.0004	0.2304

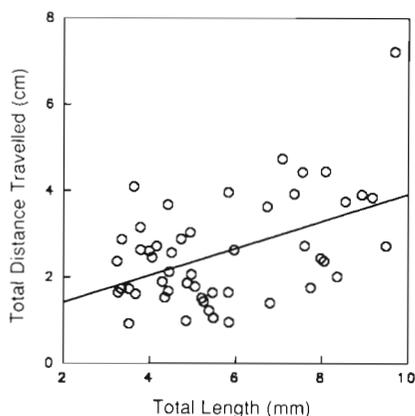


Fig. 3. *Pleuronectes americanus*. Total distance travelled during escape response by larval winter flounder vs larval total length. Each symbol represents the total distance travelled during 1 escape response. Equation for regression is given in Table 2

DISCUSSION

The escape responses performed by larval flounder in this study are qualitatively similar to those described for larval northern anchovy (Webb 1981, Webb & Corolla 1981). However, quantitative comparisons of our results with that of other studies are complicated because of the different time intervals examined in this versus other studies. For example, a number of other studies (Webb 1981, Webb & Corolla 1981, Batty 1989) have examined the initial part of the response, the c-start, but did not follow the response beyond 300 ms in elapsed time. In contrast, we examined the entire response, using the behaviour of the larvae to signal the end of the response. Consequently, our profiles (Fig. 1B) show less detail of the initial phase as compared to other studies, but cover the entire 1200 to 1400 ms of the response. We observed that maximum speeds occurred in the first 400 ms of the response, whereas other studies show maximum speeds at 80 to 100 ms (Webb & Corolla 1981, Yin & Blaxter 1987). We also observed that escape speed decreased over the duration of the escape response (Fig. 1B). Yin & Blaxter (1987) show steady decreases in escape speed until 200 ms, the point where their observations end. Likewise, Webb & Corolla (1981) show speed decreasing from the maximum, but then levelling out until 350 ms, the end of their observations. If examination of our speed/elapsed time profiles were limited to 350 ms, 4 of the 6 profiles (Fig. 1B) level out or increase after the maximum speed. However, our extended examination of the whole response indicates that mean escape speed decreases as the response proceeds.

One way of assessing how the escape response changes as larvae develop is to examine the relationship between escape response parameters and larval total length. Doing this, we found mean speed, maximum speed and total distance travelled to be significantly linearly related to larval length. The timing of maximum speed and duration of the escape response were not clearly related to larval length, although larger larvae appeared to exhibit escape responses that were shorter in duration. Webb & Corolla (1981) also reported mean and maximum escape speeds of northern anchovy increasing linearly with length, and found that time to maximum speed was unrelated to length. Webb (1981) reports that mean speed increased linearly with larval length, but the relationship between maximum speed and larval length was best described by an increasing power function. It seems therefore, that as is the case for northern anchovy larvae, the escape response of larval flounder improves with increasing larval size, with larger larvae exhibiting increased mean and maximum speeds during their responses.

The relationship between larval length and mean escape speed is a convenient measure for comparing the escape responses of different species of larval fish, however different methodologies and measurement times can lead to marked differences in performance within species (Miller et al. 1988). For example, the escape response performance of northern anchovy larvae, as elicited by electric shock (Webb & Corolla 1981), is nearly twice the magnitude of northern anchovy escape speeds resulting from attacks by a planktivorous fish (Webb 1981)(Fig. 4). When we compare the mean escape speed/length relationship of winter flounder with similar published relationships (Fig. 4), we find that in general larval flounder escape at a lower speed/larval length than other species. This comparison includes the relationship proposed by Miller et al. (1988) as a composite of 76 escape speeds measured from 9 different species of larval fish, including 8 measurements from European flounder *Platichthys flesus* and 15 measurements from the plaice *Pleuronectes platessa*.

One way to evaluate the potential effectiveness of the escape response of winter flounder is to compare their escape abilities with those of other organisms in the plankton, including other species of larval fish. These comparisons may be done in absolute terms or in terms adjusted for larval size. We feel that absolute terms are more important from an ecological point of view because they determine the effectiveness of the response (i.e. in a suction flow field of 20 cm s^{-1} , a larva with a maximum escape velocity of 7 cm s^{-1} will probably be captured, regardless of whether this velocity represents 10, 20 or 30 bls). Although young flounder

