DEVELOPMENTAL CHANGES IN ANTI-PREDATOR DEFENCES OF MARINE LARVAL FISH

PHILIP JAMES WILLIAMS

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BY

PHILIP JAMES WILLIAMS

A thesis submitted to the School of Graduate Studies in partial fulfilment of the requirements for the degree of Doctor of Philosophy

Department of Biology
Memorial University of Newfoundland

1994

St. John's Newfoundland

Abstract: This thesis describes behavioural experiments that investigate anti-predator defences employed by larval fish. The first anti-predator defence investigated was cessation of movement, or "freezing". Smaller size classes (mean length 6-10 mm) of larval lumpfish (Cyclopterus lumpus) used the freezing response in the presence of a predator, despite the fact that this behaviour precluded foraging. Interestingly, fifteen week old larvae (mean length 15 mm) no longer used this defence, presumably because the predator no longer posed a threat.

The second anti-predator defence investigated was the escape response, defined as a period of high acceleration followed by burst swimming. Escape response performance was measured in larval winter flounder (Pleuronectes americanus), ranging in size from newly hatched (3.5 mm TL) to metamorphosed juveniles (10 mm TL). All escape response performance measurements (mean and maximum speed, distance travelled during the first 100 ms of the response, and total distance travelled) increased with larval length. There was no obvious decrease in performance during metamorphosis, nor was any increased rate of improvement noted after metamorphosis.

The escape response performance of length ranges of an additional four species of larval fish, including cod (Gadus morhua), capelin (Mallotus villosus), herring (Clupea

harengus), and radiated shanny (Ulvaria subbifurcata) were measured. These results were combined with the winter flounder data to produce general models for the following performance measurements: mean and maximum speed, distance travelled during the first 17 and 100 ms of the response, and total distance travelled during the response. In all models, except that relating distance during 100 ms to larval length, the logarithm of the performance measurement was significantly linearly related to larval length. Distance travelled during the first 100 ms was linearly related to larval length.

The potential for increased drag, and subsequent reduced performance during escape responses occurring very near the surface was investigated, in an attempt to partition some of the within-length variation observed in the general models. No overall reduction in performance was detected in responses near the surface; in fact, some performance measurements actually showed significant improvement.

Dedication:

I dedicate this thesis to three generations. First of all to my father. Financial restraints and familial responsibilities prevented him from attending university, despite his excellent academic standing. Second, to Ken McNeill, who recently passed away just when things were coming together for him. Ken was always intently interested in and appreciative of my research, even though it was far removed from his profession. Finally, to my son, now fourteen months old. He was born a few weeks after the first submission of this document. I hope the memory of the first two, and the life of the third, will keep reminding me that our work should not be our life.

Acknowledgements:

First and foremost, I thank my wife, Maureen, for what could only be described as her unflagging support and encouragement these last six years. She never gave up on me, nor did she allow me to give up on myself. I couldn't, couldn't, couldn't have done this without her.

Thanks to my main man, Dr. Joe Brown. He was an excellent supervisor and friend from start to finish.

Many thanks to Vee and Pierre, for editing countless manuscripts and versions. Pierre served double duty as committee member, and was very supportive through the years.

Drs. Howard Browman and Matt Litvak were generously helpful with advice and information concerning the silhouette video system, resulting in chapters 4 and 5.

To lab buddies Grant, Donna, Rod, Leslie, Greg, Trevor, (yes, you too Sparky).

Thanks to everybody at the MSRL, may she float forever. Larry Crim, Ed Downton, Jimmy Devereaux and workshop men, Terry Harris, Connie Short, Steve Sooley, Mike Riehl, Dolores, Gen, Helen, Deanne, Gord Chaisson and the dive unit, past and present, Chris Bajdik, Craig Tuck, all of the custodians.

Thanks to everyone in the Biology Dept. at MUN for making my first year of teaching a smooth one, in particular Christine, Shirley, Gail, and Roy Ficken for lots of last

minute slides. Thanks to Bob Sheath and Ian Emerson for the opportunity to teach in a fine department.

Financial support over the years came in the form of an NSERC postgraduate scholarship, and student support from the OPEN project.

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Chapter One: General Introduction

Predation is a powerful organizing force in nature and has been demonstrated to have profound effects at the level of the community (Paine 1966, Glassen 1979, Zaret 1980, Power et al. 1992), the population (Mittelbach & Chesson 1987, Price 1988), and the individual (Havel 1987, Mattingly & Butler 1994). As an agent of natural selection, predation has been implicated in the evolution of an impressive list of anti-predator defences (Sih 1987), involving prey morphology, behaviour, and life history characteristics (Edmunds 1974, Havel 1987, Scrimshaw & Kerfoot 1987, Stemberger & Gilbert 1987).

The ecological importance of predation has prompted considerable research efforts, which may be categorized according to various criteria. For example, Helfman (1986) divides predation studies into two categories, direct and indirect studies, based on whether or not behavioural observations of predator-prey interactions are used in the study. Indirect studies do not use behavioural observations, but rather examine or analyze the end results or products of predation. These types of studies include examination of gut contents of predators, quantification of wounds on prey (van der Veer & Bergman 1987, Mushinski & Miller 1993), biochemical detection of prey consumption

(Theilacker et al. 1986), or correlation of prey populations with predator abundance or presence (Zaret 1980, Stamps 1983, Fraser & Gilliam 1992). Many indirect studies include some manipulation of predators, prey, or habitat, both in the field and in the laboratory (Brooks & Dodson 1965, Dayton 1975, Himmelman et al. 1983, Pepin et al. 1987, deLafontaine & Leggett 1988, Litvak & Leggett 1992, Pepin et al. 1992).

Direct studies, involving behavioural observations of predator-prey interactions in the field or in the laboratory, have greatly increased our understanding of predator-prey relationships (Helfman 1986). Direct studies of predation seek to elucidate the mechanisms of predation, mechanisms whereby prey are encountered, detected, attacked, captured, and ingested. The direct approach has the added advantage that it is based on the level of the individual, the same level at which selection takes place (Lomnicki 1988). Increasingly, researchers are experimenting with individual-based approaches to better understand population dynamics problems (Ohman 1988, Chambers 1993, Rice et al. 1993, Van Winkle et al. 1993, Williamson 1993). In the study of zooplankton communities, for example, the direct approach to the study of predation has been pivotal in understanding predator-prey interactions and how they relate to population and community processes (Price 1987,

Williamson 1993).

The experiments described in this thesis used direct, detailed behavioural observations to investigate predation processes that involve larval fish as prey. Larval fish are interesting subjects for behavioural study because they undergo dramatic developmental changes during the first few weeks of life (Blaxter 1988), and this accelerated development allows the researcher to investigate developmental and size effects on components of the predator-prey interaction. It is also generally accepted that predation is the main source of mortality in larval fish (Hunter 1984, Bailey & Houde 1989), suggesting that this life history stage is under strong selective pressure for effective anti-predator adaptations.

There have been many direct studies of predator-prey interactions between larval fish and predators, beginning as early as the 1920's when Lebour (1925) experimentally determined that zooplankton were capable of capturing and consuming larval fish. Some studies reported numbers captured over time, or captures per attack, at various predator-prey densities (Westernhagen & Rosenthal 1976, Brownell 1985, Folkvord & Hunter 1986, Butler & Pickett 1988, Luecke et al. 1990, Margulies 1990). Other researchers took a more mechanistic approach, assessing the effectiveness of the predator and the various adaptations

predators use in the detection and capture of larval fish (Fraser 1969, Kuhlmann 1977, Dendy 1978, Bailey & Batty 1983, Heeger & Moller 1987, Purcell et al. 1987, Yen 1987, Seale & Binkowski 1988). In recent years, the role of the larval sensory system in detecting predators and coordinating escape has been examined (Blaxter & Batty 1985, Batty 1989, Margulies 1989, Blaxter & Fuiman 1990, Fuiman & Batty 1994). Finally, details of the escape response exhibited by most larval fish have been examined experimentally (Eaton et al. 1977, Kimmel et al. 1980, Webb 1981, Webb & Corolla 1981, Bailey 1984, Bailey & Batty 1984, Blaxter & Batty 1985, Eaton & Didomenico 1986, Fuiman 1986, Yin & Blaxter 1987).

Researchers often represent the act of predation as a cycle of discrete steps. For predation processes that involve larval fish as prey, these steps include Encounter, Attack, and Capture (modified from O'Brien 1987). In recent years, understanding of the characteristics of plankton community dynamics has benefitted from experimental determination of the conditional probabilities associated with each step of the predation cycle (Price 1988, Williamson 1993). With respect to larval fish as prey, the majority of direct experimental work has concentrated on the last step in the predation cycle, capture. Responsiveness to the attack (which in turn depends upon sensory

development); and the timing, speed, and acceleration of the resultant escape response by the fish larva have been shown to affect the probability of capture (P(C)). In contrast, far less attention has been given to factors influencing the encounter and attack of larval fish by their predators. Some information affecting the probability of encounter (P(E)) has been obtained from search patterns of invertebrate (Bailey & Batty 1983) and vertebrate (Colin 1976, Hunter 1981, Christensen 1983) predators. Research pertaining to the probability of attack (P(A)) has focused on what cues predators use to detect prey. Pigmentation (Brownell 1985, Folkvord & Hunter 1986), larval size (Folkvord & Hunter 1986), and larval movement (Christensen 1983) have all been shown to affect the P(A) of larval fish.

The experiments described in this thesis use direct, behaviourally-based experiments to gain information about anti-predator defences of larval fish. Knowledge concerning these defences is important because they, in part, determine the conditional probabilities of whether or not a larva will be attacked (P(A)), or if attacked, whether or not a larva will be captured (P(C)). Because the development of larval fish is rapid, it is not sufficient to evaluate defences at one size or age of larvae. Rather, testing a range of sizes is more instructive, in order to detect the improvement, and rate of improvement, in anti-predator defences as the larvae

develop. Consequently, all of the experiments reported in the following chapters were carried out on length ranges of larvae, in order to determine how anti-predator defences may change with larval development.

Chapter Two reports the results of experiments designed to determine whether or not larval lumpfish (Cyclopterus lumpus) use a very simple anti-predator defence, cessation of movement, to reduce the probability of attack when exposed to the threat of a predator. Besides the presence or absence of a predator, two other factors were examined for their effect on use of the anti-predator defence by the larvae. Prey organisms with greater hunger levels have been shown to accept greater risk of attack by a predator in order to forage (Dill & Fraser 1984, Magnhagen 1988). In the experiments described in Chapter Two, larvae were not able to forage when using the cessation of movement (or "freezing") anti-predator defence. These experiments tested larvae reared at two food ration levels in order to detect any effect of hunger on use of the anti-predator defence. The other factor that was examined was larval size. Four size groups of larvae, corresponding to the ages of five, eight, twelve, and fifteen weeks post-hatch, were tested in order to detect any effect of larval size on the use of the anti-predator defence.

Chapters Three to Five focus on the main anti-predator

defence larval fish employ once attacked, the escape response. This response consists of a period of rapid acceleration followed by burst swimming, and is used by larval fish to avoid capture by a variety of predators. Chapter Three reports measurements of the escape response performance of larval winter flounder Pleuronectes americanus ranging in size from newly hatched larvae (3.5 mm T.L.) to metamorphosed juveniles (10 mm T.L.). Emphasis in this chapter is on the changes in performance with development of the flounder. Chapter Four adds escape response performance measurements from four additional species, cod, Gadus morhua, capelin, Mallotus villosus, herring, Clupea harengus, and radiated shanny, Ulvaria subbifurcata. This chapter emphasizes the development of general models that describe the relationship between larval length and various aspects of escape response performance. Finally, in an attempt to partition some of the observed within-length variability in escape response performance, the effect of increased drag due to surface tension is tested to determine its effect on escape responses that occur very near the surface. The results of this investigation are reported in Chapter Five.

Chapter Two: Developmental changes in foraging-predator avoidance trade-offs in larval lumpfish (Cyclopterus lumpus)

Introduction

Predation can be broken down into the following sequence of events: encounter, attack, and capture of prey (modified from O'Brien 1979). Anti-predator defences that have evolved in prey organisms act to interrupt this sequence at different steps (Endler 1986, Sih 1987). For example, prey may decrease the probability of encounters with predators by hiding, by avoiding areas of high predator density, or by being cryptically coloured (Mittelbach 1981, Endler 1986, Main 1987, Sih 1987, Pierce 1988). Once an encounter has taken place, anti-predator defences that reduce the probability of attack become important, such as cessation of movement, unpalatibility, mimicry of organisms that are poisonous or unpalatable, or flight to a refuge (Endler 1986). Finally, once an attack is initiated by a predator, defences act to reduce the probability of capture. This last type of defence includes rapid evasive movements and flight, spines or plates that make handling difficult, and active fighting (Helfman 1986, Sih 1987). To assess the anti-predator capabilities of an organism properly, all three types of anti-predator defences should be evaluated.

In the last decade, an increasing number of predation

studies have used larval fish as prey, and many of these studies have examined only anti-predator defences that operate at the last step in the predation sequence, that is, defences that reduce the probability of capture given an attack by a predator (Miller et al. 1988, Fuiman 1989, Margulies 1989, Margulies 1990, but see Blaxter & Fuiman 1990). However, as pointed out by Endler (1986), defences that operate earlier in the sequence are more efficient, due to a greater probability that the predation sequence will be interrupted without injury to the prey. It seems likely that larval fish should possess and utilize anti-predator defences that reduce the probability of attack.

Probably the simplest anti-predator defence that reduces the probability of attack is cessation of movement, or freezing. Freezing behaviour has been reported in many groups of animals (Herzog & Burghardt 1974, Zaret 1980, Dill 1987, Sih 1987, Gerkema & Verhulst 1990) including fish (Brown 1984, Wootton 1984, Helfman 1986, Huntingford et al. 1988, Radabaugh 1989). Freezing is an effective anti-predator defence because most predators key on movement in order to detect potential prey (Ware 1973, O'Brien 1979, Stein 1979, Prejs 1987), or use movement as a criteria for deciding whether or not to attack an object they are presently inspecting (Orr 1989).

All anti-predator defences have costs associated with

them (Milinski & Heller 1978, Dill & Fraser 1984, Lima et al. 1985, Dill 1987, Sih 1987). Probably the most important cost associated with cessation of movement is reduced foraging. Since many larval fish possess limited energy stores, a reduction in time available for foraging could represent a substantial cost. Therefore, it would seem adaptive for larval fish to be able to assess the level of predation threat and respond so as to minimize associated costs. Studies have demonstrated this ability in juvenile and adult fish, where the prey varied their response to potential predators depending upon the preys' hunger level (Dill & Fraser 1984, Magnhagen 1988), behaviour of the predator (Sih 1987, Helfman 1989), and predator-prey size ratio (Stein & Magnuson 1976, Sih 1980, Sih 1984, Brown 1984, Werner & Gilliam 1984, Main 1987, Prejs 1987). Other studies have shown that prey fish not only spend less time foraging in the presence of a predator, but in addition the effectiveness of their foraging decreased (Milinski & Heller 1978, Milinski 1986, Fraser & Huntingford 1986). This effect has been attributed to increased vigilance by the prey.

In this study larval lumpfish, Cyclopterus lumpus, were tested to determine whether or not they would use the freezing response to reduce the probability of attack by a predator. Larval lumpfish possess an adhesive disk that

allows them to cling to surfaces (Brown 1986). This adaptation should enhance the effectiveness of a freezing response by anchoring a larva in place. Specifically, the objectives were to determine: 1) whether or not larval lumpfish use a freezing response, and thus trade-off foraging time, to reduce the probability of attack by a potential predator; 2) whether or not hunger level of the lumpfish affects their willingness to trade off foraging time against the threat of attack by a predator; and 3) whether or not the response of larval lumpfish to a predator changes with ontogeny.

Materials and Methods;

Fertilized lumpfish eggs were collected in the spring of 1988 by divers in Conception Bay, Newfoundland, Canada, and incubated in ambient seawater until hatch. Larvae were held in an 80 l aquarium and fed live Artemia nauplii once a day at a density of approximately 300 prey/l. In the laboratory, a peak in mortality of larval lumpfish often occurs at approximately three to four weeks post-hatch (J.A. Brown, unpublished data). Accordingly, this study was initiated after this peak had occurred. Approximately 400 four week old larvae were placed into each of four, 40 l aquaria. Artemia were added once a day to these four aquaria, at two prey density levels. Two aquaria received

enough Artemia to produce a prey density of ca 100 prey/l (low food treatment), while the other two aquaria received Artemia to produce a prey density of ca 250 prey/l (high food treatment). Testing began after the larvae had been exposed to the prey levels for one week.

