TO FEED OR NOT TO FEED?: THE ONTOGENY OF FORAGING AND PREDATOR AVOIDANCE TRADE-OFFS IN LARVAL COD (Gadus morhua)

LESLIE L. LEADER

To Feed or Not to Feed?: The Ontogeny of Foraging and Predator Avoidance Trade-offs in Larval Cod (*Gadus morhua*)

by

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ABSTRACT

Animals are often forced to make ecologically important decisions when faced with potentially conflicting behavioural alternatives. For larval fish, starvation and predation are thought to be the two major causes of mortality. A larva's ability to initiate and maintain exogenous feeding, while at the same time avoid predation, often produces a situation where two necessary but incompatible behaviours conflict. The manner in which foraging behaviours are compromised under risk of predation should reflect the degree of predation threat encountered. Because the larval period is one of rapid growth and development, vulnerability to both starvation and predation will change with larval size and developmental state.

In this study, experiments were conducted which offered cod larvae the opportunity to forage in the presence and absence of a predator to determine if larvae would trade-off foraging for predator avoidance. Larvae were reared at low, medium, and high prey densities to examine if food availability influenced the timing and magnitude of this trade-off.

Larval cod displayed threat-sensitivity in their foraging activity, as trade-offs and active predator avoidance behaviours were only observed in high risk areas of the experimental aquaria. Larvae reared with high prey densities grew faster, survived longer, and in the presence of a predator showed reduced foraging and swimming behaviour at week three post-hatch. In medium food densities, larvae grew slower and did not trade-off foraging and swimming behaviour until they were four weeks old. In addition, these larvae were less likely to trade-off foraging for predator avoidance as compared to those reared at high food densities. At low food densities, larvae were not observed to trade-off foraging for predator avoidance and total mortality occurred after week two post-hatch.

In all three prey densities, yolk-sac and first-feeding cod larvae were not highly responsive to visual attack cues. However, responsiveness increased with growth and development. The timing of foraging trade-offs in larval cod were highly correlated with increased activity levels and the development of body pigmentation. In order to counter the effects of increased visibility, it may become increasingly important for larval cod to reduce foraging activity in the presence of predation threat. These results suggest that the observed timing and magnitude of trade-off behaviours in cod larvae may be size (i.e. developmentally) related.

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INTRODUCTION

1.1 Animal Decision Making and Behavioural Trade-offs

The study of animal behaviour attempts to understand the complex relationships that exist between behaviour, ecology and life history strategies. Central to this is animal decision-making (Krebs and Davies 1987). Animals often have to make ecologically important decisions, such as where to feed, when to feed, what to feed on, where to live, when and where to reproduce, and choosing mates (Lima and Dill 1990). This being the case, an organism's daily time budget is likely to be divided amongst a variety of behavioural alternatives. The time and energy allocated to these activities have associated costs and benefits (Wootton 1990). For example, although feeding results in the acquisition of energy and nutrients, it may "cost" an animal in terms of predation risk and/or reduced time available for other activities. When studying behavioural decision making processes in animals, cognitive choice is not implied, rather behaviours are measured in terms of fitness related costs and benefits.

The costs and benefits associated with decisions become increasingly important when animals are faced with conflicting goals. For example, an individual may not be able to simultaneously defend a territory and a mate, or feed and avoid a predator. Under such conditions, an animal will be forced to "choose" or select one particular behaviour from a set of possible alternatives. Decision making therefore, involves the "trading-off" of behaviours. Since costs and benefits are associated with all behaviours, the result of trade-offs among activities should represent net fitness benefits (Wootton 1990, Abrahams 1993).

Behavioural trade-offs have been widely documented in mammals (Edwards 1983, Hasselquist and Bensch 1991), fishes (Ibrahim and Huntingford 1988, Helfman 1989, Bishop and Brown 1992, Rangeley and Godin 1992, Abrahams 1993), insects (Nonacs and Dill 1990, Rayor and Uetz 1993) and invertebrates (Scarratt and Godin 1992). In studying trade-offs and the constraints that influence behaviour, it has become evident that animals have the behavioural flexibility to assess their environment and incorporate this information into decision-making processes. For example, work by Brown (1984) on parental care and the ontogeny of predator avoidance in centrarchids demonstrated that rock bass (*Amblolites rupestris*) fry trade-off other behaviours for predator avoidance much earlier than largemouth bass (*Micropterus salmoides*) fry which experience an extended period of parental care. Since predator avoidance can be costly in terms of energy expenditure and lost foraging opportunity, it would be an unnecessary cost for largemouth bass fry to employ this behaviour while guarded by the adult male. In Brown's (1984) study, centrarchid fry exhibited the ability to assess their environment and trade-off predator avoidance in a manner that maximized fitness. Rangeley and Godin (1992) studied trade-offs in convict cichlids (*Cichlasoma nigrofasciatum*) which examined the conflict between foraging and brood defence on parental behaviour. Under these circumstances reduced, parental care may result in increased off spring mortality (i.e. diminishing current investment) while decreased foraging may influence parental growth, fecundity and survival. This study showed that in the presence of a predator parental cichlids reduced foraging and increased parental care, resulting in a trade-off between food consumption and defence of current reproductive investment.

Perhaps the most intensely studied trade-off in the literature is that of foraging and predator avoidance (Lima and Dill 1990, Milinski 1993). Animals often risk being eaten while feeding. This risk can be attributed to increased conspicuousness due to movement, less time devoted to vigilance while searching for food, and often, optimal feeding habitats leave foraging individuals in vulnerable locales (Lima and Dill 1990, Milinski 1993). The failure to avoid and escape a predator is fatal, thus predation has long been recognized as an important force influencing prey behaviour (Stein 1979, Lima and Dill 1990).

1.2 Predation

Predation has become an area of fascination for behavioural ecologists because of the complex interactions that exist between a predator and its prey. For predation to be successful, a predator must encounter, detect, identify, approach, attack, capture and consume a prey item. Prey organisms respond to predation by attempting to interrupt this sequence using antipredator defenses. Antipredator defenses can be employed at any or all stages of the predation sequence (Crowder and Cooper 1982, Endler 1986). The goal of the predator, however, is to complete this sequence as quickly as possible by counter-acting the defenses of potential prey items (Endler 1986, Krebs and Davies 1987).

1.3 Prey responses to predation

If an animal is to maximize its fitness (i.e. its genetic contribution to future generations; Begon et al. 1986), it cannot exclusively avoid predators at the expense of all other activities. Therefore, some compromise might be expected between incompatible behaviours. Predation can result in a number of fitness consequences for prey; attacks can have direct effects resulting in death or injury, or indirect effects which place restrictions on the prey's activities or movements (Sih 1987, Wootton 1990). An organism's response to a predator should therefore depend on it's vulnerability to predation and the costs and benefits associated with its behavioural options (Stein 1979, Lima and Dill 1990). It would be energetically costly to trade-off foraging, or other activities, to avoid a non-threatening predator (Stein 1979). Predation threat is therefore considered a strong selective force which can influence an individual prey's behaviour.

Helfman's (1989) studies with damselfish (*Stegastes planifrons*)-trumpetfish (*Aulostomus maculatus*) interactions predicted that "...prey individuals would trade-off predator avoidance against other activities by altering their avoidance response in a manner that reflects the magnitude of the predatory threat...", thus employing threat sensitivity in decision-making processes. Results showed that damselfish displayed progressively stronger avoidance responses to model predators as the distance between predator and prey decreased. Helfman (1989) also observed stronger responses from damselfish exposed to large predator models and models oriented in threatening strike positions. In contrast, intermediate avoidance responses were employed by damselfish when predator size and orientation combinations represented an intermediate threat. Results supported Helfman's threat-sensitive hypothesis, as strong threats evoked strong responses and weak threats evoked weak ones. Helfman (1989) also observed damselfish to be threat-sensitive when reducing non-avoidance activities, such as territory defense and feeding. Work by Foster and Ploch (1990) also demonstrated that territorial male three-spine stickleback (*Gasterosteus aculeatus*) were sensitive to threats posed by four different aquatic predators: sculpin (*Cottus asper*), trout (*Oncorhynchus clarki*), nymphs (*Belostomatidae*), and newts (*Taricha granulosa*). Sticklebacks discriminated rapidly amongst these predators and performed a diverse array of antipredator behaviours reflecting the degree of threat each predator type posed. The ability to assess predator threat and modify behavioural responses appropriately should enhance survival. Such sensitivity would be expected in behavioural decision-making processes when strategies attempt to maximize fitness.

Bishop and Brown (1992) extended Helfman's threat-sensitive predator avoidance hypothesis to specifically examine the trade-off between foraging and predator avoidance in larval fish. They posed the threat-sensitive foraging hypothesis which predicts that animals should trade-off foraging for predator avoidance in a manner that reflects the degree of predation threat encountered.