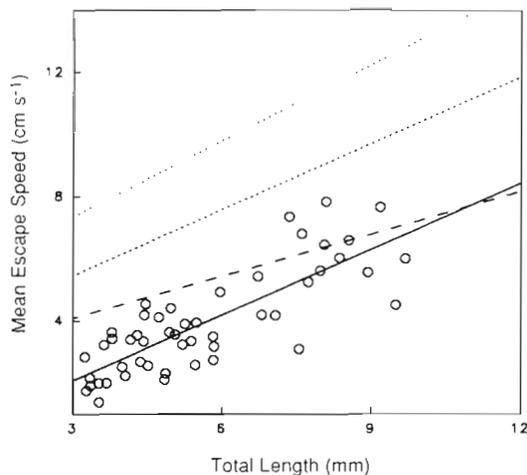


Fig. 4. *Pleuronectes americanus*. Plot of mean escape speed of larval winter flounder vs total larval length, with regression lines from other published escape speed/larval length relationships. The key for regression lines is as follows: (.....) Webb & Corolla (1981); (-----) Miller et al. (1988); (- -) Webb (1981); (—) this study. The relationships from Webb & Corolla (1981) and Webb (1981) are for northern anchovy *Engraulis mordax* larvae, while the relationship from Miller et al. (1988) is from 9 species of larval fish

larvae attain comparable mean escape speeds to the slower zooplankters, such as rotifers and *Daphnia* spp. (Fig. 5), even the metamorphosed flounder are slower than the cnidarians and copepods. In experiments using predatory freshwater cladocerans, Browman et al. (1989) found that copepods with escape speeds of 9 cm s^{-1} could escape the predator, while *Daphnia* spp. juveniles and adults with escape speeds of 2.5 and 3.2 cm s^{-1} were captured at a significantly higher rate. Newly hatched flounder larvae with escape speeds of approximately 2 cm s^{-1} would probably not survive many attacks by a marine equivalent of the predator used by Browman et al. (1989), however larger larvae may be able to survive a greater percentage of such attacks. Comparisons of the mean escape speed of winter flounder with that of other marine and freshwater vertebrates (Fig. 5) also show that newly hatched flounder larvae perform at a lower rate than other species noted. Even the 6 mm flounder larvae only achieve speeds similar to the slowest mean escape speeds listed. It seems, therefore, that winter flounder larvae, particularly newly hatched larvae, are among the slower organisms in the plankton with respect to mean escape speeds, and as such may be very vulnerable to predation from both vertebrate and invertebrate predators.

Another way to assess the potential effectiveness of the escape response of winter flounder larvae is to consider the different predator attack characteristics.

Probably the majority of predators that flounder larvae would be exposed to would be contact predators, only attacking organisms that they physically come in contact with. These types of predators include carnivorous copepods and amphipods (Westernhagen & Rosenthal 1976), cnidarians (Fraser 1969, Purcell 1985) and ctenophores (Purcell 1985). The escape response displayed by the winter flounder in this study would be effective against these types of predators in 2 ways. First, if a larva was touched, but not grasped, it would quickly swim away before being captured. Secondly, if the larva was grasped or if it made contact with an adhesive tentacle [e.g. some medusa use adhesion more than nematocysts for initial capture of prey; Fraser (1969)], the escape response would produce a thrashing motion that may break the hold of the predator and allow the prey to escape. Striped bass larvae escape cyclopoid copepods by thrashing once grasped (McGovern & Olney 1988). Similarly, bloater larvae have been shown to escape the grasp of mysids in a similar fashion (Seale & Binkowski 1988). It seems therefore that the escape response of winter flounder larvae could be effective against contact-type predators, and that given the increasing speed generated by larger larvae, the effectiveness should improve as the larvae grow.

How effective might the observed escape responses of flounder be against attacks by predators other than contact predators, for example, planktivorous fish that feed by suction? Two requirements of an effective defence from this type of attack are precise timing of the escape response, and sufficient escape velocity to enable the larva to swim out of the flow field produced by the attack (Drost 1987). Our study did not address the timing of the response, but it did measure maximum escape velocities produced by the larvae. The currents generated by suction feeders may be quite high near the mouth of the predator, with values of 26 cm s^{-1} having been reported for 6 to 8 mm carp larvae (Drost & van den Boogaart 1986) and 43 cm s^{-1} for 10 mm carp larvae (Drost 1987). However these currents drop off very rapidly as the distance from the mouth increases (Drost & van den Boogaart 1986). Considering the maximum velocities attained by flounder in this study (i.e. ranging from 3 to 15 cm s^{-1}) several conditions would determine whether or not a larva would successfully escape an attack by a suction-feeding planktivorous fish. These conditions include the size of the predator, which in turn determines its suction velocity, the timing of the response by the larva, and the distance at which the attack was initiated. Based on our results, larval flounder, particularly smaller larvae, are poorly equipped to escape attacks by planktivorous fish. This vulnerability of the smallest larvae to vertebrate predators may not translate into