The predators used in this study were three-spined sticklebacks, Gasterosteus aculeatus. Three sticklebacks (six cm total length) were maintained in separate compartments of a 40 l saltwater aquarium. In preliminary trials, hungry sticklebacks captured and consumed 5 week old lumpfish larvae. Because the intent of the study was to use sticklebacks as a predatory stimulus (but not to allow capture and consumption of lumpfish) sticklebacks were fed to satiation with capelin (Mallotus villosus) eggs prior to each experiment.

At week five post hatch, testing began. Two groups of 15 larvae were selected from each of the 4 holding aquaria, yielding 8 groups of 15 larvae (4 high food, 4 low food). Each group was then placed into a separate opaque plastic container (23 x 23 x 8 cm, containing ca 2 l of seawater) floating in a wet bench. Two test containers from each food level were randomly designated to receive a satiated predator during the experiment. After one hour of acclimation, one container, chosen at random, was gently moved into position under a suspended video camera. Each

experimental trial (i.e. each test container) began with one minute of videotaping with no food or predator present. This was followed by the introduction of food (250 Artemia/l for a high food container, 100 Artemia/l for a low food container) to the container, and, if designated, a satiated stickleback. Video recording continued for an additional 10 minutes, after which another test container was moved into position and the same procedure followed. Larvae were used in only one trial. One experiment was carried out at ca 3 week intervals at week five, eight, twelve, and fifteen post-hatch. The experiment was terminated after week fifteen because the larvae had increased in size to a point where they were no longer responding to the predator.

The behaviour of individual larvae was recorded from the video tapes with the aid of an event recorder. The variables extracted from the video were the time (s, between 0 and 120) spent clinging to a surface (i.e. freezing), and the number of bites each individual lumpfish performed (see Brown 1986 for definition of bites). The number of bites is a good indicator of feeding because capture success of lumpfish larvae feeding on Artemia nauplii is close to 100 % after the first two weeks post-hatch (Brown 1986). Lengths of each individual larva were obtained from the video tapes using an image analysis system.

The video recordings were subsampled to reduce viewing

time. To decide which time segment of the trial period would make up the sample, the entire trial for all four of the low food treatments in week five was viewed, and total time clinging and number of bites performed by each lumpfish was recorded. These variables exhibited the most variation during the initial three minutes of each trial, with no substantial changes evident during the last seven minutes. Consequently the two minute segment from minute five to minute seven was selected for analysis, thereby avoiding initial disturbance caused by predator introduction, and focusing on the final response of the larvae to the experimental situation.

The experimental design for each week was a 2 X 2 factorial experiment, with factors "food" (low or high) and "predator" (present or absent), with each food-predator combination replicated twice. Each experiment (week five, eight, twelve, and fifteen) was analyzed separately. In the analysis of time spent clinging, larval length was included as a covariable to allow examination of the effects of food and predator after length effects had been removed. This data set was analyzed using the GLM procedure in SAS (SAS 1988). The residuals were tested for normality using the Shapiro-Wilk statistic, and plots of the residuals versus the predicted values were examined to detect violations of the assumptions of independence and constant variance.

Consequently, time clinging was converted to a proportion of the total two minutes, and an arc-sine transformation performed. This procedure restored normality to the data from week five, eight, and twelve, but not the data from week fifteen. The departures from normality in week fifteen were due to a large number of observations at the boundaries (i.e. 0 and 120 seconds). Here a probit transformation was applied, which restored normality. The use of different transformations was acceptable because each week's data were analyzed separately.

In the analysis of the feeding data, the number of larvae that performed any bites was modelled as a binomial variate, with the number of trials being the total number of fish in that food-predator combination (for example, seven out of a total of thirty fish fed in the low food, no predator trial in week five). The model was fitted using a Generalized Linear Model (McCullagh & Nelder 1989) as implemented in the computer software GLIM (Payne 1987). To assess the potential for confounding length effects in this analysis, the lengths of the lumpfish were compared between each treatment combination (low food without predator, low food with predator, etc.) within each week, using the GLM procedure in SAS. Finally, to determine whether or not larval lumpfish were more vigilant when in the presence of a predator, a feeding rate/time swimming was calculated for

each fish that fed during the trial period by dividing the number of bites performed by that fish by the total number of seconds the fish was swimming (i.e. not clinging), and compared these rates using an anova (SAS procedure GLM). The level of significance for all statistical tests was set at 0.05.

Results:

When introduced into a test container, the stickleback would usually remain motionless for the first minute of the trial. During this time, the lumpfish would often perform what appeared to be a form of predator inspection (Wootton 1984), consisting of a group of lumpfish swimming to within ten cm of the stickleback, and remaining, sometimes clinging, all oriented with heads towards the predator. This behaviour was not repeated after the stickleback began to move about the container. After the initial inspection period, most larvae reacted to the approach of the predator (within ca ten cm), by clinging to the bottom or side of the container. Approximately 10 % of the lumpfish would quickly swim to a corner of the container and resume clinging immediately after the stickleback moved past. There were no obvious differences between experimental trials in the amount of time the predators spent swimming or staying motionless.

All of the interaction terms in the analysis of time clinging to a surface were not significant (Table 2.1). In the analysis of the number of fish feeding all of the interaction terms except that of week fifteen were not significant (Table 2.2). In week five post-hatch, presence of a predator significantly increased the time larval lumpfish spent clinging to a surface (Fig. 2.1; Table 2.1). In week eight, the categorical data (Fig. 2.1) show that the lumpfish spent more time clinging in the presence of a predator; however the predator term from the analysis only approaches significance at $p = 0.066$. Twelve week old lumpfish spent significantly more time clinging in the presence of a predator. By week fifteen, the presence of a predator clearly did not increase time clinging.

Analysis of the number of fish feeding (Table 2.2; Fig. 2.2) shows similar trends to the analysis of time clinging. Presence of a predator significantly decreased the proportion of fish feeding in weeks five, eight and twelve post-hatch. In addition, there was a significant food effect in week twelve, specifically (Fig. 2.2) more fish from the high food treatment than from the low food treatment fed during the experiment. The significant food-predator interaction term in week fifteen requires separate interpretation from the main effects. Examination of Figure 2.2 clearly illustrates this interaction in that the

presence of a predator did not seem to affect the number of larvae from the high food treatment that fed during the trial, whereas presence of a predator decreased the number of larvae feeding from the low food treatment. Finally, presence of a predator only significantly decreased feeding rate (bites per time swimming) for twelve week old larvae ($p=0.3341$, 0.7014, 0.0414, and 0.8782 for week five, eight, twelve and fifteen respectively). There were no significant differences in mean length (mm) of the lumpfish between treatments in any of the experiments ($p=0.1461$, 0.1408, 0.2660, and 0.1248 for week five, eight, twelve, and fifteen respectively).

Discussion:

In contrast to weeks five to twelve, fifteen week old larvae no longer significantly increased time spent clinging in the presence of a predator. One possible explanation for this is that by week fifteen, clinging has been dropped from the behavioural repertoire as an anti-predator defence. However, disturbances in holding aquaria usually elicit clinging by larval, juvenile and even adult lumpfish. Assuming that the cling behaviour was still available as an anti-predator defence, the fact that it was not used in the presence of a stickleback may indicate that these larvae had reached a size at which they were no longer vulnerable to

the predator. The mean size by week fifteen was 15.25 mm, which represents about 25 % of the total body length of the predator. Prejs (1987) considered forty percent of body length as an upper limit of prey size for most freshwater piscivorous teleosts, but considering that sticklebacks possess a relatively small mouth, the fifteen week old larvae were probably in no danger of being eaten.

An obvious, important cost associated with the freezing behaviour in larval lumpfish is reduced foraging. In this study, the increase in the time larvae spent clinging in the presence of a predator was accompanied by a significant decrease in the number of larvae feeding. In another study, Brown (1986) demonstrated that larval lumpfish are able to feed from the cling position; however prey levels in those experiments were an order of magnitude higher than those used in this study. In the present study, very few larvae were observed performing bites while clinging to a surface, even in the high food treatment. Therefore, increased time clinging by the lumpfish probably reduced their encounter rate with their prey, resulting in reduced opportunity to forage. Magnhagen (1988) and Prejs (1987) both found evidence of decreased foraging by small fish in the presence of predators, and both attributed this reduction in foraging to the increased danger of being detected by predators when moving.

Both theoretical (Mangel & Clark 1986, McNamara & Houston 1987) and experimental (Milinski 1986, Dill & Fraser 1984, Magnhagen 1988) studies indicate that an increased need for food should render an animal more willing to accept a greater risk in order to forage. However, the lumpfish tested in the present study did not show any effect of hunger level on their willingness to accept risk of attack in order to forage. In terms of actual foraging, the only significant food effect occurred in week twelve, where significantly fewer larvae from the low food treatment foraged than did larvae from the high food treatment, a result that is opposite to what one might have predicted. Similarly, fifteen week old larvae from the low food treatment responded to the presence of a predator by reducing their feeding, whereas the presence of a predator did not affect the larvae from the high food treatment. Possibly the differential in food levels used in this study was not sufficient to show this effect, as Brown (1986) found good survival when larval lumpfish were fed 100 prey/l. Support for this conclusion is that no significant differences in larval lengths were found between food treatments. Had starved versus fed groups been utilized, as in Magnhagen (1988), differences might have been observed.

The anti-predator defences displayed by larval lumpfish in this study would probably be effective in the natural

environment. Despite possessing a ventral adhesive disk, an adaptation that seems to favour an epibenthic existence, lumpfish spend the first year of life in the water column (Scott & Scott 1988). Daborn & Gregory (1983) found relatively high numbers of larval lumpfish up to 50 mm in length in the upper 0.5 m of the macrotidal Bay of Fundy, where they are often associated with masses of floating seaweed (Gregory & Daborn 1982). Association with floating seaweed would allow larval lumpfish to forage up in the plankton-rich pelagic zone, yet still be able to reduce the probability of attack by predators by clinging to the weed when a predator was detected. In areas that do not have large collections of floating seaweed, the larval lumpfish probably frequent areas closer to shore where they may seek refuge on the bottom or in and around attached seaweed.

Most pelagic larval fish do not possess a ventral adhesive disk as larval lumpfish do, however no complex morphological adaptations are required for a simple freezing response to the threat of a potential predator. In fact, the effectiveness of a freezing response by larval fish should be enhanced because of their small size and lack of pigmentation in many species. Blaxter & Fuiman (1990) suggested that reduced activity or movement might reduce the number of attacks on smaller pelagic larvae by fish predators, and Bailey & Yen (1983) proposed the same

strategy for pelagic hake larvae to reduce the number of attacks by a carnivorous marine copepod. Most of the research dealing with predation and larval fish has concentrated on the last step in the predation sequence, testing the ability of the larvae to escape actual attacks by predators. Further investigation is needed into anti-predator defences that other species of pelagic larval fish may use to reduce the probability of attacks by predators.

Table 2.1 Results of the analysis of variance for the effects of food level and predator presence on the time larval lumpfish spent clinging to a surface.

	Source	d.f. numerator	d.f. denominator	F-value	Pr. > F	
Week 5						
	Food	1	3.88	2.355	0.2019	
	Predator	1	4.08	20.020	0.0106	*
	Food * Pred	1	3.91	3.882	0.1218	
Week 8						
	Food	1	4.00	0.013	0.9144	
	Predator	1	4.04	6.209	0.0667	
	Food * Pred	1	4.01	0.842	0.4106	
Week 12						
	Food	1	3.98	0.333	0.5950	
	Predator	1	4.02	12.345	0.0244	*
	Food * Pred	1	3.97	0.000	0.9844	
Week 15						
	Food	1	4.02	0.763	0.4315	
	Predator	1	4.00	0.163	0.7066	
	Food * Pred	1	4.03	0.242	0.6485	

* indicates significance at .05 level

Note: Degrees of freedom were determined using Satterthwaite's approximation (e.g. Snedecor & Cochran 1980). Larval length was included as a covariate in all models.

Table 2.2 Results of the GLIM procedure on the effects of food level and predator presence on the number of larval lumpfish feeding.

	Terms	Observed Chi-square	D.f.	Prob.	Sig.
Week 5					
	Food	0.4677	1	0.49405	
	Predator	12.2400	1	0.00047	**
	Food X Pred	2.8360	1	0.09217	
Week 8					
	Food	1.1790	1	0.27756	
	Predator	14.4500	1	0.00014	**
	Food X Pred	0.1959	1	0.65805	
Week 12					
	Food	14.0500	1	0.00018	**
	Predator	31.3200	1	0.00000	**
	Food X Pred	2.8151	1	0.09338	
Week 15					
	Food	0.0000	1	1.00000	
	Predator	4.5950	1	0.03207	*
	Food X Pred	7.0376	1	0.00798	**

Note: * denotes significance at .05 level
** denotes significance at .01 level

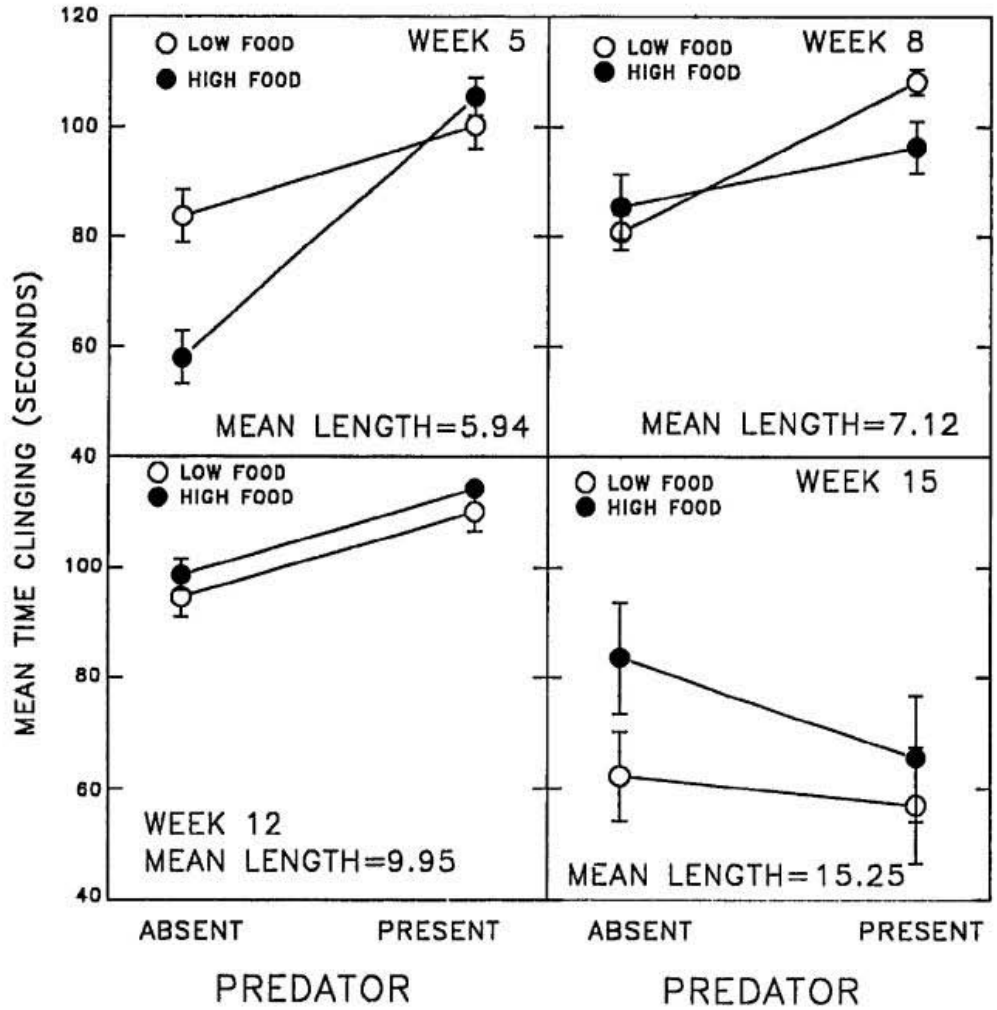


Figure 2.1 Mean (plus or minus 1 standard error) time larval lumpfish spent clinging in the presence and absence of a predator. Data are presented with respect to larval age in weeks. Each point represents a mean value for 15 larvae.