When employing foraging/predator-avoidance trade-offs, individuals can respond to predation in a variety of ways. How an individual responds will be influenced by its developmental state, habitat, and nutritional requirements as well as by the degree of predation threat. In response to predation, a foraging individual may alter it's behaviour in a manner that reduces it's risk of encountering potential predators (Lima and Dill 1990, Milinski 1993). Werner et al (1983) showed that, in the absence of a predator, all size classes of bluegill sunfish (*Lepomis macrochirus*) foraged in an open benthic habitat where food was abundant. However, when largemouth bass predators were introduced, the smallest and most vulnerable age class of bluegill moved into protected vegetative habitat where food was less abundant. This movement resulted in lowered food intake and an overall decrease in growth. Small bluegills were forced to balance foraging profitability against risk of predation. Because largemouth bass are gape-limited predators, larger bluegills did not need to employ this trade-off. Similarly, Edwards (1983), found that female moose (*Alces alces andersoni*) with calves foraged on small isolated island habitats, where food quality was poor, to reduce risk of wolf predation. In both these examples, prey individuals employed predator avoidance tactics resulting in decreased energy gains but increased safety.

Prey can also trade-off conflicting foraging and predator avoidance demands by employing alternative foraging behaviour. Work by Semlitsch (1987) found a dietary overlap between two species of salamander larvae, *Ambystoma* *talpoideum* and *Ambystoma maculatum*, and a predatory fish, *Lepomis macrochirus*. Larvae reared in the presence of this predator decreased feeding and switched prey. Dill and Fraser (1984) found that juvenile coho salmon (*Onchorhynchus kisutch*) lowered their tendency to strike at oncoming prey after sighting a model predator rainbow trout. Decreased feeding strikes influenced the salmon's encounter volume, especially for large profitable prey, thereby influencing diet selection. Three-spined sticklebacks were observed to reduce foraging and shift their diet from large, profitable, yet difficult to handle prey, to small less profitable, but easy-to-handle prey, when under the threat of predation. This resulted in a trade-off between energy gain and predator avoidance (Ibrahim and Huntingford 1988).

Activity levels have also been highly correlated with risk of predation, as in many studies moving prey are more easily detected and recognized by predators than stationary ones (Lima and Dill 1990). Movement patterns and activity levels are also related to foraging behaviour (Blaxter 1986, Kerfoot and Sih 1987). Constraints placed on an organism due to predation have been shown to reduce feeding and growth rates. For example, decreased activity in the presence of predators has been reported for the shrimp *Tozeuma carolinense* in the presence of a predator pinfish (Main 1987), three-spine stickleback exposed to model herons

(Godin and Sproul 1988), larval lumpfish (*Cyclopterus lumpus*) in the presence of predator three-spined sticklebacks (Williams and Brown 1992a), four species of larval anurans in the presence of predatory salamanders and sunfish (Lawler 1989), and the midge *Chironomus tentans*, exposed to predatory pumpkinseed sunfish (*Lepomis gibbosus*) (Macchiusi and Baker 1992).

It is clear that there are many behavioural options available to a foraging individual when faced with the risk of predation. Perhaps one of the best strategies to adopt when faced with these conflicts is suggested by Gilliam and Fraser (1987): prey should trade-off behaviours in a manner that minimizes the risk of death per unit energy consumed. This strategy implies that prey individuals have the behavioural flexibility to assess their environment and behave accordingly.

1.4 Young Animals and Vulnerability to Predation

Susceptibility to predation can be related to an animal's condition and life stage (Stein 1979). A prudent predator would be expected to select vulnerable individuals (i.e. young, or those weakened by starvation or other causes). Since differences in prey vulnerability are often attributed to size and development, young animals are readily preyed upon (Milinski 1993). Because size and vulnerability change with growth, response to predation should also vary with development. Stein (1977) examined interactions between predator smallmouth bass, *Micropterus dolomieui*, and different sizes and life stages of the crayfish, *Orconectus propinquus*. Results showed that smallmouth bass foraged on the smallest, most vulnerable size class of crayfish in sandy habitats. However, on pebble and large substrate habitats, small crayfish were not readily consumed as they took refuge within the substrate. Work by Sih (1980) on foraging and predator avoidance in the aquatic insect, *Notonecta hoffmanni*, showed that first and second instars were more susceptible to predation by adult stages than were third, fourth, and fifth instars. As a result, younger instars reduced feeding to avoid risk of predation. It, therefore, becomes extremely important for young animals to compensate behaviourally and/or morphologically for differential vulnerability. Perhaps the best strategy young animals can employ is to grow fast, thereby becoming too large for predator consumption, thus decreasing the number of potential predators.

1.5 Larval fishes

Houde's (1987) conceptualized recruitment diagram (Fig. 1) illustrates the many abiotic and biotic factors that influence survival in larval fishes. Although, all of these factors influence larval survival, starvation and predation are thought to be the two major causes of larval fish mortality (Hunter 1975). When referring to this diagram, it is clear that predation influences mortality at all stages starting with the egg and continuing through to the juvenile. In contrast, it is only after complete yolk-sac absorption that starvation begins to play a role in larval mortality. At this point the ability to initiate and maintain exogenous feeding, while at the same time avoid predation, is critical for survival.

Larval fish are extremely vulnerable to predation at hatch due to their small size and poor morphological development (i.e. sensory and motor structures are often absent or undeveloped; Blaxter 1988). Mortality throughout the larval stage is size-specific, with yolk-sac stages incurring higher rates of mortality, which decline with growth and development (Folkvord and Hunter 1986).

As larvae develop, there is a concurrent emergence of associated behaviours. For instance, the development of fins and locomotory muscles and the refinement of sensory systems will influence swimming and foraging activity as well as antipredator responses (Hunter 1975, Blaxter 1986, Noakes and Godin 1988). Numerous studies have shown larval foraging behaviour to change with size. It seems reasonable that a larva's ability to locate and capture food should improve with growth, development and experience. Browman and O'Brien (1992a) documented the ontogeny of search behaviour in white crappie larvae (*Pomoxis annularis*). Fish size was found to have a significant overall effect on foraging behaviour, as attack time and strike distance, as well as swimming and aiming speeds, increased with larval size, while the proportion of aborted attacks decreased. Similar results were reported for the golden shiner (*Notemigonus cryleucas*) (Browman and O'Brien 1992b), northern anchovy (*Engraulis mordax*) (Hunter 1972), and herring (Blaxter and Staines 1971).

In addition to increasing body size, development of the visual system also influences both foraging and predator avoidance behaviour. Increased visual acuity produces a larger visual field in which larvae can detect both predators and prey. This allows larvae to feed faster and more efficiently as well as respond more quickly to predatory threats (Noakes and Godin 1988).

Mouth size can also affect feeding behaviour in larval fish. The relationship between the gape of a larva's mouth and size of prey available for consumption at the onset of exogenous feeding can become crucial to larval survival (Blaxter 1988). Generally, larger prey items represent greater energy gains which can be channelled into growth and development.

Growth and survival of larval fish during the early developmental stages is largely influenced by feeding conditions (Frank and Leggett 1986, Van der Meeren and Naess 1993). Variability in both prey size and abundance can produce unpredictable foraging environments. When prey abundances are low or prey are of an inappropriate size, larvae may be forced to feed on energetically unfavourable prey items in order to achieve maintenance diets. As a result, larvae may be forced to search greater volumes of water and increase foraging time to obtain lower energetic gains. This in turn may increase their encounter rate with predators.

During periods of starvation, vulnerability to predation increases. Nutritional state and hunger levels become increasingly important factors in determining foraging-predator avoidance trade-offs, as hungry individuals are often more willing to accept temporary risk in order to obtain immediate gains. Since hunger levels change with prey abundance, the degree of risk taking behaviour should be proportional (Fraser and Huntingford 1986, Lima and Dill 1990, Milinski 1993). Growth is often slow or negligible during starvation, and larvae can experience degeneration of muscle and other tissue types, thereby resulting in impaired behavioural responses. For example, preliminary work by Folkvord and Hunter (1986) demonstrated a reduced predator avoidance response in starved northern anchovy larvae. A larva's susceptibility to starvation may become less important as larvae grow, establish energy reserves and develop an extended behavioural repertoire.

Predator detection and avoidance behaviours in larvae develop as a result of maturation. Folkvord and Hunter (1986) demonstrated an interaction between larval growth and size-specific vulnerability to predation in northern anchovy, whereby as larvae grew they were more likely to initiate predator escape responses. Fuiman (1989) also found a 10 fold increase in responsiveness to predator attack in larval Atlantic herring at lengths between 26-30mm. At this time major morphological advances were found in both the acoustic and visual sensory systems. The development of such systems may improve predator detection and assessment abilities, response time and direction, and the magnitude of anti-predator responses. Over time, experience may also improve evasive behaviours. Williams and Brown (1992b) also documented an increase in escape response with larval size in winter flounder (*Pleuronectes americanus*) when exposed to predatory amphipods. Since larvae become more easily detected by predators with increased size and pigmentation the development of predator detection and escape behaviours becomes increasingly important. It is evident that the ontogeny of behaviour is directly related to the development of structure in many larval fish species.

1.6 Experimental Rationale

In the past, larval fish research has focused on examining starvation and predation separately. However, using the threat-sensitive foraging paradigm, we can examine the interactions between foraging and predator avoidance. Since both are critical to the survival of larval fishes, it is appropriate to examine this trade-off.

Bishop and Brown (1992) were the first to test this hypothesis using larval three-spined stickleback, (*Gasterosteus aculeatus*). Sticklebacks have a unique early life history involving parental care, schooling behaviour, the development of dorsal and ventral spines, and a relatively short larval period (i.e. 30 days to metamorphosis). These larvae were observed to trade-off foraging for predator avoidance at week two post-hatch in the presence of medium and large sized predators. However, larvae exposed to small predators did not significantly reduce their foraging. These results indicate that early in ontogeny, sticklebacks have the ability to distinguish among different levels of predation threat, and alter their foraging behaviour in an threat-sensitive manner.