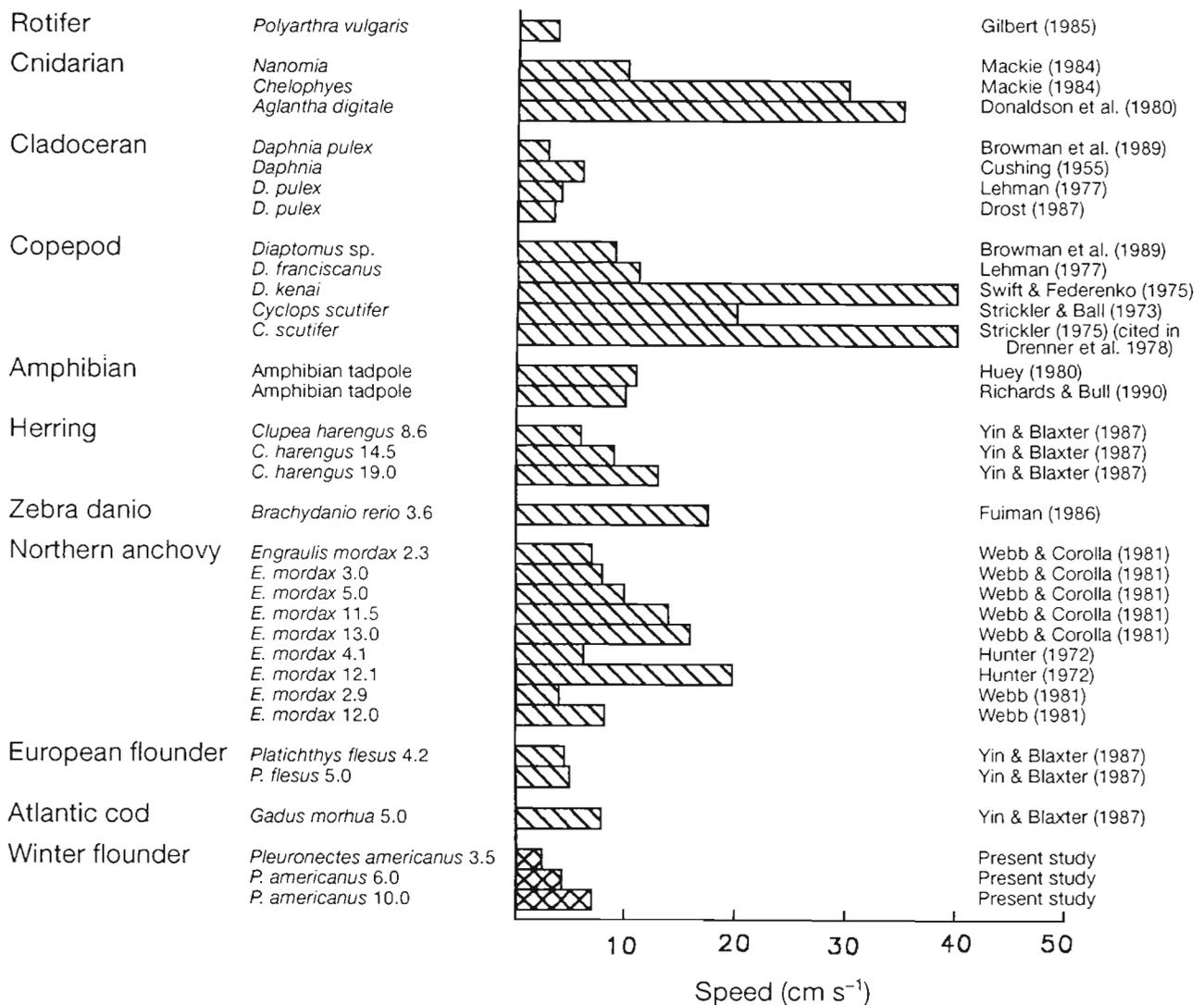


Fig. 5. Comparison of escape speeds of different taxonomic groups, including larval fish. Lengths of larval fish (in mm) are provided after species name

high mortality, because the attack rate of vertebrate predators has been shown to be lower on smaller larval fish (Pepin et al. 1987).

In this study, no obvious demarcations or breaks in the speed/larval length relationships were noted, despite the extensive reorganization flounder undergo during metamorphosis. Amphibians also go through extensive changes during metamorphosis (Werner 1986), and in 2 studies, tadpoles undergoing metamorphosis (called climax tadpoles) were found to be more susceptible to predation (Huey 1980, Richards & Bull 1990). Huey (1980) provides an effective description in stating that the climax tadpoles are stuck between being good tadpoles and good frogs. Richards & Bull (1990), testing 3 species of Australian tadpoles, attributed the increased vulnerability to predation to decreased swimming speed during the transition.