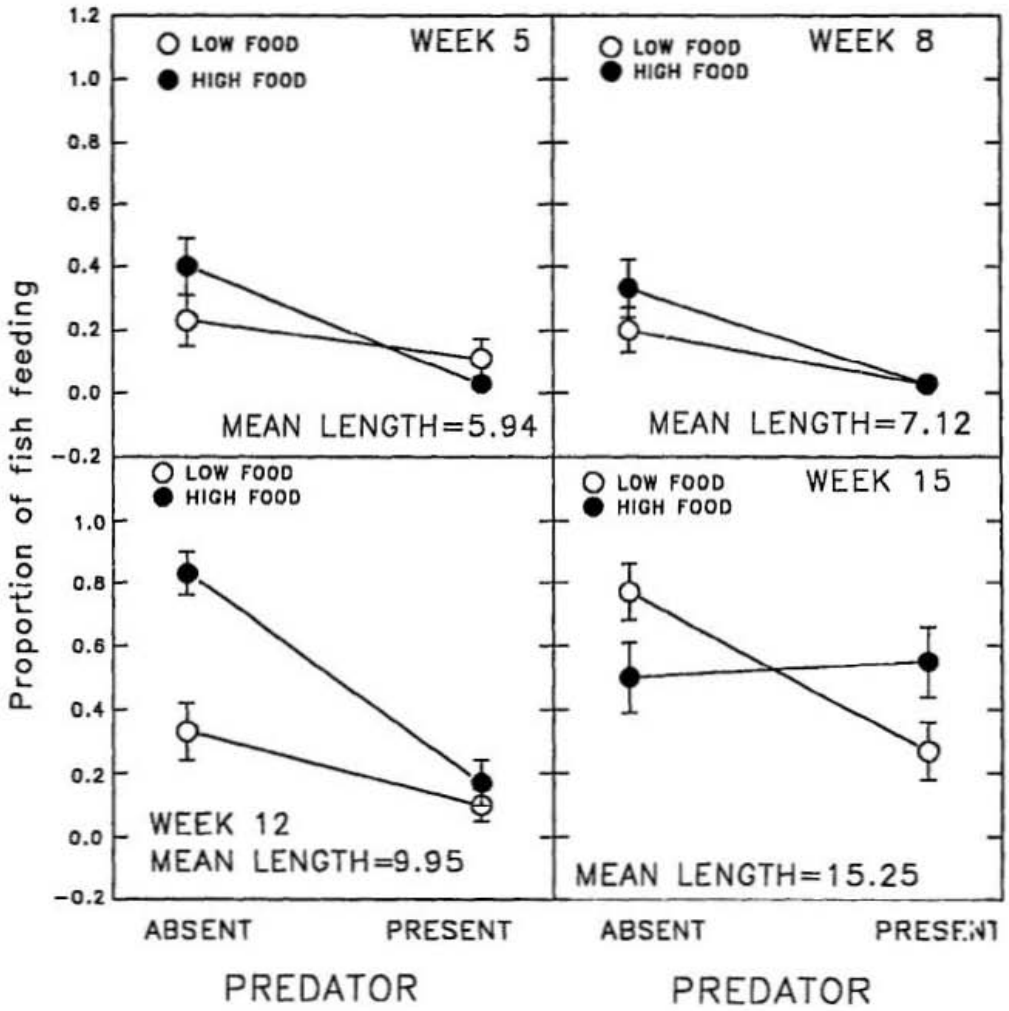


Figure 2.2 Proportion of the total number of larval lumpfish feeding in the presence and absence of a predator. Data are presented with respect to larval age in weeks.

Chapter Three: Developmental changes in the escape response of larval winter flounder (Pleuronectes americanus) from hatch through metamorphosis

Introduction:

Many marine fish are egg-scattering pelagic spawners which produce larvae that 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 (Bailey & Houde 1989). 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 or 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 1986b). 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). In the present study, the term is used to encompass the entire response (i.e. both the c-start and the period of burst swimming). This definition is consistent with that used by researchers studying other taxonomic groups (e.g. 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. 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, 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 (Blaxter 1988). In order to identify "windows" of vulnerability to predators, it is necessary to determine the quantitative and qualitative

changes in anti-predator defences that occur as larvae develop. If one is studying the escape response, it is important to know when the response becomes operative, and to know the relationship between this response and larval size. Webb (1981) and Webb & Corolla (1981) reported positive linear relationships between escape response speed parameters of Northern anchovy (Engraulis mordax) larvae and larval length. Miller et al. (1988) summarized data from nine 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 are 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 might logically expect such a reduction in performance 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 versus 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 40-70 days 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 one week to complete (Chambers & Leggett 1987). Considering the extensive reorganization during this transition phase, some reduction in efficiency of the escape response might be expected.

The objectives of this study were to measure and describe the escape response of larval winter flounder from hatch through metamorphosis, and compare the performance of larval winter flounder with that of other organisms found in the plankton, including other larval fish.

Materials and Methods:

Experimental animals: Winter flounder eggs were fertilized in the spring of 1990, and incubated in plastic petri dishes (Harmin & Crim 1992). Hatched larvae were maintained in 40 l aquaria containing static filtered seawater. Aquaria were partially immersed in a running ambient seawater wet bench to maintain temperature between 9 and 14° C. Because testing temperatures were at the upper end of the range to which flounder larvae would be exposed 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 plicatilus) at an approximate density of 10 prey/ml for the first 30 days post-hatch. From 30 days onward, newly-hatched brine shrimp nauplii (Artemia salina) were added at a density of approximately 1/ml. Larvae from different female-male pairings fertilized on different dates were used in the experiments.

Individual Calliopius laeviusculus, a common free-swimming epibenthic amphipod (DeBlois & Leggett 1991), were used to elicit the escape responses in the larval flounder. Calliopius are omnivorous, consuming algae, detritus, and live zooplankton (Hudon 1983). They are contact predators, grasping and biting prey they come in contact with.

Calliopius 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. The amphipods used in this experiment served as a predatory stimulus only, 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: Rearing of larvae and experimentation took place at the Ocean Sciences Centre, Logy Bay, Nfld. All experimental trials were carried out in a circular, 80 cm diameter, flat-bottomed plexiglas 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 (Panasonic 5010 digital SVHS 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: Between 10 and 15 larvae were

placed in a 20 cm diameter glass dish containing 1.5 cm seawater. This dish was floated in the water bath, restrained directly over the biconvex lens. After one minute, 2 amphipods were pipetted into the dish, and the video recording initiated. Video recording continued for 20 minutes, after which the larvae were pipetted from the dish, anaesthetized in MS-222, 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. Because individual larvae were not followed, there was potential for repeated measures of escape responses by the same larva. If repeated responses by an individual were very similar, a reduction in within-length variability could occur. This remote possibility was not considered important compared to the logistic difficulty of tracking individual larvae. 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 (on Panasonic AG-1960 SVHS video cassete recorder), by tracing the movements of the end of the snout of the larva at single field (1/60 s, 17 ms) intervals on an acetate overlay of the monitor. These tracings were then digitized, and the distance larvae travelled (mm) during each 1/60 s interval of the response was recorded. From these data, mean and maximum larval speed were calculated, as well as the distance travelled during the first 100 ms of the response, and the total distance travelled. Total length of the larva, total duration of the response, and the point in the response where the maximum speed occurred were also noted.

Scatterplots of all performance variables versus larval length appeared to describe linear relationships, with no violations of the assumptions of linear regressions. Linear regressions were performed on these four variables using the GLM procedure in SAS (SAS 1988). The residuals 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. The residuals generated by maximum speed were not normally distributed, therefore a log-10 transformation was performed. This transformation restored normality.

The mean escape speed/ larval length relationship

generated by the present study was compared to that proposed by Miller et al. (1988).

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. Fifty larval-amphipod interactions were used in the analyses (Table 3.1). Examination of the preserved larvae after the experiments showed that only the 50 day 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 began with a series of contractions which caused the larvae to bend alternately in a shape that resembled a "c" or reverse "c", when viewed from above. These first couple of contractions represented the c-start portion of the response. These initial contractions were followed by a period of burst swimming. 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 speed (cm/s) during each 1/60 s interval versus time elapsed since contact with the predator

exhibited considerable variation (Fig. 3.1A). Part of this variability can be attributed to the framing rate of the video system, which at 1/60 s intervals has been shown to be too slow to record details of the beginning of the escape response, the c-start (Eaton et al. 1977). In order to see general trends, the data were smoothed using a six-point running average, as in Fuiman (1986). General trends from the smoothed data (Fig. 3.1B) are that the maximum speeds occur in the first 400 ms, speed decreases with elapsed time, and there is an increase in maximum and mean speed as age increases. All subsequent statistical analyses were performed on raw data (without modification by the six-point running average).

The distance travelled during the first 100 ms of the response (Fig. 3.2, Table 3.2) was measured in order to examine the contribution of the c-start portion of the response. This performance measurement was linearly related to larval length. Mean speed during the escape response was also linearly related to total larval length (Fig. 3.3, Table 3.2). Newly hatched larvae attained mean escape speeds of 4 cm/s (11.4 body lengths per s, bl/s), while metamorphosed flounder performed at 12-14 cm/s (15.2 bl/s). The logarithm of maximum speed was linearly related to larval length, indicating a non-linear relationship of the untransformed data (Fig. 3.3, Table 3.2). Newly hatched

larvae reached maximum speeds of approximately 8 cm/s (22.8 bl/s), while metamorphosed flounder reached maximums of 20-22 cm/s (24.6 bl/s). Total distance travelled during the response was quite variable for any given length of larva, and although the regression was significant, it had little predictive value with an r^2 value of 0.23 (Fig. 3.4, Table 3.2). 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 significantly related to total larval length.

The slope of the mean escape speed larval length relationship was significantly different from the slope of the model proposed by Miller et al. (1988), $F=10.53$, $p < 0.0015$, $n=126$.

Discussion:

With respect to speed profiles within a response, the responses of larval flounder in this study are qualitatively similar to those described for larval Northern anchovy (Webb 1981, Webb & Corolla 1981). Detailed quantitative comparisons of the speed-elapsed time profiles from the present study 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 concentrated on the initial part of the response, the c-start, but did not follow the response beyond 300 ms in elapsed time. In contrast, the present study examined the entire response, using the behaviour of the larvae to signal the end of the response. Consequently, speed profiles (Fig. 3.1B) show less detail of the initial phase as compared to other studies, but cover the entire 600-700 ms of the response. Maximum speeds generally occurred in the first 200 ms of the response, whereas other studies show maximum speeds at 80-100 ms (Webb & Corolla 1981, Yin & Blaxter 1987). In the present study, escape speed decreased over the duration of the escape response (Fig. 3.1B). Yin & Blaxter (1987) show steady decreases in larval escape speed until 200 ms, the point where their observations end. Likewise, Webb & Corolla (1981) show speed decreasing from an early maximum, but then levelling out until 350 ms, the end of their observations. If examination of the present speed/elapsed time profiles were limited to 350 ms, 4 of the 6 profiles (Fig. 3.1B) level out or increase after the maximum speed. However, extended examination of the whole response indicates that mean escape speed decreases as the response proceeds.

The relationship between escape response performance and total larval length illustrates how the escape response

changes as larvae develop. In the present study, three performance variables (mean speed, distance travelled during the first 100 ms, and total distance travelled during the response) increased in a linear fashion with increasing larval length. Maximum speed also increased with increasing larval length, however it increased exponentially. Despite the extensive reorganization flounder undergo during metamorphosis, no obvious demarcations or breaks in the speed/larval length relationships were noted. Amphibians also go through extensive changes during metamorphosis (Werner 1986), and in two 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 three species of Australian tadpoles, attributed the increased vulnerability to predation to decreased swimming speed during the transition. Given this information from amphibians, one may expect some reduction in the escape response of flounder approaching metamorphosis. The data, however, do 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.

The relationships between performance and length are also useful when comparing results among studies. Two studies carried out with Northern anchovy larvae, Webb (1981) and Webb and Corolla (1981), are particularly useful for comparison with the present study. These studies comprehensively tested a broad size range of larvae, and calculated escape response performance- larval length relationships. Both the present study and Webb and Corolla (1981) report linear relationships between larval length and distance travelled during the first 100 ms of the response; examination of the two regression lines shows that they are not widely separated (Fig. 3.2). Webb and Corolla (1981) report that maximum speed increases linearly with increasing length. In the present study, maximum speed was found to increase exponentially with increasing larval length. This difference may be due to the fact that the larger flounder larvae had metamorphosed, and possibly their relatively high performance had a significant effect on the slope of the relationship. As was the case in the present study, Webb and Corolla (1981) report a positive linear relationship between total distance travelled and larval length. Webb (1981) found that this relationship could best be described as a power function. The level of variability observed from

the flounder data is such that the resultant regression, although significant, has little predictive value. Finally, in the present study the timing of the occurrence of maximum speed was not clearly related to larval length. Webb and Corolla (1981) also report that the time to maximum speed was unrelated to larval length.

All three studies report linear relationships between mean escape speed and larval length, although the slopes of the two Northern anchovy studies seem to be less than that of the flounder results (Fig. 3.5). Statistical comparison between the flounder data and the relationship proposed by Miller et al. (1988) indicates that the slope of the flounder model is significantly greater. The model proposed by Miller et al. (1988) includes 76 escape speeds measured from nine different species of larval fish, including eight measurements from European flounder (Platichthys flesus) and fifteen measurements from the plaice (Pleuronectes platessa). There are insufficient data to speculate on whether the observed higher rate of improvement by winter flounder is a species difference, a reflection of differing testing methodology, or possibly due to the fact that the larger flounder tested had metamorphosed.

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. It can be argued 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/sec, a larva with a maximum escape velocity of 7 cm/sec will probably be captured, regardless of whether this velocity represents 10 or 20 or 30 body lengths/sec). Young flounder larvae attain mean escape speeds comparable to those of slower zooplankters, such as rotifers and cladocerans (Fig. 3.6), however even metamorphosed flounder are slower than some cnidarians and copepods. In experiments using predatory freshwater cladocerans, Browman et al. (1989) found that copepods with escape speeds of 9 cm/sec could escape the predator, while Daphnia juveniles and adults with escape speeds of 2.5 and 3.2 cm/sec were captured at a significantly higher rate. Newly hatched flounder larvae with escape speeds of approximately 4 cm/sec would probably not survive many attacks by a marine equivalent of the predator used by Browman et al., however larger larvae may be able to survive a greater percentage of such attacks. With their relatively low mean escape speed, it is likely that winter flounder larvae, particularly newly-hatched larvae, are 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. Many predators that flounder larvae would be exposed to would be contact predators, attacking only 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 two 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 might 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). Bloater larvae have also 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). The present study did not address the timing of the response, but 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 having been reported for 6-8 mm carp larvae (Drost & van den Boogaart 1986) and 43 cm/s 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 6-30 cm/s) 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 the present 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 high mortality, however, because the attack rate of vertebrate predators has been shown to be lower on smaller larval fish (Pepin et al. 1987).

In conclusion, larval winter flounder responded to contact with amphipods by an escape response consisting of c-start acceleration followed by burst swimming. Mean speed, distance travelled during the first 100 ms, and total distance travelled increased linearly with total larval length. Maximum speed increased in a non-linear fashion with increasing larval length. The escape performance of larval flounder was found to be intermediate compared to other organisms found in the plankton, including other species of larval fish. With these mean escape speeds, flounder larvae would probably not survive many attacks by suction-feeding planktivorous fish. The escape response of larval flounder would, however, be effective against contact predators, and effectiveness would improve as the larvae get larger.

Table 3.1 Summary of ages and total lengths of larval winter flounder tested. Larvae tested originated from several batches

Age (days)	N	mean length (mm)	Std. err.	Temp	Date Tested
1	5	3.38	0.06	9.0	July 4
7	4	5.23	0.14	12.0	July 28
8	6	4.05	0.22	12.5	July 31
10	4	5.24	0.30	12.5	July 31
12	4	3.84	0.11	13.0	August 9
20	5	4.80	0.14	14.0	August 12
24	4	5.17	0.42	14.0	August 16
30	1	4.51	----	10.0	July 15
30	2	8.77	0.72	12.5	August 4
43	5	6.80	0.28	12.5	July 28
50	5	7.75	0.13	12.0	August 3
50	5	8.94	0.23	14.0	August 6

* N denotes the number of amphipod-larva interactions used in the analysis

Table 3.2 Regression equations for larval winter flounder escape response parameters versus larval length. All speed values are in cm/sec, total distance travelled is in cm, and larval length (L) is in mm.