To extend Bishop and Brown's (1992) work, I decided to use the threat-sensitive foraging paradigm to study a species that has a very different early life history. Larval cod, (*Gadus morhua*), are smaller and much less developed at hatch than three-spined stickleback. Adults do not provide parental care and larvae do not develop specialized external antipredator structures (e.g. spines). Finally, the vulnerable larval period is much longer, as time to metamorphosis is anywhere between 45-60 days depending upon temperature.

In this thesis, I investigated the behaviours associated with foraging and predator avoidance in larval cod over an extended period of growth and development. My specific objectives were to:

1. **Determine if larval cod alter foraging activity in the presence of a predator (i.e. will larvae trade-off foraging for predator avoidance).**

2. **Determine if prey density will influence behaviour and the timing of foraging vs predator avoidance trade-offs.**

3. **Examine how growth and development influence the ontogeny of behaviour.**

METHODS

2.1 Experimental Animals

2.1.1 Larval cod

Atlantic cod inhabit the cool temperate to subarctic waters of the north Atlantic ocean (Scott and Scott 1988). Cod are broadcast spawners and individual females produce millions of pelagic eggs. Eggs rise to upper layers of the ocean for incubation. Upon hatching, these transparent larvae are relatively small (4.6 mm) and poorly developed. At this point, fins are not developed nor are the mouth and eyes functional. Yolk-sac reserves generally last for 7-10 days, depending upon water temperatures. Cod larvae will remain pelagic until they metamorphose, approximately 25-40 mm in length, and become demersal.

Fertilized cod eggs were collected from a naturally spawning captive broodstock maintained at the Ocean Sciences Centre, Logy Bay, Newfoundland. Eggs were incubated in floating rectangular baskets with slight aeration, natural photoperiod and filtered seawater until hatch. Upon hatching, larvae were carefully transferred from incubation baskets to the experimental aquaria described below. Stocking density in the experimental aquaria was 20 larvae/l.

2.1.2 Experimental Predator

Three-spine sticklebacks, *Gasterosteus aculeatus*, were used as the experimental predator. Sticklebacks were considered an appropriate predator as they are a common visually feeding, generalist predator which include larval fish in their diets (Wootton 1984, Delbeek and Williams 1988). They are also easy to collect, maintain, and train for behavioural experiments. This was demonstrated in studies by Gotceitas and Brown (1993) wherein sticklebacks were found to actively forage on larval cod.

Two sticklebacks were housed in the predator chamber of each of six treatment tanks (see below) for a total of 12 fish. Predators had a mean weight (± SD) of 1.0 (± 0.09) grams and a mean total length of 5.0 (± 0.04) cm at the onset of experimental observations. Upon completion of the experiment, predators weighed 1.19 (± 0.09) grams and measured 5.1 (± 0.06) cm. Predators were fed a maintenance diet of frozen brine shrimp every third day. This resulted in hunger levels that produced aggressive predators. Larval cod were incorporated into the sticklebacks diet so as to ensure and maintain an attack image of larval cod as a prey item.

2.2 Experimental Tanks

Twelve, 30-L aquaria were used to rear and test larval cod. All aquaria were housed in a cool room maintained at approximately 7 °C (± 1 °C). Tanks were supplied with a constant flow of filtered seawater (flow rate approx. 200-500 ml/min), and slight aeration. Overhead fluorescent lights (700 lux at the surface) maintained a 24 hr light photoperiod. To reduce outside disturbance three sides of each tank were covered externally with black plastic.

Each tank was divided into two chambers, one predator chamber measuring 12.5 (L) x 26 (W) x 30 (H) cm, and a larger larval rearing chamber measuring 37.5 x 26 x 30 cm (Fig. 2). These chambers were separated by two adjacent partitions, one being transparent and non-removable, and the other removable and opaque. These partitions allowed the experimenter to visually expose larval cod to the predators in their chamber by raising the opaque partition, while preventing physical contact between the predators and cod larvae. The larval rearing chamber was further subdivided into three, 12.5 cm wide grids demarcated by vertical lines drawn on the front and back walls of each aquaria. The grid closest to the predator chamber was designated the "predator grid" (p), the grid furthest away was designated the "non-predator grid" (np), and the grid in between these the "middle" grid (m) (Fig. 2).

Six of the twelve tanks were arbitrarily designated as treatment aquaria. These housed two predators in the predator chamber. The remaining six tanks did not house predators, and constituted the control aquaria. Control trials were used to determine whether observed larval behaviour was due to the presence of the predator and not to the disturbance associated with the removal of the opaque partition. Larvae were fed at three prey densities, resulting in two replicate tanks for each prey density in both control and treatment aquaria.

2.3 Larval rearing

Cod larvae were initially fed rotifers and tanks were stocked with the appropriate prey density for low (500 prey/l), medium (1500 prey/l), and high (4500 prey/l) prey levels. Experimental prey densities were selected on the basis of previous laboratory studies which found increased larval growth and survival (i.e. larvae developed through to metamorphosis) at high (4500 prey/l) prey densities, whereas growth and survival was significantly reduced in larval cod reared at low (500 prey/l) prey densities. 1500 prey /l was selected as an intermediate density.

Larvae were provided with food beginning at day two post-hatch. An up-welling aeration system was used to ensure a homogeneous prey distribution within the tank. To maintain a constant daily prey density within each experimental tank, ten 1-ml aliquots of seawater were pipetted from arbitrarily selected regions of each tank. The prey density of this sample was counted, providing an estimate of the total tank prey density. Prey was then added as needed to achieve the desired prey density in each aquaria. At week two post-hatch, prey densities were changed to a 50:50 mixture of rotifers and newly hatched *Artemia salina* nauplii. By the end of week three post-hatch larvae had grown to a sufficient size to consume nutrient-enriched nauplii exclusively. For the first 12 days post-hatch, 400 mls of algae (*Isochrysis sp.*) was added daily to each experimental aquaria.

2.4 Behavioural observations

Larvae were observed three times a week during the study period (April-June 1992). The sequential order in which aquaria were selected for observations was arbitrarily determined. Prior to an observation session, the desired quantity of food was introduced evenly into the larval chamber and the opaque partition removed. Removing this partition allowed predator sticklebacks to direct attacks at larvae through the transparent partition, but rendered attacks unsuccessful. The observer sat quietly at eye level and approximately 60 cm from the aquaria. Experiments commenced after an acclimatization period of approximately 1 min.

Seven Modal Action Patterns (MAP's), defined in Table 1, were recorded. Barlow (1968) defined a MAP as a discrete and quantifiable unit of behaviour that has a typical and recognizable form. The frequency of attempt and success MAP's were pooled together to create the variable "attack" which was used to calculate feeding success. Orient, attempt, success and pass MAP's were also pooled to create a variable that represented larval "foraging activity".

The focal animal technique (Altmann 1974) was used to observe an arbitrarily selected larva for 1 minute. During this period, the frequency and duration of all MAP's, as well as location within the larval chamber, were recorded using a Tandy 102 event recorder. The event recorder was programmed to accept keyboard inputs as codes for defined behaviours and locations. This procedure was repeated for 10 larvae within each tank. Because larvae could swim freely throughout the rearing chamber (i.e. between all three grids) observations were initiated from each grid to ensure that larval behaviour was recorded in all areas of the tank. Individuals were carefully observed to ensure that they were only recorded once during an observational period and notes documenting unqiue larval behaviour were recorded. During an observation session predator behaviour was also examined to ensure that sticklebacks were posing a threat to the larvae.

2.5 Morphometric Measurements

Throughout the course of this experiment gross morphometric characteristics of the larvae were recorded every five days. Five larvae from each tank were arbitrarily selected and measured individually under a dissecting microscope using an eyepiece micrometer. The following characteristics were recorded:
standard length (snout to tip of notochord) , eye diameter (along body axis), myotomal height (posterior to the anus), the proportion of food in larval stomachs (i.e. gut fullness), which was defined as being either empty, 1/4, 1/2, 3/4 or full, and the presence or absence of yolk reserves (Fig. 3). Measuring larval standard length (mm), eye diameter (mm), and myotomal height (mm) provided an indication of larval growth, visual development and accumulation of muscle mass. Monitoring larval gut fullness and presence or absence of yolk reserves provided a measure of larval foraging success and the need for exogenous feeding. After these measurements were recorded individual larvae were placed on pre-weighed pieces of numbered foil and left in a drying oven (90 °C) for two days, after which, larvae were re-weighted on an electrobalance and dry weights

(mg) calculated. These measurements were used as indictors of larval growth and stage of development at high, medium and low prey densities and in the presence and absence of a predator over the study period.

2.6 Data analysis

Prior to analysis, data were tested for the assumptions required to perform multivariate and univariate parametric statistics. Normality was tested for by using the Kolomogorov statistic (proc univariate procedure in SAS, 1988) and plots of residuals versus predicted values were examined to detect violations of homogeneity and independence.

Feeding in larval cod consisted of four Modal Action Patterns: orient, attempt, success and pass. For analysis, the frequency of attempt and success MAP's were added together to create the variable attack and, in turn, the frequency of orient and pass MAP's along with attack were summed to create a variable that represented larval "foraging activity" (Table 1).