Given this information from amphibians, we had expected some reduction in the escape response of flounder approaching metamorphosis. Our data, however, does not show any consistent decrease in performance during metamorphosis. Unfortunately, larvae at what may be considered transition lengths provided the fewest responses suitable for analysis, most of the responses occurring near the sides of the arena and resulting in early contact with the sides of the arena.

In conclusion, we found that larval winter flounder responded to contact by amphipods with an escape response consisting of c-start acceleration followed by burst swimming. Mean and maximum speed of the responses increased linearly with total larval length. The escape performance of larval flounder was found to be generally lower than that of other organisms found in the plankton, including other species of lar-

val fish. With mean escape speeds among the slowest of many organisms found in the plankton, flounder larvae would probably not survive many attacks by suction-feeding planktivorous fish. Based on our results, we feel that the escape response of larval flounder would be effective against contact predators, and that any effectiveness would improve as the larvae get larger.

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Errata

Re: P. J. Williams, J. A. Brown

Mar. Ecol. Prog. Ser. 88: 185–193 (1992)

- The above article incorrectly reports mean and maximum escape speeds of larval winter flounder. The actual speeds are greater than reported by a factor of 2. For example, if a speed of 4 cm s⁻¹ is listed in the article, the actual speed is 8 cm s⁻¹. Figs. 1, 2, 4 & 5 are affected by this change. The regressions provided in Table 2 for calculating mean and maximum speed should read:

Mean speed (U):

$$U = 1.353(L) + 0.348, \quad \text{with } F\text{-value} = 94.93, \quad p > F = 0.0001, \quad r^2 = 0.6641$$

Maximum speed (M):

$$M = 2.000(L) + 2.5498, \quad \text{with } F\text{-value} = 57.50, \quad p > F = 0.0001, \quad r^2 = 0.5450$$

Both speeds are in cm s⁻¹, and lengths are total lengths in mm.

One of the main conclusions of the article was that flounder larvae exhibited escape speed parameters lower than values published for other species of larval fish (paragraph 3 of 'Discussion'). We now feel that this is not the case, and we report that flounder larvae perform at similar levels as had previously been reported for other species of larval fish. The other conclusions of the article, including the description of the escape response and the relationship between length and escape performance, remain qualitatively unchanged. The authors apologize for the error, and regret any inconvenience the incorrect values may have caused. Anyone wishing further clarification may contact P. J. Williams at the address below.

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Re: M. P. Hoch, D. L. Kirchman

Mar. Ecol. Prog. Ser. 98: 283–295 (1993)

- Table 2, on p. 288, contained 3 misprinted values. The corrected table appears below.

Table 2. Summary of biological properties for the upper, middle, and lower regions of the Delaware Estuary, 1986 to 1988. The ratio of bacterial production to primary production is given as Bprod:Pprod

	Chl <i>a</i> ($\mu\text{g l}^{-1}$)	Primary production ($\text{mmol C m}^{-2} \text{d}^{-1}$)	Bacteria			Bprod:Pprod
			Abundance (10^6 ml^{-1})	Growth rate (d^{-1})	Production ($\text{mmol C m}^{-2} \text{d}^{-1}$)	
Upper region						
Mean \pm SD	11.2 \pm 10.3	19.0 \pm 19.9	3.0 \pm 2.0	0.336 \pm 0.216	27.3 \pm 26.2	4.32 \pm 6.32
(Max, min)	(70.0, 1.1)	(82.4, 0.17)	(12.7, 0.78)	(1.32, 0.048)	(147, 1.6)	(34.10, 0.20)
n	107	103	89	88	89	88
Middle region						
Mean \pm SD	15.0 \pm 15.6	61.4 \pm 66.3	3.3 \pm 2.1	0.240 \pm 0.144	23.3 \pm 21.1	0.65 \pm 0.73
(Max, min)	(81.7, 2.6)	(422, 0.93)	(9.1, 0.93)	(0.720, 0.024)	(88.4, 1.20)	(5.24, 0.06)
n	89	87	73	70	72	72
Lower region						
Mean \pm SD	10.8 \pm 9.0	75.1 \pm 101.1	3.7 \pm 2.3	0.216 \pm 0.168	24.0 \pm 25.1	0.51 \pm 0.54
(Max, min)	(56.3, 1.1)	(735, 1.3)	(11.1, 0.65)	(0.984, 0.024)	(138, 1.11)	(3.48, 0.05)
n	108	103	90	85	82	77