Variable	Relationship	F-value	Sig.	R^2
Distance after 100 ms (D100), in cm	D100=0.162(L)-0.035	130.45	0.0001	0.7310
Mean Speed (U), cm/sec	U=0.707(L)-0.043	91.41	0.0001	0.6557
Maximum Speed (M), cm/sec	log(M)=0.065(L)+0.434	53.72	0.0001	0.5281
Total Distance (D), cm	D=0.311(L)+0.796	14.37	0.0004	0.2304

N = 50 in all analyses

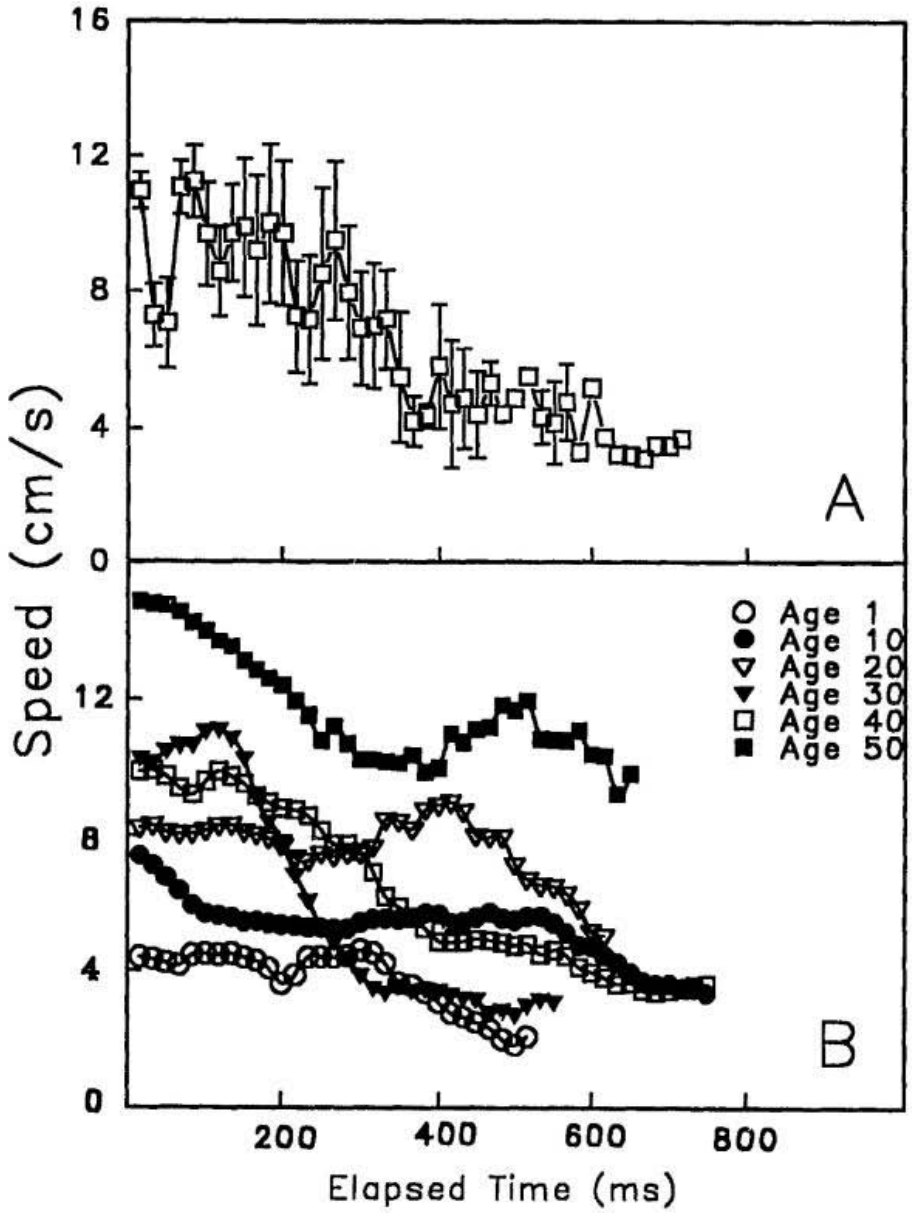


Figure 3.1 Larval winter flounder escape speed versus elapsed time from contact with amphipod. A. Mean escape speed of 40 day old larvae presented in order to demonstrate variation present in all six age classes plotted in B. Error bars represent standard error. B. Plots of six age-groups of flounder, after smoothing with a six-point running average. Ages in days post-hatch.

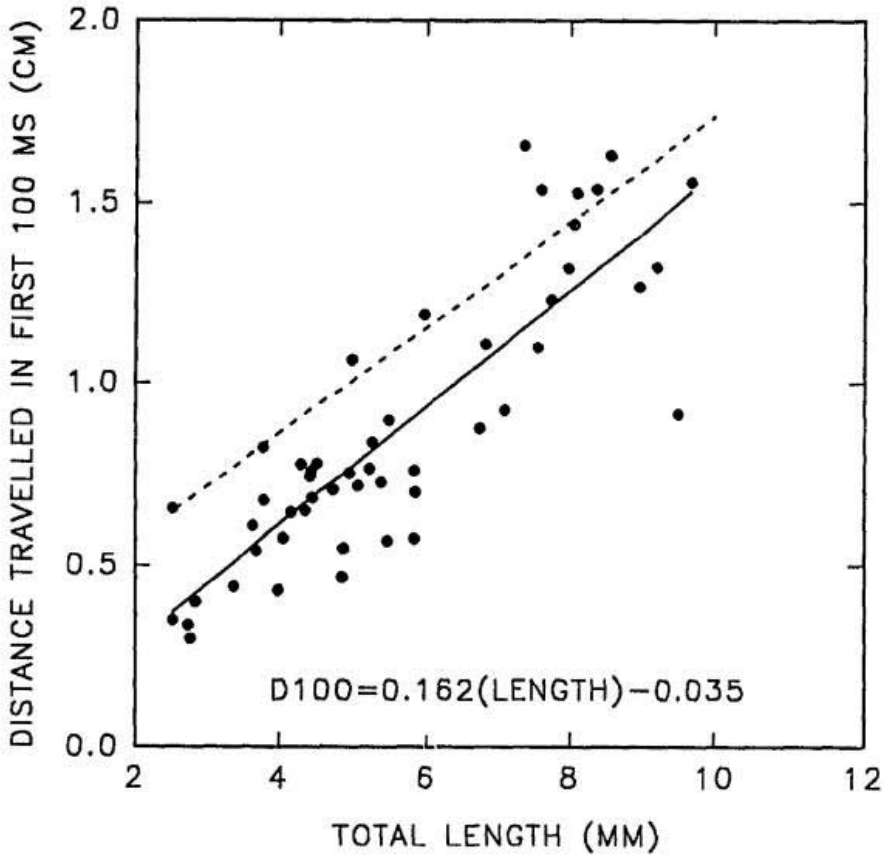


Figure 3.2 Distance travelled by flounder larvae during the first 100 ms of their escape responses, plotted against total larval length. r^2 = 0.73, n = 50. Filled circles and solid regression line represent flounder data. Dashed regression line represents similar measurements from Northern anchovy larvae, from Webb and Corolla (1981).

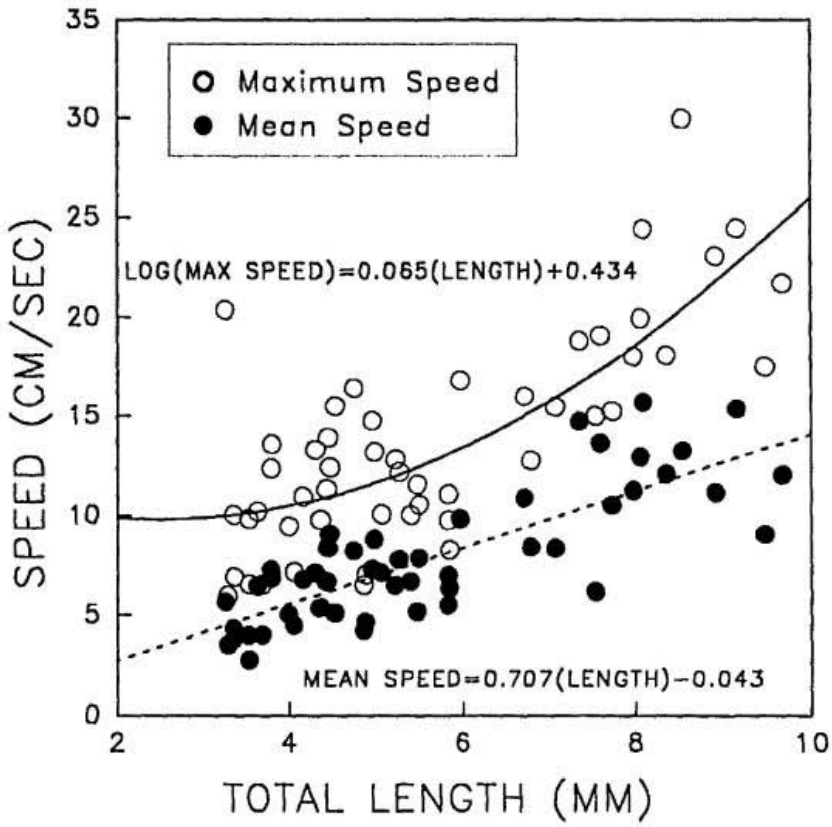


Figure 3.3 Mean and maximum speeds of flounder larvae during escape responses, plotted against total larval length. Each symbol represents the mean or maximum speed during one escape response. Hollow circles and solid regression line represents maximum speed (r^2=0.66), filled circles and dashed regression line represents mean speed (r^2=0.53). N=50 for both plots.

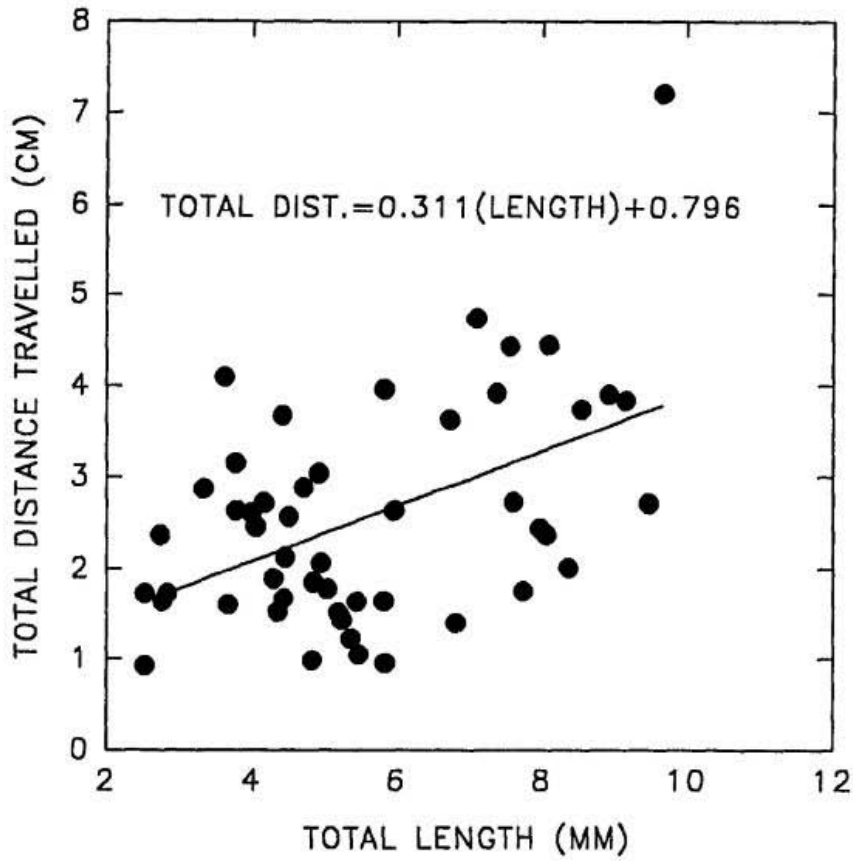


Figure 3.4 Total distance travelled during escape responses by flounder larvae, plotted against larval length. Each symbol represents the total distance travelled during one escape response. r^2 =0.23, n=50.

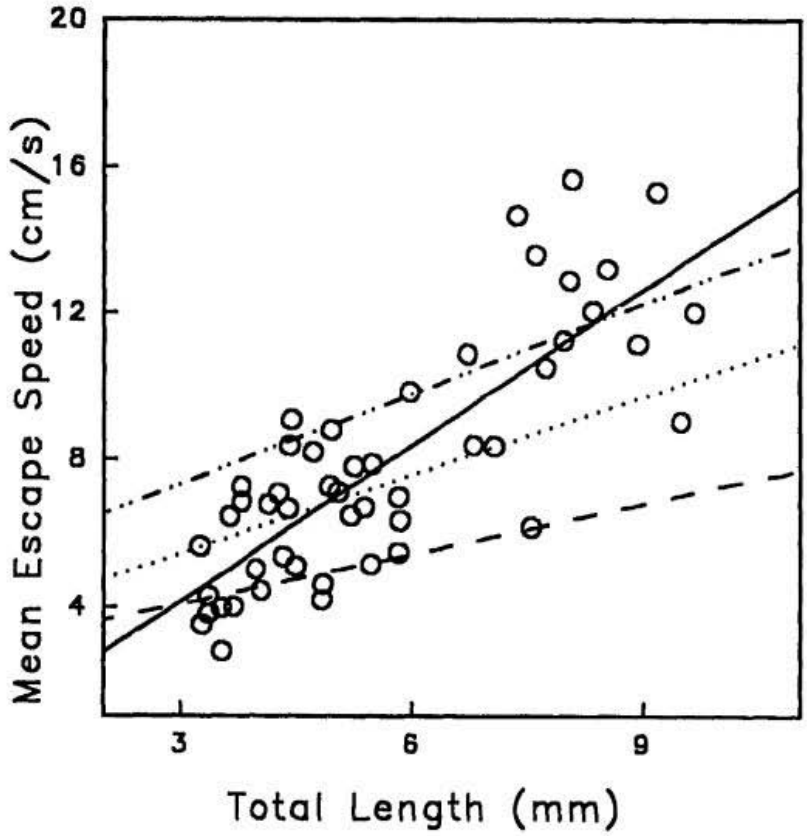
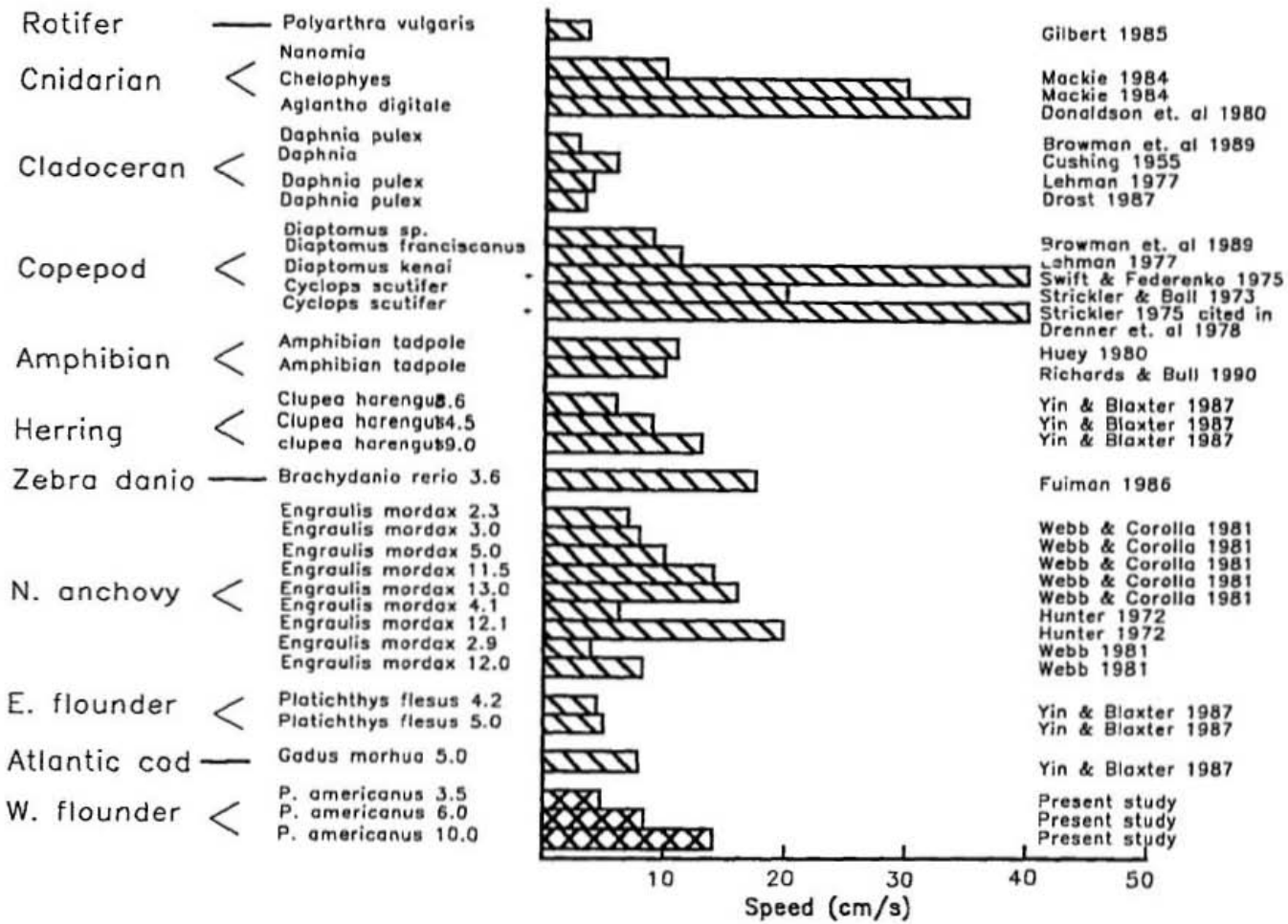


Figure 3.5 Plot of mean escape speed of larval flounder versus total larval length, with the addition of regression lines from similar relationships from other studies. Key as follows: Open circles and solid regression line, flounder data from the present study. Large dash: Webb (1981). Dotted line: Miller et al. (1988). Dash and dotted line: Webb and Corolla (1981).