Initially, larval foraging in the absence of a predator was examined to determine the effect of prey density on larval foraging activity. A Two-way Analysis of Variance, testing for week and food levels effects, was performed on data collected from control observations. Bonferroni post-hoc comparisons were employed when significant results were obtained. To provide an indication of larval feeding ability with growth and development, the frequency of attempt and success MAP's were used to calculate larval capture success (i.e. success:attack) on a weekly basis.

To examine the effects of predation threat on larval behaviour, multivariate analysis was used to determine if the total time larvae spent within each grid of the larval rearing chamber differed between control and treatment aquaria. Similarly the total frequency of active MAP's (i.e. frequency of swim + orient + pass + attempt + success + flee) performed by larvae within each grid was analyzed (MANOVA, Proc GLM, SAS 1988). When significant results were obtained, Bonferroni post-hoc tests were employed to determine which means differed significantly.

Larval MAP's were then analyzed in more detail to determine the effects of week, food level and the presence or absence of a predator on larval behaviour. Because larval swimming behaviour was associated with foraging MAP's, multivariate analysis of variance (MANOVA) (using the GLM procedure (SAS)) was used to examine these larval activities. Separate MANOVA's were performed on larval swimming duration and foraging activity, and larval swimming duration and the individual MAP's which constitute foraging activity (i.e. orient, pass and attack).

Behavioural data collected from within each of the grids (i.e. "p", "np", and "m") in the larval chamber were initially summed, yielding total duration of swimming and total frequency of foraging MAP's. As discussed above, MANOVA's were performed on these totals to determine overall trends in swimming activity, foraging, and predator responses within the experimental tanks. When significant overall MANOVA results were obtained, univariate results were examined. Where significant univariate F-values were found Bonferroni multiple comparisons were performed using the LSMeans procedure to determine which means differed significantly. The level of statistical significance for the experiment was initially set at $p<0.05$ and $p<0.1$. According to LSMeans procedure to calculate a per comparison alpha level p values are divided by the number of mean comparisons examined thus producing comparison wise alpha levels which were used to determine statistical significance.

To examine the influence of proximity of larvae to the predator, foraging activity, feeding MAP's and swimming duration were examined in each of the predator, middle, and non-predator grids separately (MANOVA, Proc GLM, SAS 1988). When significant multivariate and univariate F-values were found, Bonferroni LSMeans procedures were performed to determine which means differed significantly.

To further examine the effects of predation threat on larval behaviour, treatment aquaria were analyzed separately to determine if larval swimming and foraging activity differed between predator, middle and non-predator grids (MANOVA, Proc GLM, SAS 1988). Duncan's multiple range tests were used when significant results were obtained.

Analysis of Variance was performed on morphometric data to test for food level, tank, week, and treatment effects. Where results were found to be nonsignificant data was pooled appropriately. Bonferroni post-hoc comparisons using the LSMeans procedure or Duncans multiple range test were employed on significant results to determine which means differed. Again, the overall experimental level of statistical significance was set at $p<0.05$ and $p<0.1$.

RESULTS

3.1 Assumptions

Behavioural data were not normally distributed. After having attempted various transformations of these data, I was still unable to restore normality. However, according to the central limit theorem, normality can be relaxed in cases where sample size is large and in this experiment n=1472 (Johnson and Wichern, 1992). Olson (1976) also found that when dealing with large sample sizes, deviations from normality exerted little effect on MANOVA analysis. Log transformations were performed on morphometric data to restore normality. Homogeneity of dispersion matrices was achieved for morphometric data, but was violated for behavioural data. Again, due to a large sample size, MANOVA is robust to this violation. Independence was implied within the experimental design.

3.2 Foraging Activity with no Threat of Predation

Feeding in larval cod consisted of four Modal Action Patterns (MAP's): orient, attempt, success, and pass. These behaviours were lumped together to create the variable "foraging activity" (Table 1).

Control tanks were examined to determine the effect of prey density on larval foraging activity. Two-way analysis of variance showed a significant interaction between week and food level (Table 2). Overall larval foraging activity was highest under 4500 prey/l across all weeks (Fig. 4). The frequency of foraging activity increased dramatically at week two in medium and high food treatments and decreased slightly in low food treatments. Larvae in low food aquaria foraged significantly less than larvae reared in high food aquaria during weeks one and two (Table 3). Similarly, cod larvae reared at low prey densities foraged significantly less than larvae reared at medium prey densities during week two (Table 3). When comparing foraging activity under high and medium prey densities larvae foraged significantly more at week three and week five at high prey densities (Table 3).

Both day ($F_{6,126}$=14.96, p=0.0001) and food level ($F_{2,126}$=5.75, p=0.004) were found to significantly influence the quantity of prey found in larval stomachs. Considering all days together, larvae reared at high prey densities possessed significantly fuller guts than those reared at lower prey densities, while larvae reared at intermediate densities had significantly fuller guts than those reared at the low prey density (Duncan's, p<0.05, high $\bar{x}$=0.5, medium $\bar{x}$=0.32, low $\bar{x}$=0.12) (Fig. 5). The amount of food observed in larval stomachs increased rapidly up to day 11, which coincides with the complete absorption of yolk reserves and the need for exogenous feeding. After week two, the proportion of food observed in the stomachs of larvae ranged from 50-70% and 35-55% in high and medium food densities, respectively. First-feeding larvae reared at low prey densities were able to capture prey items (i.e. mean gut fullness was 30%), however, mass mortality occurred after week two (Table 4, Fig.5). These results suggest that ingestion rates of larvae under low prey densities were not sufficient to satisfy larval energy requirements for growth and survival.

To determine if feeding success varied over the experimental period, the number of attempt and success MAP's were used to calculate overall capture success. During the first week, larvae exhibited relatively low capture success (Table 4), however, this increased at week two for all food levels. At high prey densities, success remained above 85% from week 2 through to the completion of the experiment, while a slight decrease was observed over weeks four and five at medium prey densities. The frequency of attacks (i.e. attempt + success MAP's) were highest at 4500 prey/l and decreased with relative prey density (Table 4).

3.3 Larval Response to Predation Threat

In all twelve experimental tanks, cod larvae could move freely throughout the larval rearing chamber, thereby spending varied amounts of time in each of the three designated grids. The presence of a predator did not significantly influence the total amount of time larvae spent within each of these grids (Hotelling Lawley trace (HL) F=0.569, p=0.635) (Figs. 6-8).

Overall larval activity (i.e. frequency of all active MAP's) were examined to determine if the presence of a predator influenced activity levels among these three grids. MANOVA results showed significant week*treatment and week*food level interactions (Table 5) and univariate results found a significant treatment effect for the predator grid only (Table 6). Larvae in the grid adjacent to the predators were significantly less active (i.e. performed fewer MAP's) than larvae in other grids. On a weekly basis, larvae reared on 4500 prey/l were less active in the predator grid of treatment aquaria than larvae in control aquaria during weeks three, four, five and six (Fig. 9). Bonferroni post-hoc comparisons showed larvae were significantly less active in the presence of a predator during weeks four and five (Table 7). At medium prey densities, a non-significant decreasing trend in larval activity in the predator grid of treatment aquaria was observed across all weeks (Fig. 9). In contrast, larval activity was not significantly influenced by the presence of a predator in the middle and non-predator grids. This was true for all three prey densities, (Table 6, Appendix 1;

Figs. 1a-2a).

In the predator grid of treatment aquaria, larval response to direct predator attack varied with growth and development. Observed behaviours included no response, active fleeing, and avoidance followed by turning back towards the predator and remaining motionless. Larvae in the middle and non-predator grids of treatment aquaria and in control aquaria were not observed to perform fleeing or avoidance behaviours.

One-week-old larvae generally did not respond to predator attacks. Predators displayed aggressive behaviours by swimming throughout the predator chamber and frequently attacking larvae through the clear partition. Fleeing responses by larvae were initially observed in high food treatments at day 6 (Fig. 10).

During week two, larvae began to display a higher frequency of flee responses. These were only elicited in response to direct head-on attacks by the predator but not consistently so for every attack. Predators attacking the posterior portion of larvae through the glass partition did not elicit a response. However, with frontal attacks, larvae would flee from the predator, followed by remaining motionless or quickly resuming routine swimming behaviour. It should be noted that in many cases several attacks by the predator were necessary in order to initiate any response from the larvae.

There was a continuous increase in flee responses through to week three from larvae reared in high food treatments. In contrast, flee behaviour was noted to decrease in medium food treatments (Fig. 10). By the end of week three, larvae decreased the number of rapid flee responses employed and replaced them with a more moderate avoidance response to predator attacks (i.e. swimming away from predators at a substantially slower speed than that seen in flee responses).

At week four, larvae began to display fewer flee responses (Fig. 10) and incorporated avoidance into their behavioural repertoire. Often, what appeared to be the precursor of predator inspection behaviour accompanied this avoidance response (i.e. larvae would move away from the predator, stop, and turn 180°, fixating on the predator while remaining motionless).

During the last two weeks of observations and in high food treatments, the frequency of flee responses decreased steadily, with none observed during week six. At this stage, attacks by predators caused larvae to turn and swim away from the potential threat. When threatened, larvae would also remain motionless for some time and move out of the predator grid only when the predator's activity level decreased. Again, in most cases, several attacks would be necessary for larvae to swim out of the predator grid.