Figure 3.6 Comparison of escape speeds of different taxanomic groups, including larval fish. Lengths of larval fish (in mm) are provided after species names.


Rotifer
Polyarthra vulgaris
Gilbert 1985
Cnidarian
Nanomia
Chelophyes
Aglantha digitale
Mackie 1984
Mackie 1984
Donaldson et. al 1980
Cladoceran
Daphnia pulex
Daphnia
Daphnia pulex
Daphnia pulex
Browman et. al 1989
Cushing 1955
Lehman 1977
Drost 1987
Copepod
Diaptomus sp.
Diaptomus franciscanus
Diaptomus kenai
Cyclops scutifer
Cyclops scutifer
Browman et. al 1989
Lehman 1977
Swift & Federenko 1975
Strickler & Ball 1973
Strickler 1975 cited in Drenner et. al 1978
Amphibian
Amphibian tadpole
Amphibian tadpole
Huey 1980
Richards & Bull 1990
Herring
Clupea harengus 8.6
Clupea harengus 4.5
clupea harengus 9.0
Yin & Blaxter 1987
Yin & Blaxter 1987
Yin & Blaxter 1987
Zebra danio
Brachydanio rerio 3.6
Fuiman 1986
N. anchovy
Engraulis mordax 2.3
Engraulis mordax 3.0
Engraulis mordax 5.0
Engraulis mordax 11.5
Engraulis mordax 13.0
Engraulis mordax 4.1
Engraulis mordax 12.1
Engraulis mordax 2.9
Engraulis mordax 12.0
Webb & Corolla 1981
Webb & Corolla 1981
Webb & Corolla 1981
Webb & Corolla 1981
Webb & Corolla 1981
Hunter 1972
Hunter 1972
Webb 1981
Webb 1981
E. flounder
Platichthys flesus 4.2
Platichthys flesus 5.0
Yin & Blaxter 1987
Yin & Blaxter 1987
Atlantic cod
Gadus morhua 5.0
Yin & Blaxter 1987
W. flounder
P. americanus 3.5
P. americanus 6.0
P. americanus 10.0
Present study
Present study
Present study
10
20
30
40
50
Speed (cm/s)

Chapter Four: Developmental changes in the escape response performance of five species of marine larval fish

Introduction:

Predation is an important cause of mortality in larval fish (Bailey & Yen 1983, Batty 1989, Blaxter & Fuiman 1990), resulting in strong selection for anti-predator defences. One anti-predator defence that has been demonstrated in many species of larval fish is some form of escape response, employing rapid acceleration and burst swimming (Webb & 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 & Batty 1984, McGovern & Olney 1988, Seale & 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 & Houde 1989, Blaxter 1986, Miller et al. 1988, Pepin 1991). Earlier studies (Bailey & Batty 1984, Blaxter 1986, Yin & Blaxter 1987) proposed a linear relationship between larval length and burst swimming speed, an important component of the escape response. Miller et al. (1988) formalized the relationship by using published values of burst swimming speed from nine species of larval

fish to generate a quantitative relationship between larval size and burst swimming speed. However, Miller at al. (1988) also point 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 (e.g. escape response performance of larval Northern anchovy Engraulis mordax in Webb 1981 versus Webb & Corolla 1981). 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) originates from two species of clupeoid fishes, Northern anchovy and Atlantic herring (Clupea harengus). Body flexibility and morphology have been shown to affect fast-start acceleration rate (Webb 1986a, Harper & Blake 1990) and general fast-start performance (Domenici & 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.

Chapter Three represents a first step in evaluating Miller et al.'s model. Measurements were made of the escape response performance of larval winter flounder (Pleuronectes americanus) from hatch through metamorphosis. The resulting mean escape speed-larval length relationship for winter flounder was compared to 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-dependant 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 (Pleuronectes americanus), 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 a deeper body 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:

1. To measure, using the same protocol, the escape response parameters for five species of larval fish.

2. To develop a model or models to describe the relationship between escape response performance and larval length.

3. 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 & Blake 1991, Harper & Blake 1990). In the present study, an escape response is defined as consisting of the three kinematic stages described by Weihs (1973). In stage one, the musculature on one side of the body contracts, and the larva assumes a "c" or reverse "c" shape. Stage two 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 a period of continuous high speed swimming, also called burst swimming.

Experimental animals: Fertilized eggs from Atlantic cod were collected from broodstock tanks. The eggs were

incubated in mesh sided baskets in a running ambient seawater wetbench. 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 to maintain 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 30 days onward, newly hatched brine shrimp nauplii (Artemia salina) were added at a density of approximately 1/ml. The flounder larvae were reared similarly to cod.

Fertilized eggs of the other three species tested were collected from the wild. Separate masses of radiated shanny eggs were brought into the lab, incubated, and the resultant larvae reared in a fashion similar to that used for cod, with the exception that shanny larvae were fed Artemia from hatch onwards. Batches of beach substrate containing fertilized capelin eggs, and vegetation with attached herring eggs were brought into the lab, incubated in meshed baskets as above, and reared in the same manner as were flounder and cod.

Calliopius laeviusculus, a common free-swimming epibenthic amphipod (DeBlois & Leggett 1991), was used to elicit the escape responses in the larvae. Calliopius 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 & Yen 1983, Bailey & 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.

Test Chamber: All experimental trials were carried out in a 20 cm diameter glass dish ("experimental chamber") containing 1.5 cm seawater. This dish was floated in a circular 80 cm diameter, flat-bottomed plexiglas 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 (Panasonic 5010 digital SVHS video camera). Low light levels (less than 10 lux 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 restrained directly over the biconvex lens.

Experimental protocol: Between ten and fifteen larvae (sample sizes were smaller with some of the oldest larvae due to reduced availability) were placed in the experimental chamber for one minute, after which two amphipods were pipetted into the dish and the video recording initiated. Video recording continued for 20 minutes. All video recording and playback was carried out on a Panasonic AG-1960 SVHS video cassette 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, leaving 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 measurements (Harper & Blake 1989).

The location of the end of the snout of each larva was digitized to measure the distance larvae travelled (mm) during each 1/60 s 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:

- the distance travelled after 17 ms, which represents displacement resulting from the first c-shaped contraction of the larva.
- distance travelled after 100 ms, which represents the contribution of the fast-start portion of the response. Webb and Corolla (1981) report that maximum speed was attained by larval Northern anchovy (Engraulis mordax) after 100 ms of an escape response, after which speed decreased.
- mean speed for the entire response, which is indicative of the larva's ability to escape a chasing predator, such as some juvenile fish (Webb & Corolla 1981) and some invertebrates.
- maximum speed during the response, which may be important in swimming out of the flow field of a suctorial predator (Drost & van den Boogaart 1986).
- 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 GLM procedure (SAS 1988). The observations for each species were weighted depending on sample size. The residuals 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 dependant variable was $\log_{10}$ transformed. This transformation restored normality.

Finally, the data on mean escape speed and larval length were combined with the corresponding data from Miller et al. (1988), and an analysis of covariance (Zar 1984) was used to test for significant differences between the collections.

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. 4.1), and a regression that is

of little predictive value (r-square of 0.22, Table 4.1). However, the regression is significant, and examination of the plotted data indicates that there is improvement in this performance measurement 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 cm and total length in mm.

Measurements of the distance travelled during the first 100 ms of the response, representing the fast-start portion of the response, were unique in that they did not require log_{10} transformation in order to produce normal residuals. The variation for this measurement was considerably less than that observed for displacement after 17 ms (Fig. 4.2, Table 4.1). The 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 tested. The formula for the best-fit regression model is:

Distance after 100 ms = 0.1405(Length) + 0.1133

with distance in cm and total length in mm.

The mean speed during the entire response was found to increase with larval length (Fig. 4.3, Table 4.1). The formula for the best-fit regression model is:

Log_{10}(Mean speed) = 0.0591(Length) + 0.5624

with speed in cm/s and total length in mm.

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 ($n=460$, $F=42.93$, $p<.0001$). Examination of a plot of both relationships with accompanying data points (Fig. 4.4) shows that the present relationship generally predicts greater mean escape speeds than does the relationship reported by Miller et al. (1988).

The regression of maximum speed versus larval length (Fig. 4.5, Table 4.1) shows 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:

$\text{Log}_{10}(\text{Maximum speed}) = 0.0538(\text{Length}) + 0.8258$

with speed in cm/s and total length in mm.

The data for total distance travelled during the escape response (Fig. 4.6, Table 4.1) 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:

$\text{Log}_{10}(\text{Total distance}) = 0.0504(\text{Length}) + 0.1242$

with distance in cm and total length in mm.

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 value, beyond showing that this measurement improves with increasing larval length. Webb and Corolla (1981) also report a relatively low r^2 value (0.31, versus 0.19 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 cite measurement error associated with the very small distances travelled as a probable cause for the variability around the Y-axis. In the present study the framing rate of the video system (60 Hz, as compared to 250 Hz in Webb and Corolla) also contributed to the low r^2. It produced an image 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 introducing variation about the regression line. Despite the high

variability, the resultant regression is not dissimilar in magnitude 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 in order 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 similar to that reported by Webb and Corolla (1981) for electrically stimulated Northern anchovy larvae escape responses, 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. Mean speed is also useful for comparing experimental results between researchers because it is often reported in the literature. One other regression of mean escape speed versus larval length is superimposed on the plot from the present study (Fig. 4.3). This regression was calculated from data reported by Bailey (1984) for mean escape speed of five species of larval fish (excluding one speed measurement for 21.1 mm larval herring). This study was appropriate for comparison with the present study

because both sets of experiments tested a number of 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 slopes appear 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 by the amphipods in the present study.

Comparison with the mean burst speed-larval length relationship suggested by Miller et al. (1988) (Fig. 4.4) yielded significant differences in slopes. The slope of the relationship suggested by Miller et al. (1988) appears to be reduced (i.e. the regression line "flattened") by the influence of speeds corresponding to larvae greater than 12 mm in length. The two sets of data appear more similar if one only considers speed measurements from larvae less than 12 mm. It is inappropriate to extrapolate the results of the present study and predict mean escape speeds for a length range of larvae not used to generate the model (Zar 1974). Possibly length-specific mean larval escape speeds exhibit a demarkation or break after larval lengths of approximately 12 mm. For larvae less than 12 mm in length, however, 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 summarised by Miller et al. (1988), a problem they acknowledge in their synthesis. The model for length-specific mean escape speed from the present study is recommended over that from Miller et al. (1988) because the present study used the same protocol to test all five species. The examination, revision, and refinement of models such as those presented by Miller et al. (1988) represent the natural evolution of conceptual frameworks.

Maximum speed during the escape response is important in allowing larvae to escape attacks by lunging predators (Webb & Corolla 1981). Within the size range tested, maximum speed clearly increases with increasing larval length. In a similar fashion to the distance travelled during the first 17 ms of the response, measurement of maximum speed had the potential to be affected by the slow framing rate of the video system. Suprisingly, the resultant model is very similar to that recorded using a much higher framing rate by Webb and Corolla (1981) for Northern anchovy.

In contrast to maximum speed, total distance travelled, because it is measured over the entire response, has the least potential for error due to measurements of small distances and framing rate. Despite this condition, this

measurement displayed considerable variation, and the resultant model, although significant, is of little predictive value.

The escape response is considered to be somewhat stereotyped, yet all performance variables measured displayed considerable variability. There are several potential contributors 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 & Blake 1990). It is possible that larval fish also use different types of fast starts. Another potential source of variation in performance within a larval size range is the effect of the air/water interface on escape performance. For adult trout, the drag during a fast start can increase by as much as a factor of five if the fish is at or near the air/water interface (Webb et al. 1991). Many of the escape responses observed in the present study involved production of surface waves, indicative of their occurring at the air/water interface. The potentially

reduced performance of these escape responses could result in additional variability for the general relationship. This possibility will be explored in Chapter Five. Finally, some of the observed variability is probably due to differences among species.

Obviously any suggested general relationship will not describe all species equally well. What one seeks is a framework that is as universally applicable as possible. If the data consistently show considerable variability, as was the case for the distance travelled after 17 ms and total distance travelled, the relationship is only useful in testing the nature of the relationship (in both of these cases, for example, there was a statistically significant improvement in the performance with increasing larval length). The models developed for the other three parameters have some predictive value, and may be useful in generating hypotheses or constructing predator-prey simulation models.

A positive linear relationship was determined between the logarithm of escape speed parameters and larval length, yet researchers have found that the relationship between vulnerability to various predators and larval length is usually non-linear (for examples see Bailey & Houde 1989). In some cases, vulnerability has even been shown to increase with increasing larval length (Litvak & Leggett 1992, Pepin

et al. 1992). How may a linear improvement in escape speed parameters be reconciled with a non-linear decrease (or in some cases even an increase) in vulnerability? The answer lies in making the distinction between vulnerability, and the component probabilities that combine to equal gross vulnerability.

Vulnerability may be represented as follows (O'Brien 1979):

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

Similarly, it is overly simplistic to expect that,

based on the results of the present study, P(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 the P(C) decreases with increasing larval length (Lillelund & Lasker 1971, Folkvord & Hunter 1986, Butler & Pickett 1988, Leucke et al. 1990, Litvak & 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, or more important than, the escape velocity (Webb 1976, Webb 1981, Eaton & Didomenico 1986, Fuiman 1986, Fuiman 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 non-linear decreases in P(C) with increasing larval size. This was elegantly demonstrated by Fuiman (1989) and Blaxter & 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 of 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(C) of a larval fish is detected, that decrease should not be attributed to improved swimming ability. Instead, researchers should look to sensory systems or neural pathways for the cause of abrupt improvements.

Table 4.1 Results of the regression analyses of measurements of larval escape performance versus total larval length (mm). N=384 for all analyses.

Distance travelled during the first 17 ms of response

Source	DF	S.S.	M.S.	F-value	Sig.
Length	1	13.4557	13.4557	109.54	0.0001
Error	382	46.9236	0.1228		
r^2=0.22					

Distance travelled during the first 100 ms of response

Source	DF	S.S.	M.S.	F-value	Sig.
Length	1	130.3366	130.3366	498.00	0.0001
Error	382	99.9770	0.2617		
r^2=0.57					

Mean escape speed during entire response

Source	DF	S.S.	M.S.	F-value	Sig.
Length	1	23.1106	23.1106	509.27	0.0001
Error	382	17.3349	0.0454		
r^2=0.57					

Maximum escape speed during entire response

Source	DF	S.S.	M.S.	F-value	Sig.
Length	1	19.1304	19.1304	342.56	0.0001
Error	382	21.3329	0.0558		
r^2=0.47					

Total distance travelled during entire response

Source	DF	S.S.	M.S.	F-value	Sig.
Length	1	16.7655	16.7655	84.26	0.0001
Error	382	76.0057	0.1990		
r^2=0.18					

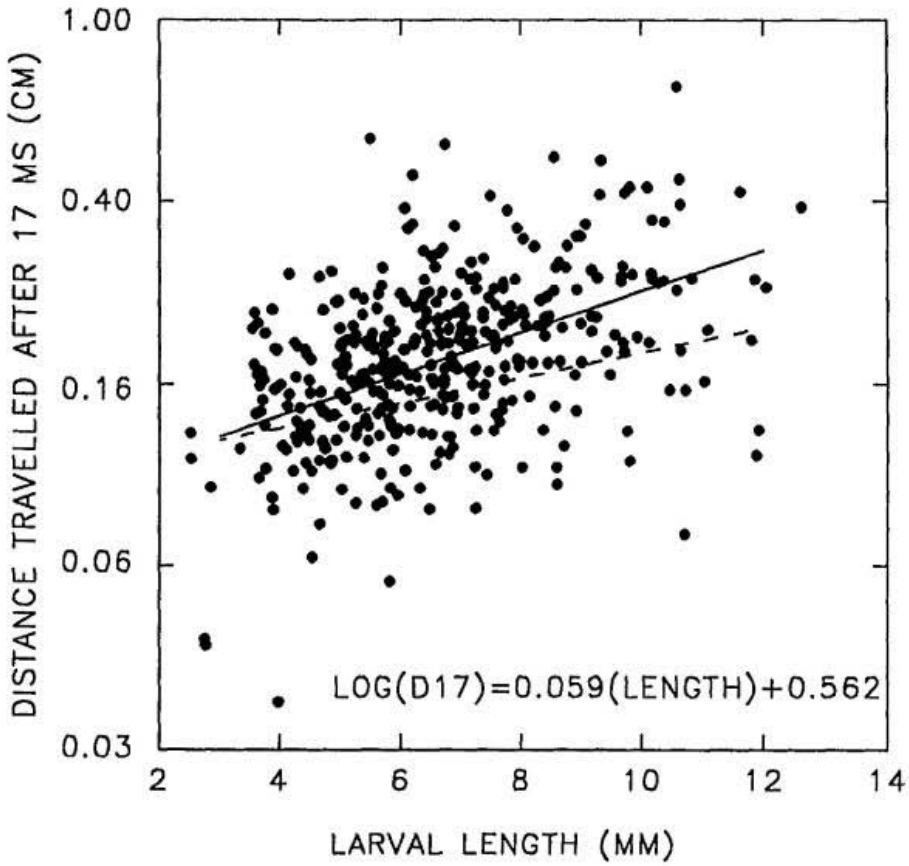


Figure 4.1. Distance travelled (in cm) during the first 17 ms of larval escape responses versus total larval length (in mm). Solid line represents least squares regression line (r^2=0.22, n=384. Dashed line is the regression line of similar relationship from Webb and Corolla (1981). Note Y-axis is Log_{10} scaled.

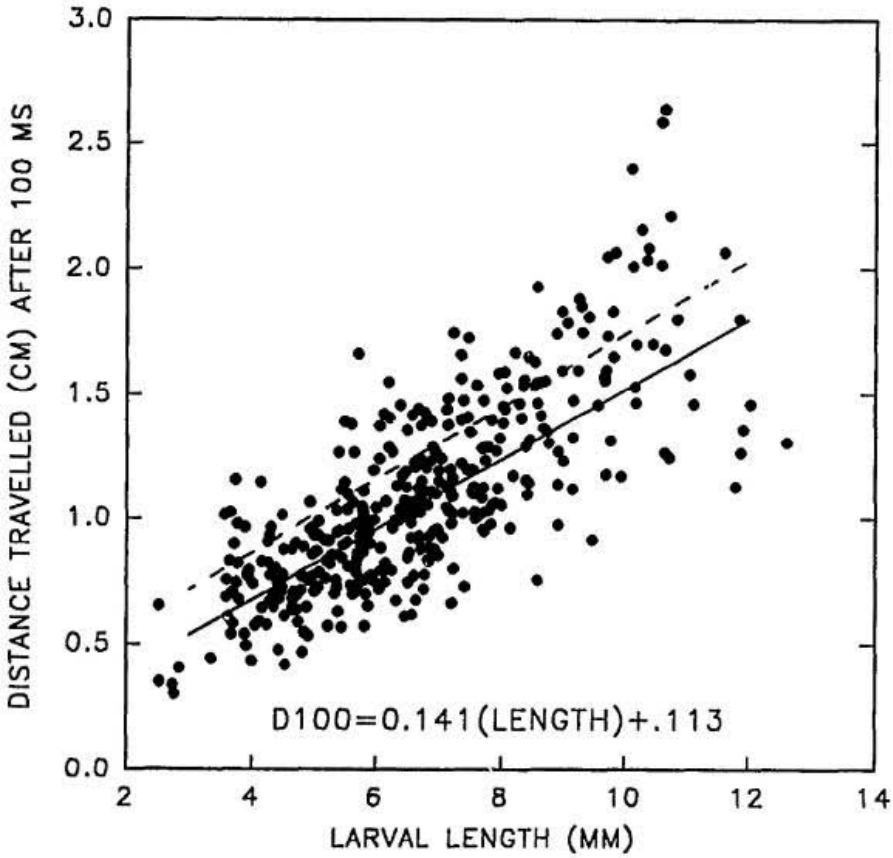


Figure 4.2. Distance travelled (in cm) during the first 100 ms of larval escape responses versus total larval length (in mm). Solid line represents least squares regression line. (r^2=0.57, n=384). Dashed line is the regression line of similar relationship from Webb and Corolla (1981).

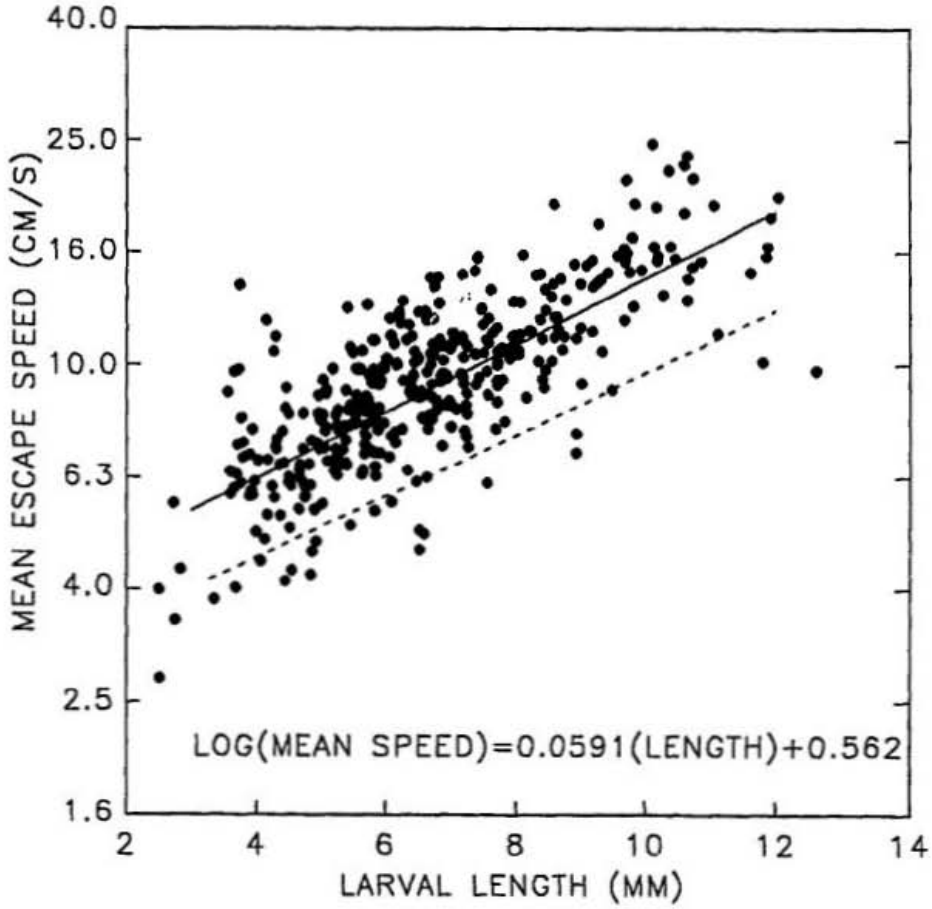


Figure 4.3. Mean escape speed (in cm/s) during the entire larval escape response versus total larval length (in mm). Solid line represents least squares regression line (r^2=0.56, n=384). Dashed line is the regression line of similar relationship calculated from Bailey (1984). Note Y-axis is Log_{10} scaled.

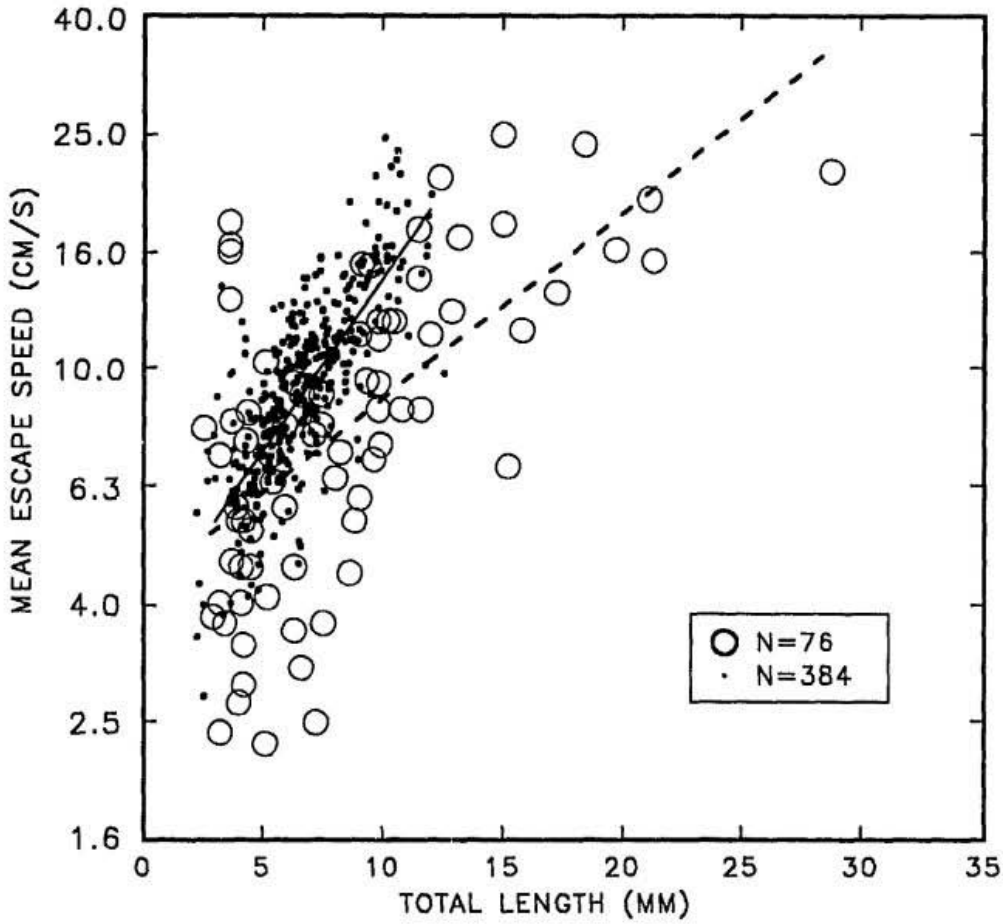


Figure 4.4. Mean escape speed (in cm/s) during the entire larval escape response versus total larval length (in mm) for the present study (filled dots, solid regression line) and for Miller et al. (1988)(open circles, dashed regression line). Note Y-axis is Log_{10} scaled.

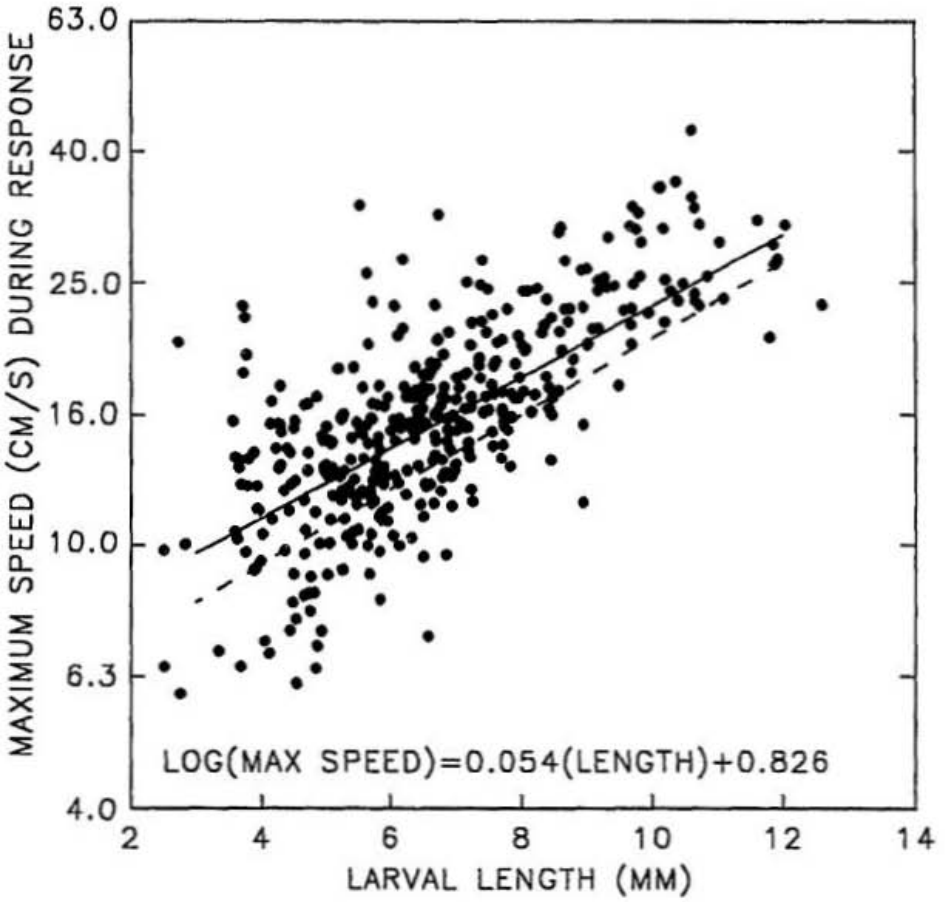


Figure 4.5. Maximum escape speed (in cm/s) during the entire larval escape response versus total larval length (in mm). Solid line represents least squares regression line (r^2=0.47, n=384). Dashed line is the regression line of similar relationship from Webb and Corolla (1981). Note Y-axis is Log_{10} scaled.

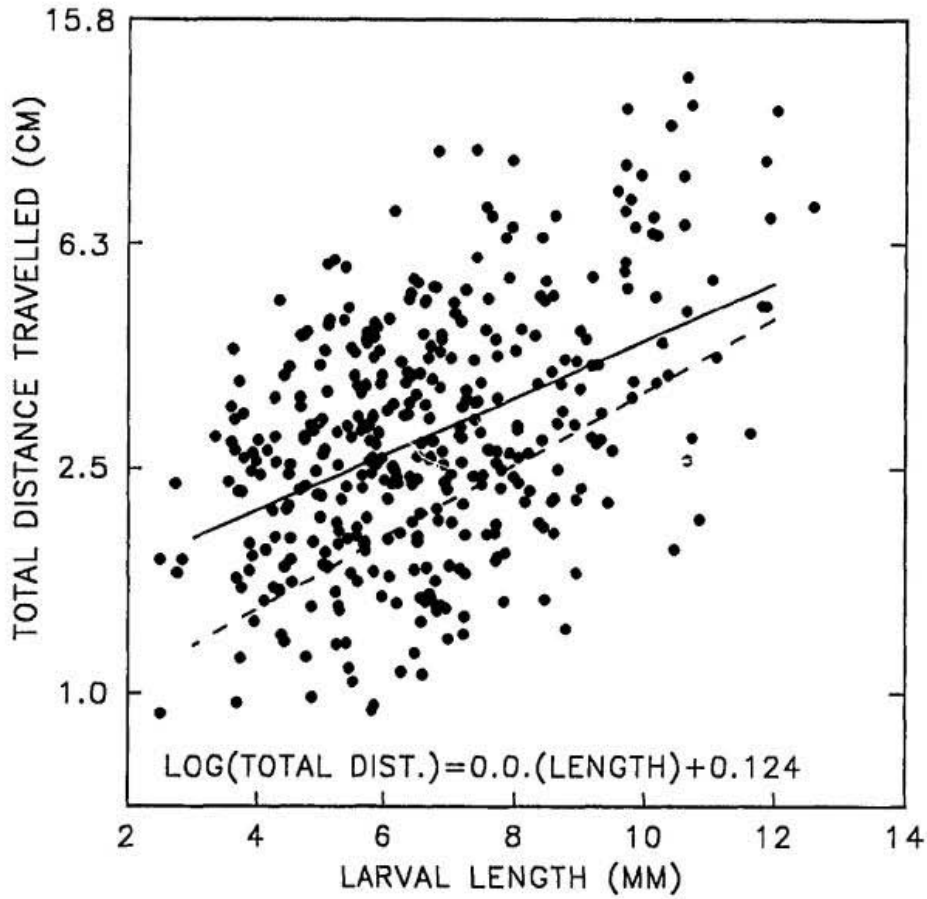


Figure 4.6. Total distance travelled (in cm) during the entire larval escape response versus total larval length (in mm). Solid line represents least squares regression line (r^2=0.18, n=384). Dashed line is the regression line of similar relationship from Webb and Corolla (1981). Note Y-axis is Log_{10} scaled.

Chapter Five: Effects of surface tension on the escape response performance of five species of marine larval fish

Introduction:

Many species of larval fish spend significant amounts of time near the air-water interface. Some species are positively buoyant at hatch (Blaxter & Ehrlich 1974, Blaxter 1986) and remain at the surface for the first few days of life. Other species must go to the surface either occasionally (Sclafani et al. 1993) or daily (Blaxter 1988) to inflate their swim bladders. Finally, larvae in poor condition tend to be positively buoyant (Blaxter & Ehrlich 1974, Neilson et al. 1986). Proximity to the air-water interface has implications with respect to nutrition and threat of detection by predators, but in particular may have a profound effect on larval fish locomotion.