3.4 Foraging/Predator Avoidance Trade-offs

The foraging data analyzed in this section were obtained by combining the frequency of foraging MAP's (i.e. orient, attempt, success and pass) from all three grids in the rearing chamber (i.e. total foraging activity). Multivariate and univariate analyses revealed that week*treatment and week*food level interactions significantly influenced foraging activity in the presence of a predator (Tables 8 and 10, Fig. 11) As discussed earlier, mean foraging activity was found to increase at week two in medium and high food conditions. This increase was maintained over the course of the experiment in control aquaria. However, exposure to a predator in predator treatments resulted in a decrease in foraging at week three.

Examining the data on a weekly basis and within each food level, I found that cod larvae foraged significantly less under high food densities at weeks three, four, five, and six, and under medium food conditions at week four, when exposed to a predator (Table 11, Fig. 11). Overall foraging activity was low in larvae fed 500 prey/l and was not influenced by the presence of a predator (Fig. 11). Associated with decreased foraging was high mortality after week two in the low food aquaria.

MANOVA results indicated that the total frequency of orient, attack, and pass MAP's performed by larvae were significantly influenced by the presence of a predator and this in turn differed depending upon age (i.e. week) and food level (Table 9). Under high and medium food densities these MAP's increased at week two. In the presence of a predator, however, the frequency of orient, attack and pass decreased at week three and thereafter (Figs. 12-14). Results examining these data on a weekly basis within each food level are summarized in Table 10. As expected, these results are similar to those for foraging activity (Fig. 11).

To examine larval MAP's in more detail, data from the predator, middle and non-predator grids were analyzed separately. Foraging activity in the middle and non-predator grids were not significantly influenced by the presence or absence of a predator (Tables 12,14,15,17, Appendix 1;Figs. 3a-4a). However, a significant multivariate week*treatment interaction was observed in predator grids (Table 18, Fig. 15). Examination of univariate analysis also showed a significant week*treatment interaction (Table 20). This interaction indicates that the predator-mediated effect on larval foraging activity varied with larval age (i.e. week). Qualitative observations indicated that for both medium and high food treatments, larvae in the predator grid of treatment aquaria foraged less than larvae in the predator grid of control aquaria. Examining these differences on a weekly basis, and within each food level, larval foraging activity was found to significantly decrease in the presence of a predator at week three and thereafter when reared at 4500 prey/l (Table 21, Fig. 15). A decrease in foraging activity was observed at week four in larvae fed 1500 prey/l, but this was not significant (Table 21, Fig. 15).

The components of foraging activity (i.e. orient, attack and pass) were examined in more detail to further characterize larval foraging behaviour. As expected, these results were similar to those observed for overall foraging activity. Non-significant treatment effects were obtained for all feeding MAP's performed by larvae in the middle and non-predator grids (Tables 13,14,16,17, Appendix 1; Figs. 5a-10a). In contrast, within the grid adjacent to the predator, MANOVA revealed that age (i.e. week), food level, and the presence of a predator significantly influenced the frequency of orient, attack, and pass performed by larval cod (Table 19). Subsequent examination of univariate results found similar significant main effects, as well as a significant week*treatment interaction, for these MAP's (Table 20).

Overall decreases in orient, attack, and pass were observed in predator grids for high and medium prey abundances (Figs. 16-18). Specifically, orient and pass were performed significantly less often in high food treatments during weeks three and thereafter (Table 21, Figs. 16 and 18) in the presence of a predator. When exposed to a predator, larvae in the high food treatments also performed fewer attacks during week three and thereafter, but these differed significantly from control larvae only during week 4 (Table 21, Fig. 17). Larvae reared at 1500 prey/l performed fewer orients, attacks, and passes in the predator grid of treatment aquaria, but these did not differ significantly from those performed in the predator grids of control aquaria (Figs. 16-18). The frequency of orient, attack and pass performed by larvae reared in low food conditions was not influenced by the presence of a predator (Figs. 16-18).

3.5 Swimming Behaviour in the Presence of a Predator

Swimming behaviour of larval cod was typically characterized by short, intermittent bursts produced by caudal fin action, followed by periods where larvae remain motionless.

Initially, time swimming was summed across all grids to produce a value for total swimming duration. Significant multivariate week*treatment (HL trace F=3.00, p=0.0001) and week*food level interactions were obtained (HL trace F=2.7, p=0.0001). Similarly, univariate results yielded the same significant interactions (Tables 8-10).

A peak in swimming duration was observed at week three in larvae reared in control tanks and fed 1500 and 4500 prey/l (Fig. 19). Under high food conditions this increase in swimming duration remained relatively constant throughout the experimental period. A slight decrease in mean swimming duration was observed at week four in control aquaria maintained at medium prey densities. In contrast, commencing at week three, and for every week thereafter, larval cod in the medium and high prey densities spent less time engaged in swimming behaviour when in the presence of a predator. Bonferroni post-hoc t-tests showed that larval cod significantly reduced the amount of time swimming in the presence of a predator in high food aquaria at weeks three, four, five, and six, and at weeks three and five in medium food aquaria (Table 11, Fig. 19).

To examine swimming behaviour more closely, data from the predator, middle, and non-predator grids were analyzed separately. In middle and non-predator grids, the presence of a predator did not significantly influence the amount of time larval cod spent swimming during an observational session. However, time spent swimming increased with age and food density (Tables 12-17, Appendix 1; Figs. 11a-12a).

In the grid adjacent to the predator, larval swimming was significantly influenced by the presence of predators (Tables 18-20). In this grid, larvae reared at high and medium prey densities began to show decreases in the amount of time spent swimming at week three (Fig. 20). Further examination of swimming duration on a weekly basis and within each food level showed that larvae reared at 4500 prey/l swam less in the presence of a predator at week three, four, five and six. This decrease was significantly different from control observations at weeks four, five, and six (Table 21, Fig. 20). Larvae reared at 1500 prey/l showed a non-significant decrease in time spent swimming at weeks three, four, and five when in the presence of a predator.

The magnitude of the decrease in swimming was related to prey density, with larvae reared at high food densities swimming less than larvae reared at medium food densities. In control tanks, a peak in swimming duration was observed at week three for high and medium prey densities. In these tanks, at high prey densities, mean swimming duration remained relatively constant over time (i.e. as larvae grew). In control, medium food aquaria a slight decrease in swimming duration was observed at weeks four and five (Fig. 20). The presence of a predator did not influence swimming duration of larval cod in the predator grid at low food densities. Larvae did, however, decrease the amount of time spent swimming during week two.

3.6 Larval Behaviour within Treatment Aquaria

Because a grid effect was found when comparing control and treatment aquaria (i.e. larvae decreased foraging and swimming behaviour in the predator grid of treatment tanks), a within-tank examination was employed to determine if the frequency of MAP's performed by cod larvae varied between the predator, middle and non-predator grids of treatment aquaria. A significant grid effect was observed (HL trace $F_{4,1329}$=14.26 p<0.0001). Duncans post-hoc tests showed that larval foraging activity and swimming duration did not differ significantly between middle and non-predator grids, but each of these grids differed significantly from the predator grid (Table 22). Larvae in treatment tanks swam and foraged significantly less in the grid adjacent to the predatory stickleback (Figs. 21-22) indicating trade-offs between these behaviours and risk of predation. The magnitude of these trade-offs was greater in high food treatments when compared to medium food treatments (Figs. 21-22) and these trade-offs appeared one week earlier in the high food treatment. No such trade-offs occurred in the low food treatment.

3.7 Growth and Morphological Development

At hatching, larval cod were relatively transparent with a yolk sac, an undifferentiated gut, non-functional mouth and gills, partially pigmented eyes, and a mean standard length of approximately 5.3 mm (SD±0.07). At the onset of first feeding (day 4 post-hatch), the jaw had become functional, eyes fully pigmented, and the gut had grown and differentiated.

Feeding in larval cod began on day 3 post-hatch, when algae was first noted in the guts of many of the larvae. The following day, rotifers were observed in the stomach. By day 6, yolk-sac reserves were nearly consumed in some larvae and complete absorption was noted on day 11. Larvae began to consume *Artemia* on day 14.

Analysis of variance showed that the presence of a predator did not significantly influence growth parameters. Examination of replicate tank effects within each food level were also found to be non-significant. Consequently, treatment and replicate tank data were pooled for further analysis. Two-way analysis of variance, testing for day and food level effects, was performed on this combined data. A significant day*food level interaction was found for all variables except dry weight (Table 23).

Growth in cod larvae was directly related to food density. At high prey densities, larvae grew faster and survived longer than larvae reared at lower prey densities (Figs. 23-24). An increase in mean values for all growth variables was found commencing on day 11 (Figs. 23-24). The magnitude of this increase was greatest in high food treatments. This increase coincides with an increase in feeding behaviour (Fig. 11) and, as a direct consequence, an increase in the amount of food observed in larval guts (Fig. 5). Post-hoc comparisons performed for each day and within each food level showed significant differences in standard length, eye diameter, and myotomal height at day 31 for medium versus high food larvae (Table 24, Figs. 23-24). A significant difference in myotomal height was also observed at day 11 for larvae reared under low food densities when compared to larvae reared at high food densities (Table 24, Fig. 24). Taking all sample days together larval mean dry weight was significantly higher for larvae reared at 4500 prey/l ($\overline{x}$=0.233) when compared to larvae reared at 1500 prey/l ($\overline{x}$=0.180) and 500 prey/l ($\overline{x}$=0.107). Also, the dry weight of larvae reared at 1500 prey/l differed significantly from the dry weight of larvae reared at 500 prey/l.

Survival was directly related to prey abundance, as larvae did not survive beyond week two at 500 prey/l and week five (day 36) when reared at 1500 prey/l conditions. Due to decreasing numbers of larvae, experiments were terminated at week six in the 4500 prey/l tanks. However, the remaining larvae from this treatment survived to metamorphosis indicating that this level of prey was sufficient for successful larval development.

DISCUSSION

Past research examining larval cod behaviour has been of short duration and focused mainly on larval activity, and few studies have described foraging and predator avoidance behaviours (Skiftesvik 1993, MacKenzie and Kiorboe 1993, Solberg and Tilseth 1984, Ellersten et al. 1980). My study, however, specifically defines Modal Action Patterns (MAP's) for foraging, swimming and predator avoidance behaviours in larval cod over an extended period of growth and documents the ability of cod to trade-off behaviours.

4.1 Foraging Activity

Foraging in larval cod consisted of four feeding MAP's: orient, pass, attempt, and success. These MAP's remained in the behavioural repertoire of the larvae throughout the experimental period. Feeding MAP's occurred between intermittent swimming bouts. This type of foraging behaviour; where larvae travel short distances, stop and move again if prey are not observed, has been termed a saltatory search strategy. Browman and O'Brien (1992 a,b) documented similar prey search strategies in golden shiner and white crappie larvae.

The frequency of foraging in larval cod varied with their growth and ambient prey density. Larvae reared at high prey densities foraged more, grew faster, and survived longer than larvae reared at lower prey densities. Overall, larval survival was found to be related to foraging environment (i.e. prey density). Other laboratory studies examining the effects of prey density on larval fish have also reported increased foraging rates, growth, and survival at high prey densities (Wyatt 1972, Laurence 1974, Houde 1977, Munk and Kiorboe 1985).

Under natural conditions, the density of prey organisms available to first-feeding larvae will range from sub-optimal to patches that exceed average prey densities (Frank and Leggett 1986). Unpredictable changes in prey densities due to hydrographic conditions can significantly influence larval mortality. The timing of such fluctuations in prey availability during a larva's ontogeny can result in variable survival. For example, in my experiments, I observed total mortality in larvae reared at low food densities during week two. This result suggests that prey densities during the transition from endogenous to exogenous feeding were not sufficient for larval growth and survival.

Increased survival associated with optimal prey densities early in development is thought to be linked with the ability of larvae to forage prior to total yolk-sac absorption. Under such conditions larvae have the potential to become larger, obtain surplus energy, and increase foraging efficiency, thereby making the transition from endogenous to exogenous feeding more successfully. For example, Atlantic halibut (*Hippoglossus hippoglossus*) larvae were observed to begin feeding as early as four weeks prior to yolk absorption (Pittman et al. 1990). Similar behaviour was documented in herring (Hunter 1980), cod, flounder (Yin and Blaxter 1986) milkfish (*Chanos chanos*), seabass (*Lates calcarifer*), and rabbitfish (*Siganus guttatus*) larvae (Bagarino 1986). My observations that both algae and rotifers were found in the guts of four day-old larvae also indicated that cod larvae begin foraging prior to complete yolk absorption.

Cod larvae, like the larvae of many other marine fish species, have been observed to ingest algae via filter feeding prior to yolk-absorption (Ellersten et al. 1980, Van der Meeren 1991, Thompson and Harrop 1991). Algal material appears to be important in preparing the gut and digestive system for first-feeding. Reitan et al. (1993) found that the addition of microalgae during first-feeding of larval turbot (*Scophthalmus maximus*) significantly improved initial growth rates and survival to metamorphosis. Since filter feeding does not require the development of a fully functional jaw, ingesting algal material may represent an additional nutrient source in undeveloped yolk-sac larvae.

It has been observed that if larval fish do not successfully initiate and maintain feeding behaviour by a "critical point" after yolk absorption, then swimming, foraging and survival will be reduced. This is termed the point of no return (PNR) or the time to irreversible starvation (i.e. even if larvae ingest food after this point they will be unable to digest prey items and death due to starvation is inevitable; Blaxter 1986). Time to reach this point is temperature and species dependent. Ellertsen et al. (1980) found that if cod larvae reared at 5°C did not feed by day 11 post-hatch they would reach a point of irreversible starvation marked by decreased foraging activity and increased buoyancy. Laurence (1978) reported this critical point to be day 10 in starved cod reared at 7 °C.

In my study, cod larvae which were reared at 7 °C and fed low prey densities decreased foraging and swimming behaviour during week two. Total mortality occurred in all low prey aquaria prior to week three. These results suggest that a prey density of 500 prey/l was not sufficient for larval survival. Even though small traces of food were observed in larval stomachs at low prey densities, this amount was not sufficient to prevent larvae from starving.

Yin and Blaxter's (1987 a,b) studies on larval herring, cod and flounder, and Skiftesvik's (1992) studies on cod and turbot larvae, documented similar declines in foraging and locomotor activity as starved larvae reached a PNR. Even though higher activity levels should increase the likelihood of encountering prey, lower activity levels associated with starvation in larval fishes may be a strategy employed to conserve energy, perhaps delaying time to irreversible starvation. In contrast, these trends were not observed in my experiment when cod larvae were reared at higher prey densities. Under these conditions, foraging and swimming activity increased at week two, coinciding with the successful transition from endogenous to exogenous feeding. Increased activity would increase a larva's probability of encountering prey items. Successful foraging by larvae in high food treatments was reflected in their growth patterns as well as gut fullness.

Associated with foraging is prey capture success, commonly defined as the ratio of feeding attempts to the number of successful bites (Drost 1987). A larva's ability to feed is not always exclusively dependent upon the development of specific structures (i.e. mouth parts), as feeding generally involves some degree of learning (Blaxter, 1986). In my experiment, larval cod initially attempted to feed by biting at prey items, but these early feeding attempts were not always successful. Failure to successfully capture a prey item may be the result of larvae aiming inaccurately, not attacking fast enough, or the prey item moving out of the larva's visual field. From my results it was evident that feeding success varied with larval age and prey density. Feeding success increased with larval age, and the frequency of attempt and success MAP's, which define "capture success", was highest at 4500 prey/l . At high food densities, encounter rates with prey items should increase, thus providing larvae with increased foraging opportunities. As prey densities decrease, search volumes and search times increase, resulting in fewer foraging opportunities. The energy expenditures associated with locating food items should therefore be higher at lower prey densities. Survival is highly dependent upon a larva's ability to encounter and capture prey items. In this study, two week-old cod larvae reared at 500 prey/l showed high capture success rates, but relatively low frequencies of attacks. These results indicate low encounter rates with prey items, but these encounters typically resulted in larvae successfully consuming prey items. Conversely, at higher prey densities, both capture success and frequency of attacks increased at week two post-hatch, indicating that larvae were encountering and consuming adequate numbers of prey for both growth and survival.

In many species of fish larvae, capture success improves rapidly with experience and morphological development (Blaxter 1986, Drost 1987, Noakes and Godin

1988). For example, Ellersten et al. (1980) observed that at the onset of exogenous feeding, larval cod had a feeding success of 32-62% which increased to 90 % towards the end of yolk absorption (days 7-12 post-hatch). Ellersten et al. (1980) has attributed these increases in capture success rates to improved manoeuvrability at the time of first feeding. Similarly, in my experiments larval cod were observed to have a feeding success ranging from 33-65% during week one post-hatch which increased to over 90% by the end of complete yolk absorption. In other marine fish species, capture success at the onset of first-feeding is much lower: 6% in herring (Rosenthal and Hempel 1970), 10% in northern anchovy (Hunter 1972) and 17% in american shad (*Alosa sapidissima*) (Ross and Backman 1992) all of which increased with growth and development.

It does not seem unreasonable that a larva's ability to locate and capture prey increases with both morphological development and experience. Miller et al. (1992) observed dramatic improvements in the foraging abilities of larval alewife (*Alosa pseudoharengus*), yellow perch (*Perca flavescens*), and bloater (*Coregonus hoyi*) as they developed. Browman and O'Brien (1992a) reported similar results for white crappie larvae. Cod larvae reared at high and medium prey levels demonstrated similar improvements in foraging capabilities (i.e. attack success) with age (i.e. week).

Increases in gut fullness, standard length, and myotomal height reflect this foraging success. In larval cod, it appears that the development of efficient foraging behaviour is closely associated with morophlogical development. For example, as sensory systems become refined, larvae become better equipped to detect and respond to prey individuals, while the development of fins, muscle mass, and increased body length should improve a larva's manoeuvreability, attack speed and swimming behaviour (Noakes and Godin 1988). Together, these features would be expected to play a role in improving foraging behaviour in larval cod. Conversely, under sub-optimal foraging conditions, starvation can seriously hinder larval growth and in turn the development of associated behaviours. Little or no growth observed in poorly fed larvae often results in the deterioration of body tissue, such as musculature, which can hinder locomotor capabilities, and impair the development of sensory systems. Under such conditions, larval foraging behaviours can become less efficient. The small traces of food observed in the guts of cod larvae which were reared at low prey densities during week two of the experiment suggests poor nutritional state. Energy requirements may have been met through the larva's ability to break down its own body tissue, thereby resulting in weaker larvae which quickly approached a point of starvation. As a result of this deteriorating condition, a decline in foraging behaviour was observed.