Organisms that swim at or near the surface are subjected to more drag than are organisms that swim at greater depths. The additional drag at the surface is attributed to the energy lost in the production of surface waves (Webb et al. 1991). Hertel (1966) found five times as much drag on an object moving just below the surface as compared to an object moving at three body-depths below the surface. Williams and Kooyman (1985) measured drag on towed harbour seals (Phoca vitulina) at the surface and at depth,

and found the surface-towed seals experienced 2.5 times the drag of the deeper seals. Webb et al. (1991) investigated the effect of proximity to the surface on fast start performance by adult rainbow trout (Oncorhynchus mykiss). They found a significant reduction in performance as depth decreased, and these effects were most evident very early in the fast-starts (i.e. during the first 70 ms). Results from the above-mentioned studies suggest that larval fish swimming at the surface should experience additional drag compared to larvae swimming at greater depth.

The escape response which larval fish use to escape from predators begins with a fast start similar to that studied by Webb et al. (1991). This fast start is generally followed by a period of burst swimming. Speed and distance travelled during the escape response determines its effectiveness. Therefore, if the response takes place very near the surface, thereby subjecting the larva to additional drag, the potential exists for reduced escape performance. This reduced performance could be expressed as slower speeds, and less total distance travelled during an escape response. The following analysis was performed to determine whether or not proximity to the surface reduced the escape-response performance of larval fish.

Materials and Methods:

Video recordings of 384 escape responses by larval fish were reviewed. These escape responses were experimentally elicited from five species of larval fish: winter flounder (Pleuronectes americanus), Atlantic cod (Gadus morhua), Atlantic herring (Clupea harengus), capelin (Mallotus villosus), and radiated shanny (Ulvaria subbifurcata). The amphipod Calliopius laeviusculus was used as a predator stimulus. Contact by the continually swimming amphipods elicited the escape responses in the larval fish (for more details of testing protocol see Chapter Four).

Escape responses were classified into two groups according to whether or not surface waves were produced by the larva during the response. If surface waves were evident, the response was classified as having occurred at the surface. If no surface waves were evident, the response was classified as having occurred at depth. The amphipods used as the predatory stimulus also created surface waves, which sometimes obscured the path of the larva. Omission of those responses in which there was interference from turbulence by the amphipods left 306 responses for subsequent analysis, 19 by herring, 35 by cod, 40 by flounder, 81 by capelin, and 131 by shanny larvae.

The two groups of escape responses, those with and those without surface waves, were then compared using the

following five measurements: (1) Distance travelled during the first 17 ms of the response. This distance represents the very beginning of the fast-start portion of the escape. It is thought to be important in escaping predators such as suction-feeding fish. (2) Distance travelled during the first 100 ms of the response. This distance represents average speed during the fast-start portion of the escape response. (3) Mean speed during the entire escape response, which is important in the event of a chase by a predator after an initial attack. (4) Maximum speed during the response, which can also be important during a chase by a predator, or if the larva is attempting to swim out of a flow field caused by a suctorial predator. (5) Total distance travelled during the entire escape response which is important in removing a larva from the perceptual field of an attacking predator in the event of a missed attack.

The first step in each analysis was to calculate the performance variable-larval length relationship for the two sets of data, responses at the surface and responses at depth. These two regressions were then compared using an analysis of covariance (PROC GLM, SAS 1988). If there was insufficient evidence to reject the null hypothesis that the two slopes were equal, an analysis of covariance was performed to determine whether there was a significant effect of depth on the particular performance measurement.

Residuals were tested for normality, and plots of predicted values versus residuals were examined for departure from the assumptions of linearity and independence of error terms (Anderson et. al 1980). All measurement values required $\log_{10}$ transformation. Results indicated considerable variation within depth groupings, suggesting the possibility of variation among species. Consequently, two of the species of larval fish for which there were sufficient numbers of recorded responses, capelin and radiated shanny, were also tested separately from the other four species of larvae.

Results:

Distance travelled during the first 17 ms of the response: The data from this performance measurement exhibited considerable variability (Fig. 5.1). The analysis of covariance indicated no statistically significant effect due to depth ($F=0.20$, $p=0.6584$, $n=306$). This was also the case for the separate analyses of capelin and shanny ($F=0.44$, $p=0.5131$, $n=81$; and $F=1.10$, $p=0.2955$, $n=131$, respectively).

Distance travelled during the first 100 ms of the response: In this analysis, the hypothesis of equality of slopes was rejected, with $F=5.69$, $p=0.02$, $n=306$ (Fig. 5.2).

The slope of the responses performed at depth was greater than that of responses performed near the surface. Capelin data showed no significant difference due to depth ($F=0.48$, $p=0.5005$, $n=81$). The shanny data did show a significant effect due to depth, specifically that the larvae that produced surface waves travelled significantly further during the time interval ($F=7.08$, $p=0.0088$, $n=131$).

Mean escape speed: There was a significant effect of depth on mean speed ($F=5.33$, $p=0.02$, $n=306$), with larvae that produced surface waves travelling at higher mean speed (Fig. 5.3). Capelin data showed a significant effect due to depth ($F=4.69$, $p=0.0334$, $n=81$), however the larvae travelling at the surface attained significantly lower mean escape speed. Analysis of shanny data resulted in no significant effect due to depth ($F=1.05$, $p=0.3084$, $n=131$).

Maximum speed: Maximum speed was not significantly related to depth ($F=3.28$, $p=0.0710$, $n=306$)(Fig. 5.4). Capelin and shanny analyses echoed the combined species results with no significant effect due to depth ($F=3.21$, $p=0.0771$, $n=81$; and $F=0.38$, $p=0.5402$, $n=131$ respectively).

Total distance travelled during the response: Depth had a significant effect on total distance travelled ($F=11.24$, $p=0.0009$, $n=306$)(Fig. 5.5). Escape responses that produced surface waves resulted in significantly greater total distance travelled. Capelin data showed no effect due

to depth (F=2.04, p=0.1569, n=81). The shanny data did show an effect due to depth, however it was the opposite to that from the combined data; specifically that the larvae at the surface travelled significantly less distance (F=5.35, p=0.0223, n=131).

Discussion:

Webb et al. (1991) observed reduced fast-start performance of rainbow trout with decreased relative water depth, and attributed the reduced performance to energy dispersion by the production of surface waves. In the present study, only capelin mean escape speed and shanny total escape distance indicated reduced performance during larval escape responses that produced surface waves. In fact, the other significant depth effects (shanny distance after 100 ms, combined mean speed, combined total distance) were in the opposite direction, with larvae near the surface travelling farther and faster during their escape responses. These results seem counter-intuitive. However, two assumptions underlie the initial hypothesis that escape response performance would be lessened in responses that produced surface waves. These assumptions are: (1) that the larvae performing escape responses that produced surface waves are experiencing greater drag than larvae swimming at a greater depth; and (2) that larvae from both depth groups did similar amounts of work during their escape responses.

One or both of these assumptions may not be justified.

There is one scenario in which larvae swimming at the surface may have been subjected to similar, or less, drag than were larvae swimming at greater depth. Theoretical work with models in flume tanks indicate that a half-submerged body would experience less drag than a similar body moving just under the surface (Hertel 1966). If the larvae that produced visible surface waves were actually "porpoising" to some degree (i.e. swimming half submerged), and the other larvae that did not produce surface waves were very close to the surface of the water, it is possible that drag was similar for the two sets of responses. Unfortunately, this explanation is impossible to evaluate without a side view video recording.

Assuming the larvae that generated surface waves during their escape responses were experiencing more drag than the other larvae, the only way the surface swimming larvae could have produced the higher performance values was to have put more energy into their escape response. There are several possible reasons why this might have occurred. Physical impact by the amphipods with the larvae, the stimulus that initiated the escape responses, may have been greater for the larvae very near the surface of the water than it was for larvae swimming at greater depth. The amphipods usually produced well defined wakes as they swam in the test

chambers, indicating that they were swimming near the surface. This could have lessened the impact by amphipods on larvae at greater depth, possibly resulting in a more glancing type of contact. Another possible reason for increased effort by the surface swimming larvae is that they may have perceived the extra resistance produced by the surface tension as continued contact with a predator. Webb (1981) reported that larval anchovy did not respond to predatory stimuli with maximal fast-start speeds except during chases. Possibly, the "tug" of the surface tension on larvae swimming at the surface mimicked continued contact and attack by the predator, and thus stimulated the larvae to expend more energy in order to escape. Under these conditions, larvae performing escape responses at the surface may be expected to travel faster and further, as was observed for mean speed and total distance measured for all larvae.

Webb et al. (1991) showed significant effects of proximity to the water surface on fast-start performance of adult rainbow trout. There are several key methodological differences between that study and the present one that could have led to the apparently disparate findings. Webb et al. (1991) used electric shock to elicit the escape responses. This type of stimulus produces reproducible fast-start responses in fish (Webb 1976). In the present study,

the stimulus for the larval escape responses was impact by an amphipod. Clearly there is potential for variation in this stimulus, depending upon speed of the amphipod, angle of impact, and portion of the larva that was contacted. While Webb et al. (1991) used a 250 Hz framing rate to film the fast-starts, the present study used 60 Hz, also providing potential variability. Webb et al. (1991) tested similarly-sized rainbow trout adults. The present study examined a size range of different species of larval fish. All of the cited differences have the potential to contribute to within-depth-group variability in the present study, and this within-depth group variability may have obscured differences due to depth.

It is worth noting that Webb et al. (1991) concentrated on the fast-start portion of the escape response, and most of their significant differences were detected within 100 ms of the initiation of the response. There were two measurements of fast-start performance in the present study, distance travelled during the first 17 and 100 ms, however the results are difficult to interpret. The considerable variation exhibited by the measurements from the first 17 ms, due in part to the relatively slow framing rate of the camera, would have required a very large between-depth difference in order to be significantly different. The results from the measurements over 100 ms show much less

variability (r^2 of 0.60 versus 0.18), but a significant interaction term prevented analysis of covariance for all larvae combined. Separate examination of the two largest groups of larvae, capelin and shanny, yielded no significant depth effect for capelin larvae, however there was a significant increase in distance after 100 ms for shanny larvae swimming at the surface compared to larvae swimming at depth. It is possible that shanny larvae were affected because they were the largest larvae tested, but there is no obvious mechanism for a size effect. Differential Reynold's numbers were considered as a possible mechanism for a size effect, but this explanation is unlikely as only a small difference in Reynold's number would exist between shanny and the next largest larvae, and even the escape response of the smallest larvae generate Reynold's numbers in the zone where inertial forces dominate (Fuiman & Webb 1988).

In summary, the variability within each depth group may have obscured any differences between depth groups, especially during the fast-start portion of the escape responses. The higher mean speeds and greater distances travelled exhibited by the larvae swimming at or near the surface may have been due to continued stimulation by surface tension, or possibly due to reduced drag for "porpoising" larvae at the surface.

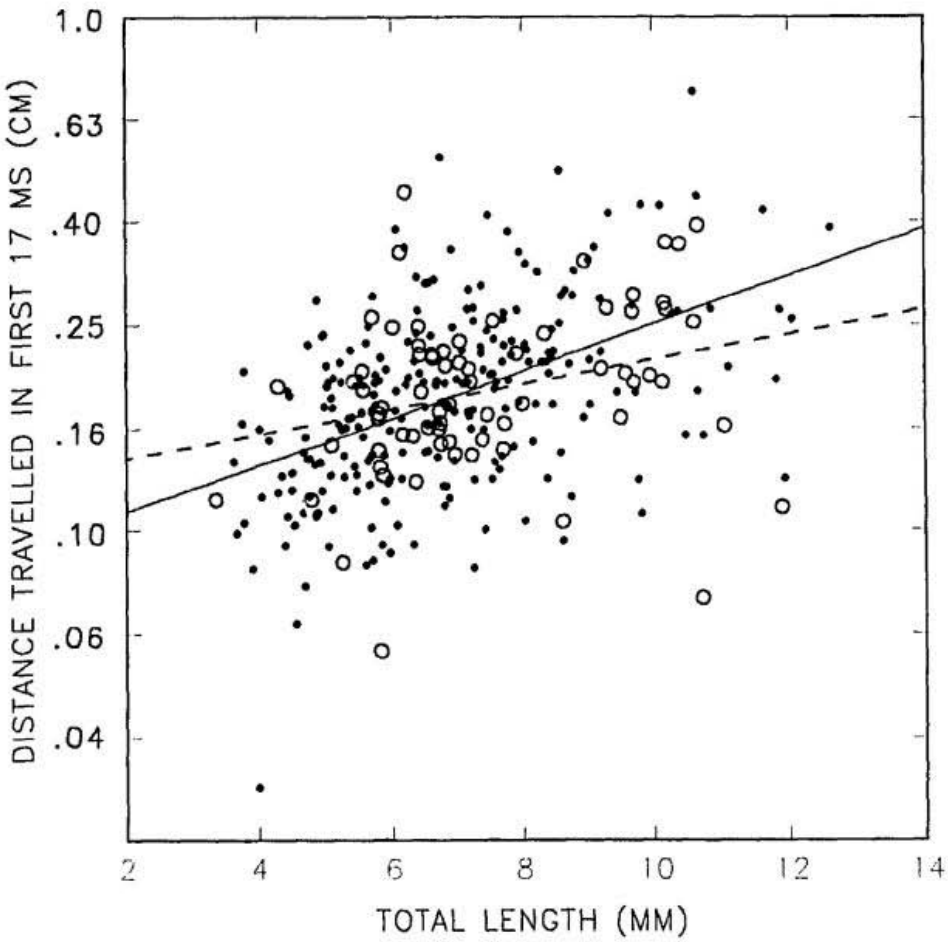


Figure 5.1 Distance travelled by fish larvae during the first 17 ms of an escape response. Open circles and broken regression line correspond to responses that occurred at the surface, indicated by the production of surface waves. Filled circles and solid regression line correspond to responses that occurred at greater depth. Note $\log_{10}$ scale for Y-axis.

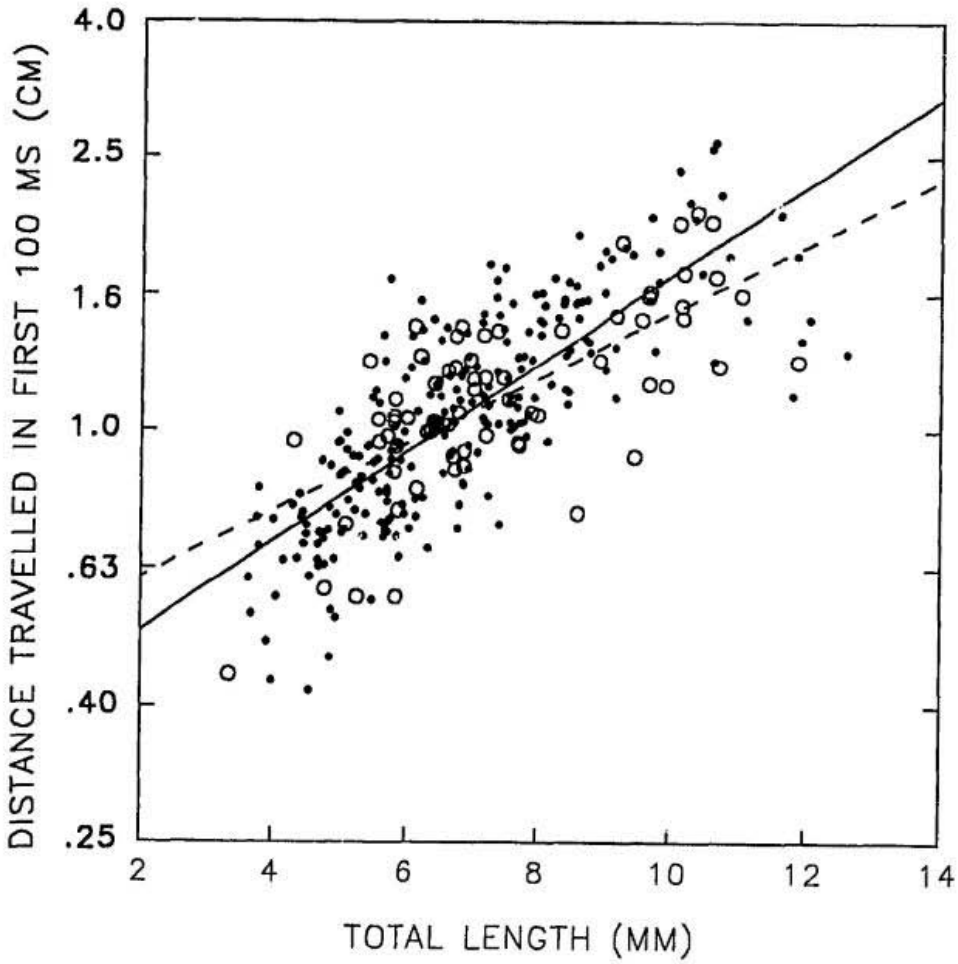


Figure 5.2 Distance travelled by larvae during the first 100 ms of an escape response. Open circles and broken regression line correspond to responses that occurred at the surface, as indicated by the production of surface waves. Filled circles and solid regression line correspond to escape responses that occurred at greater depth. Note $\log_{10}$ scale for Y-axis.