Kjorsvik et al. (1991) studied the early development of the digestive tract in larval cod, as well as some of the consequences associated with starvation and their effects on larval morphology. She observed that starved larvae had a gut morphology markedly different from that of feeding larvae. Starvation induced cellular degeneration, shrunken epithelial cells, reduced microvilli, and liver and pancreas degeneration. Periods of starvation were reported to cause irreversible damage to the gut, which ultimately reduced digestive and absorptive efficiencies. These results suggest that the early effects of starvation may still allow larvae to consume prey items, but not digest them. This may explain the presence of small amounts of food in the guts of dead larvae reared at low prey densities. In comparison, under optimal feeding conditions where gut morphology has not been affected by periods of starvation, Kjorsvik et al. (1991) reported an increased ability of the gut to absorb lipids and proteins. Therefore, the increased standard length and myotomal height observed in larval cod reared at high and medium prey densities may reflect an increased ability in the gut of these larvae to absorb such food nutrients.

In conclusion, it is evident that morphological development and survival can be drastically influenced by a larva's foraging environment. In the absence of predators and at high prey densities, cod larvae have the ability to feed efficiently, grow and develop quickly, thereby shortening the 'critical' larval period and increasing their overall potential for survival.

4.2 Larval Response to Predation Threat

In this study, larval response to predator attack varied with growth and development. At hatching, responsiveness to predator attack was low. However, as larvae grew, they began to exhibit fleeing behaviours and later incorporated avoidance responses into their behavioural repertoire.

Vulnerability of newly-hatched, yolk-sac and first feeding larvae to predation is associated with undeveloped sensory and motor structures. Typically, during predatory attacks, fish larvae are exposed to a variety of stimuli (i.e. visual, auditory, mechanical, tactile, and olfactory; Fuiman 1986, Batty 1989). In early life history stages, poorly developed sensory systems can hinder a larva's ability to interpret such stimulii, thereby resulting in low responsiveness to predation threat.

In my study, predators were maintained behind a transparent partition and it was assumed that larvae would only be exposed to visual stimuli. In these experiments, cod larvae did not actively respond to predator attacks until day six (at high food densities). Due to the fact that the eyes in newly-hatched cod larvae are not fully pigmented until approximately day three post-hatch, the lack of a well developed visual system early in development could explain this initial lack of responsiveness to attacking predators. Batty (1989) found a similar result in smaller, younger herring larvae (i.e. up to 20.4 mm total length). These larvae did not begin to elicit an escape response to visual, stimuli until reaching a total length of 25.5 mm. They did, however, initially respond to tactile and mechanical stimuli.

Early in development, many larval species are highly reactive to tactile stimuli (Eaton and DiDomenico 1986, Noakes and Godin 1988). For example, Yin and Blaxter (1987a,b) found that a startle response could be elicited in yolk-sac cod, flounder, and two species of herring larvae when touched with a fine probe or by creating suction with a pipette. Initial response rates in larval cod were 34-40% when touched with the probe, but increased to 70-80% when a suction stimuli was produced by the pipette. This increase in responsiveness may represent an adaptative response to planktivorous fish predators which feed through suction mechanisms. In our laboratory, P.J. Williams (unpubl. data) has observed that predatory amphipods elicited an escape response in yolk-sac cod larvae when they came in physical contact with the larvae. It appears that larval cod may be dependent on tactile cues rather than visual stimuli in the early stages of development. During this vulnerable period, cod larvae likely rely on being relatively inconspicuous (i.e. transparent body) to avoid detection from visually feeding predators.

Little is known about the visual system in larval cod. It is thought however, that acuity improves with growth of the eye (Blaxter 1975, Johns 1981, Noakes and Godin 1988). In my study, eye diameter in cod larvae increased with larval size, indicating the potential for improved visual capabilities. As a larva's visual system becomes refined, associated foraging, predator detection, and predator avoidance behaviours would be expected to develop accordingly.

Braum (1967) determined that the visual field of *Coregonus wartmanni* larvae consisted of a spherical region measuring 10 mm in diameter. This was approximately equal to one larval body length. Hunter (1981) also estimated the maximum reaction distance for some fish larvae to be one body length. Similar reactive distances were used by Skiftesvik and Huse (1987) and Coughlin et al. (1992) when studying feeding and swimming behaviour in larval cod and clownfish (*Amphiprion perideraion*), respectively. Assuming one body length is an acceptable criterion for estimating visual fields, it is evident that larval cod respond to visual stimuli within a relatively small reactive space. For instance, in my experiment, larval cod reared at high prey densities and sampled at days 6, 11, 21, 31 and 46 post-hatch would possess reactive distances of 5.7, 5.8, 7.2, 8.7, and 9.6 mm, respectively (i.e. corresponding to one larval body length). Solberg and Tilseth (1984) found similar results when examining perceptive distances in first-feeding cod larvae. In larvae 5-8 days post-hatch, they observed perceptive fields to vary in distance from 0.5 to 1 standard body length. They also noted that larvae could respond to prey both above and below the horizontal body axis. H. Browman (per comm) studied foraging behaviour in larval cod measuring 8-9 mm in length. He observed that the visual perceptive field for larvae of these lengths extended a maximum distance of 12 mm and had a maximum reactive angle of 80-90°. However, as these distances were calculated for small particles (i.e. rotifers), one might expect larvae to possess larger perceptive fields for larger objects such as attacking predators. Browman's results do suggest that at some point in larval development perceptive fields become greater than one body length. This is likely correlated with increased eye diameter and the development of retractor muscles which allow the eye to focus at greater distances (O'Connell 1981).

Based on the estimated values stated above, it would be reasonable to assume that larvae in the middle and non-predator grids would not respond to predator attacks as attacks would be outside their visual range. My results showed that fleeing and foraging trade-offs in cod larvae only occurred within the grid adjacent to the predator, possibly reflecting their relatively small visual field. It was also observed that larval cod only responded to predator attacks directed at their head region, and in most cases, several attacks were necessary to elicit a response. These results suggest that in the early developmental stages, cod larvae lack a refined visual system which results in low responsiveness to predatory threat.

The ability of fish larvae to detect movement and discriminate contrast is thought to be related to the presence of rods in the retina, while cones are responsible for acuity and colour vision (Johns 1981, Blaxter 1986). One could speculate that larvae, possessing upon hatch eyes with high concentrations of rods, would exhibit improved feeding, predator detection, and avoidance behaviours. For example, rods found in the retina of newly-hatched guppies (*Poecilia reticulata*), presumably evolved to allow fry to avoid parental predation (Blaxter 1986). In contrast, Batty (1989) observed the absence of rods in the eyes of newly-hatched herring larvae. However, once the larvae had reached a length of 28 mm, rods had begun to develop within the retina. The presence of these cells corresponded with the emergence of a startle response towards visual stimuli. It has been suggested that rods do not develop in larval cod until they metamorphose (Adoff 1985) and descend to benthic habitats of low light intensities. Prior to metamorphosis, cod larvae may rely solely on cones in the retina to detect potential prey items and predators. Regardless of eye development, it is quite obvious that larval cod exhibit increased responsiveness to visual attack cues with age, suggesting improved visual capabilities with growth.

Fleeing behaviour is a characteristic escape (i.e. startle) response documented in many larval fish studies (Fuiman 1986, Yin and Blaxter 1987a,b, Pittman et al 1990, Williams and Brown 1992a,b). Escape responses are probably the only defence mechanisms many larval fish employ once an attack has been initiated. An escape response is characterized by very fast and simultaneous contractions of the body musculature, known as a quick or c-start, followed by a period of rapid burst swimming (Eaton and DiDomenico 1986, Williams and Brown 1992). In my study, larval cod began to respond to visual strikes by fleeing from attacking predators. These responses were not observed until day 6 and then only in larvae from high food treatments. The frequency of fleeing behaviours increased with larval age (i.e. week), suggesting that growth and development are important in the ontogenic appearance of this behaviour. Such increases in larval escape response with growth have been documented in northern anchovy (Folkvord and Hunter 1986), winter flounder (Williams and Brown 1992b), and Atlantic herring (Fuiman 1993). These increases have been attributed to the maturation of visual and lateral line systems, as well as increased body length.

Size-dependent vulnerability to predation has been documented in many larval fish species, whereby smaller bodied, slower growing larvae incur higher rates of mortality (Webb 1981, Bailey 1984, Folkvord and Hunter 1986, Fuiman 1989, Margulies 1990). Since growth rate is largely a function of prey availability, size-specific vulnerability to predation can be influenced by a larva's foraging environment. Larval cod reared at medium prey densities initiated fleeing responses later and to a lesser extent than did cod larvae reared at high prey densities, while larvae reared at low prey densities did not respond to predator attack. These results are consistent with the proposal that larval size and condition are probably influencing response rates at these prey densities.