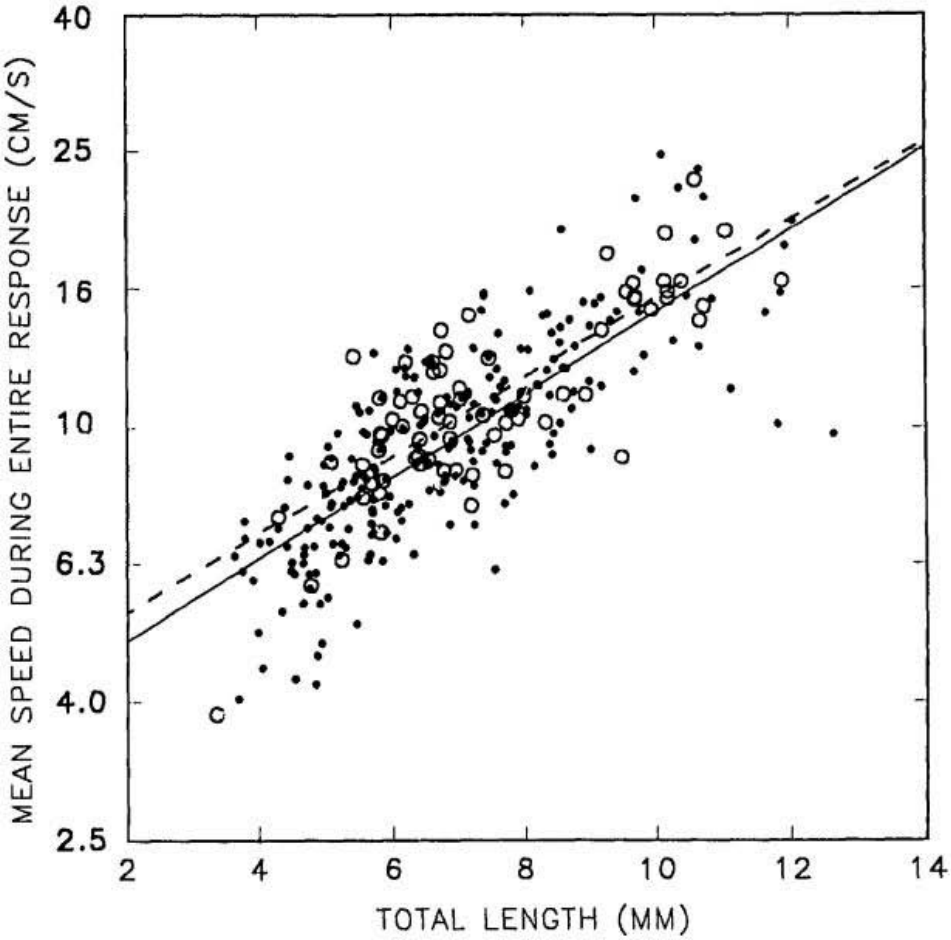


Figure 5.3 Mean speed by fish larvae during escape responses. Open circles and broken regression line correspond to escape responses that occurred at the surface, as indicated by the production of surface waves. Filled circles and solid regression line correspond to escape responses that occurred at greater depth. Note $\log_{10}$ scale for Y-axis.

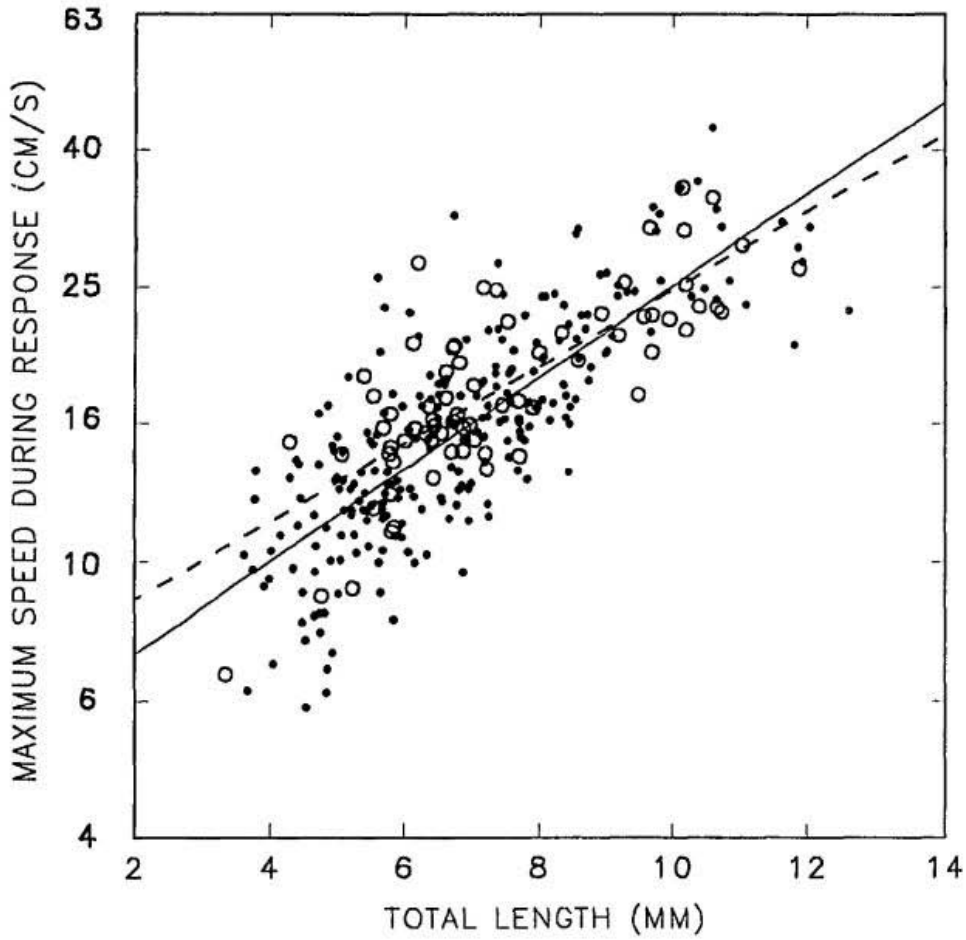


Figure 5.4 Maximum speed by fish larvae during escape responses. Open circles and broken regression line correspond to escape responses that occurred at the surface, as indicated by the production of surface waves. Filled circles and solid regression line correspond to escape responses that occurred at greater depth. Note $\log_{10}$ scale for Y-axis.

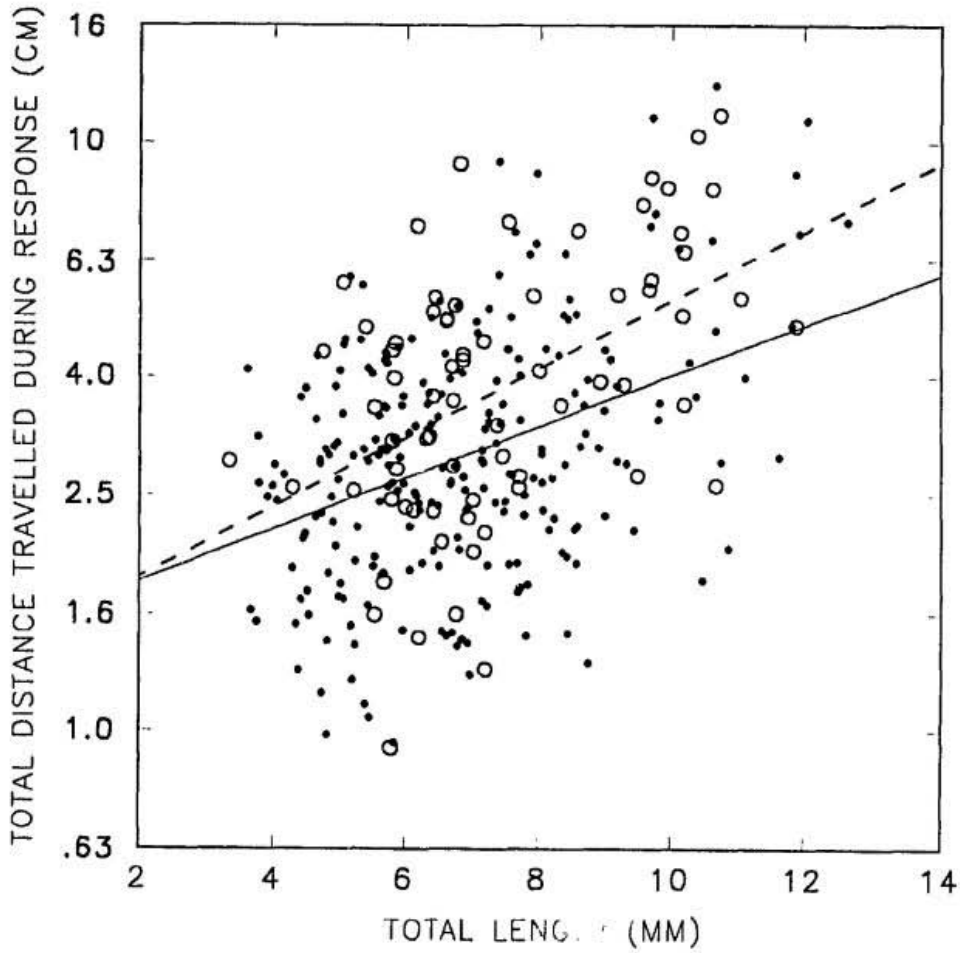


Figure 5.5 Total distance travelled by larvae during escape responses. Open circles and broken regression line correspond to responses that occurred at the surface, as indicated by the production of surface waves. Filled circles and solid regression line correspond to escape responses that occurred at greater depth. Note $\log_{10}$ scale for Y-axis.

Chapter Six: General Discussion

The experiments described in this thesis used behavioural observations of predator-prey interactions involving larval fish as prey. The goal of these experiments was to learn more about the mechanisms employed by larvae to avoid attack and capture by predators. In each chapter, the results are discussed in the context of current knowledge concerning larval fish and predation. In this concluding discussion, the contributions of the behavioural approach will be emphasized, and suggestions made for future research.

The experiments described in Chapter Two represent the first rigorous demonstration of the use of cessation of movement (or freezing) as a behavioural, antipredator defence by larval fish. The potential for use of this defence by larval fish had been suggested previously (Bailey & Yen 1983, Blaxter & Fuiman 1990), but not confirmed experimentally. Lumpfish larvae are somewhat unique in that they possess a ventral disc for adhesion to surfaces, a morphological adaptation which may facilitate the use of "freezing" as an anti-predator defence. Therefore, other behavioural experiments using different fish species are needed to address the generality of the freezing response as a defence used by larvae when confronted by a predator. If

the response is demonstrated, manipulation of hunger level of prey, species, and size of predator should prove fruitful areas for future experimentation.

Perhaps the most interesting result from Chapter Two is that fifteen week old lumpfish "turned off" the freezing behaviour in the presence of a predator, presumably because the predator was no longer perceived as a threat. What criteria did these predator-naive larvae use to assess the threat from the predator? Predator size alone would not be a reliable measure of threat, because a sculpin or cod of similar length to the stickleback predator would have been capable of ingesting the fifteen week old lumpfish (personal observation). Further experiments using other fish as predators should allow us to address this question, the results of which would also increase our knowledge concerning the mechanisms of predator recognition in fish larvae.

Chapters Three to Five outlined a series of experiments that examined the escape response of larval fish. The experiments described in Chapter Three investigated how the escape response of larval winter flounder (Pleuronectes americanus) changed with length and level of development. Obvious improvement in escape response performance was observed with increasing larval length. Suprisingly, there was no obvious decrease in performance during metamorphosis

of the larvae, and no clear increase in the rate of improvement (i.e. increase in slope of the performance-length relationship) after the transition. Given the redistribution of red and white muscle fibres, and improved support for the fins after metamorphosis, one would have expected accelerated improvement after metamorphosis. The only performance variable where this trend was suggested was maximum escape speed, which did show an increase in the rate of improvement after metamorphosis.

The observation that the flounder larvae exhibited significantly greater mean escape speed than would be predicted by a general model proposed by Miller et al. (1988) prompted the testing of an additional four species of larval fish (Chapter Four). To address the major deficiency in the composite paper by Miller et al. (1988), all five species were tested using the same protocol. As was the case using only the winter flounder data, the resultant model derived from the data for all five species still described a statistically higher rate of increase in performance (i.e significantly greater slope) than that proposed by Miller et al. (1988). The slope of the five-species model also appeared greater than that developed during two studies on Northern anchovy (Webb 1981, Webb & Corolla 1981), but appeared similar to a model calculated from data derived from another five-species comparison

reported in Bailey (1984).

Two questions arise from these results. First, would the general models developed in the present study provide good approximations of larval escape response performance? With the caveat that the models should only be used to predict escape response performance for larvae between 3.5 and 12 mm in length (the length range of larvae used to develop the models), there are two reasons why the general model developed in the present study may be preferable to earlier ones. The same protocol was used to test all five species, which represents an advantage over Miller et al.'s (1988) compilation. Secondly, the stimulus used in the present study was contact with a natural predator, rather than a touch with a wire probe as was used in Bailey (1984). The uniform protocol and natural stimulus for escape, coupled with the relatively large number of measurements, result in models that represent improvement over existing ones.

The second area of consideration prompted by the results of Chapter Four is the nature of the relationship between larval length and mean escape speed. The two regressions developed for Northern anchovy (Webb 1981, Webb & Corolla 1981), the compilations by Blaxter (1986) and Miller et al. (1988), and the results from the flounder larvae reported in Chapter Three all show linear improvement

in mean escape speed with increasing length. However, the relationship calculated for the five species tested in the present study is clearly non-linear, with the rate of improvement in performance (slope) increasing with increasing larval length. Is the real relationship linear or non-linear? It is certainly possible that the relationship is non-linear. A reasonable expectation for a mean escape speed-length relationship for the entire period from hatch through to adult may be a form of sigmoid curve, as was demonstrated for routine swimming attributes for the age range of zebra danio (Danio rerio)(Fuiman & 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 post-metamorphic period, and finally a gradual leveling-off in late-adult through senescence. Under this scenario, a mean speed-length relationship would only be linear within various stanzas of development, i.e. hatch through pre-metamorphosis, metamorphosis through adult, adult through senescence. In the present study, the larger larvae tested may extend into the region of higher improvement in performance.

It is also possible that the observed increase in rate of improvement with size was due in part to species differences. The majority of the larger larvae tested were

radiated shanny larvae. Therefore, the higher end of the mean escape speed-length relationship could have been influenced upwards if the shanny larvae were performing at a higher level than other similar-sized larvae, thereby resulting in increasing slope with increasing length. Species differences within a general model are to be expected, in the same fashion as one expects differences among individuals in single species functions (such as weight-length relationships). In the present study, the data appear to describe one relationship, with reasonable r^2 values. More testing, modifying, and re-evaluating will either refine the models to make them more universally applicable, or determine that universal or general models are not useful in predicting larval escape performance across species.

The analysis described in Chapter Five represents an attempt to further partition some of the variation in escape response performance observed within each length of larvae. Webb et al. (1991) reported evidence that adult fish performing fast-starts at the surface exhibited significantly reduced performance compared to fish swimming at greater depth. In this chapter, some of the larval fish escape responses did take place at the surface (as evidenced by the production of surface waves). As such, it seemed

possible that an effect of depth on the escape response performance of the larval fish could exist, adding to the within-length variability. Further analysis indicated that this was not the case, suggesting that the variation was the result of protocol (variable stimulus strength from the impact by the amphipods), measurement (slow framing rate of the video camera), species or individual variation.

The information reported in this thesis adds substantially to our understanding of the mechanisms associated with the predation cycle and larval fish as prey. Chapter Two reports the first rigorous demonstration of a behavioural anti-predator defence that may serve to reduce the probability of attack of larval fish. Chapters Three to Five extend our knowledge with respect to the escape response performance of larval fish, an anti-predator defence that reduces the probability of capture by predators. The behaviourally based approach used in this body of work has much to contribute to our understanding of predator-prey interactions involving larval fish as prey.

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