Due to the lower responsiveness exhibited by cod larvae reared at low and medium prey densities, one could predict that predation rates would be higher on these smaller larvae compared to similar aged, but larger, larvae from high food treatments. One would expect that with growth, development, and experience, a larva's ability to escape predatory attacks would increase. Such an increase is often necessary as larger, highly pigmented larvae are more readily detected by predators (Folkvord and Hunter 1986). Webb (1981) correlated increases in body size with increased escape speeds and total distance travelled by larvae, which resulted in declining predator attack success. Bailey (1984) also correlated body length with escape ability in larval cod, plaice, herring, and flounder. He found that in the presence of three planktonic invertebrate predators, longer larvae employed faster, more effective escape responses, and that the timing and speed associated with these escape responses was found to influence predator success rates. Margulies (1990) reported similar results for larval white perch, whereby larger larvae initiated escape responses more rapidly than smaller ones (i.e. predator attack success decreased from 100% at hatch to 10% at day 38 post hatch).

Larval condition will also influence responsiveness to predation threat. During periods of starvation, deterioration of muscle tissue and sensory systems can inhibit a larva's ability to detect and respond effectively to predatory attacks. For example, degradation of white muscle tissue associated with burst swimming behaviour, may influence both speed and timing of larval escape responses. Both Yin and Blaxter (1987b), and Bailey (1984) observed larval condition to influence behaviour, as starved larvae exhibited decreased response rate, swimming behaviour, and escape speeds. This may explain why flee MAP's were not observed in larvae reared at 500 prey/l. Ellersten et al. (1980) also observed starved cod larvae to increase in buoyancy, presumably due to the degradation of body tissue and an increase in water content. Increases in buoyancy and decreases in body mass may have serious implications for larvae with respect to risk of predation. Poorly-fed larvae which become increasingly buoyant can become associated with surface waters where they may be detected more readily by predators.

In my study, larval cod reared in high food treatments began to change their response to predatory attacks during week four. Rapid fleeing responses decreased and larvae began to employ avoidance behaviours (i.e. larvae would swim several centimetres away from the point of attack, turn 180°, and remain motionless). This behaviour may be a precursor to predator inspection and suggests that larval cod are assessing the threat of predation by modifying their response. Similar behaviours were observed in larval sticklebacks ranging in length from 11.8 to 12.5 mm (Bishop and Brown 1992). Using one body length as an indicator of visual field, larvae which initially swim away from predator attacks followed by turning back 180°, would not be expected to detect the predator. The advantage of this behaviour, however, is that it would allow larvae to determine if the predator was still in pursuit, and if so further avoidance behaviour could be employed if necessary.

Approaching or turning to face a predator may at first appear to be paradoxical: why would an individual remain in the vicinity of a potential predator? For larvae to employ such risky behaviour, one would assume an associated fitness benefit. Prey individuals which approach potential predators have the opportunity to obtain information regarding the predator's identity and motivation patterns (Dugatkin and Godin 1992). Such behaviours may, however, be energetically less costly when compared to the energy expenditure associated with fleeing. These behaviours may, however, increase the risk of predator attack and would, therefore, not be expected to appear in a larva's behavioural repertoire until sensory and locomotory systems were adequately developed.

Experience may also play a role in modifying larval behaviour. A decrease in larval fleeing may therefore be attributed to learning (i.e. larvae were never consumed during a predatory attack due to the transparent divider). In this experiment, because larvae were exposed to predation threat for relatively short periods during observation sessions learning through experience may have been minimal.

In conclusion, the ontogeny of predator detection and avoidance responses in larval cod is closely linked to morphological development. The foraging environment in which a larvae hatches will greatly influence its risk of mortality due to both starvation and predation. Larvae in a good foraging environment will have opportunity to forage early and grow quickly, thereby developing the sensory and locomotory capabilities necessary to detect and avoid predators.

4.3 Foraging/Predator Avoidance Trade-offs

Prey organisms should possess the ability to assess their environment and behave flexibly towards potential predators. In order to balance energy costs and benefits, activities which are compromised under the threat of predation should be traded-off in a manner that reflects the magnitude of predator threat (i.e. threat-sensitivity; Helfman 1989). In this study, larval cod reduced foraging and swimming behaviour in the presence of a predator and in high risk areas of treatment aquaria, thus showing threat sensitivity. These reductions, however, did not emerge until after a period of growth and development. The timing and magnitude of these trade-offs differed between larvae reared at medium and high prey densities.

Foraging trade-offs in larval cod were only observed in the grid adjacent to the predator. Larval foraging behaviour and activity levels in middle and non-predator grids were not significantly influenced by the presence of a predator. Two possible explanations can be used to interpret these results. First, Helfman's (1989) threat-sensitive predator avoidance hypothesis predicts that prey individuals should possess the ability to assess risk and trade-off behaviours in an appropriate graded manner. If this was the case, larvae in the middle and non-predator grids would have determined predation risk to be minimal (i.e. predator distance was too great to pose immediate threat). Under these circumstances, reducing foraging for predator avoidance would be costly, especially since feeding is crucial for larval survival in the early developmental stages. The second explanation, however, may be more realistic as it would suggest that in the middle and non-predator grids, larvae did not possess the visual ability to detect predators. Again, foraging trade-offs would not be expected.

Focusing on the predator grid, larvae reared at high food densities began to reduce foraging at week three.

Larvae significantly decreased their foraging and swimming activity in this grid. Several studies have documented that when faced with a threat of predation, prey individuals will reduce activity levels (Main 1987, Godin and Sproul 1988, Macchiusi and Baker 1992, Williams and Brown 1992). Since moving individuals are more noticeable to predators, prey organisms may decrease the probability of being detected and attacked by remaining motionless in the presence of visually feeding predators (Kerfoot and Sih 1987). However, potential costs associated with reduced activity levels include decreased encounter rates with prey and inefficient foraging. The effects of predator induced reductions in foraging on larval survival will depend on larval size and developmental state (i.e. amount of energy reserves), as well as nutritional demands (i.e. hunger level).

When prey densities are high, the costs of reduced activity levels and lost foraging opportunities may be minor, as lost energy could be easily regained once the threat of predation is removed. In this experiment, larvae were exposed to predation threat for short observational periods. Under these conditions (i.e. high prey density and limited predator exposure), the costs associated with reduced foraging were likely minimal, as evidenced by the lack of a predator effect on larval growth rates over the 6-week study period. Also, as larvae become satiated, the likelihood of starvation decreases, making alternative activities such as predator avoidance increasingly important. Conversely, at low prey densities, there are increased costs associated with searching for items (i.e. fewer prey, more swimming). Therefore, under low prey conditions, larvae may become more willing or may have to accept a higher potential risk of predation in order to obtain neccessary foraging gains. For example, if an organism is near the point of starvation, engaging in potentially life threatening behaviour (i.e. foraging in the presence of predator) becomes more of a behavioral option, especially if the potential exists to obtain food. Hunger level therefore has the potential of playing an important role in shaping decision making processes.

In my experiments, food availability was shown to influence the magnitude of larval response to predation threat. Such a reduction in foraging was greatest at week four in larvae reared at medium prey densities, one week later than for larvae reared at high prey abundances. Work by Magnhagen (1988) on sand gobys (*Pomatoschistus minutus*) and black gobys (*Gobius niger*) found that in the presence of a predator, starved gobys were more willing to forage than fed gobys, thus trading-off risk of predator attack for immediate energy gains. Since organisms are expected to employ behaviours that maximize fitness, the tendency to take higher risks at increased hunger levels should result in fitness benefits.

As stated previously, the timing of foraging/predator avoidance trade-offs in larval fish is strongly correlated with size and developmental state. Because the larval period is one of rapid growth and development, changes in larval behaviour are expected (Noakes and Godin 1988). My results indicate that faster growing larval cod reduced foraging for predator avoidance at week three and at a standard length of 7.2 mm, while larvae reared at medium prey densities began to show this reduction one week later but at a similar size (i.e. 7.3 mm standard length). The timing of these trade-offs also corresponded to a rapid increase in myotomal height, eye diameter, and standard length. Larval cod may therefore be exhibiting a size-dependent, developmental response to the timing of this trade-off. It is clear that the ability to respond in a threat-sensitive manner requires that a prey individual possesses the ability to assess its environment. As fish larvae grow and develop, they become better equipped to evaluate their environment resulting in the emergence of behavioral trade-offs which can change with vulnerability over the larval period.

Several larval fish studies have documented changes in behavioral trade-offs during early developmental stages.

Williams and Brown (1992a) demonstrated that 15-week-old lumpfish larvae no longer reduced foraging in the presence of a predator. At this size, predators were no longer perceived as a threat, and consequently, larvae shifted their behavioral response. Bishop and Brown (1992) also found larval stickleback to increase foraging in the presence of predators, as they increased in size relative to the size of predators. In the presence of small predators ($\overline{x}$=4.12 cm total length) two-week-old larval stickleback did not reduce foraging, however, in the presence of medium ($\overline{x}$=5.0 cm) and large ($\overline{x}$=6.4 cm) predators, larval foraging was significantly reduced. By week five, post-hatch larvae exposed to medium sized predators no longer reduced foraging. These results indicate that sticklebacks have the ability to assess risk and modify foraging behaviour in a threat-sensitive manner early in ontogeny. This early response to predation threat is likely a result of stickleback larvae hatching well-developed (i.e. notochord flexed, mouth funtional, eyes developed, relatively large), having parental care through week one post-hatch, as well as a relatively short larval period (approx. 30 days) marked by rapid growth and development. In comparison to larval sticklebacks, larval cod hatch poorly developed (i.e. mouth and eyes not functional, small), and grow more slowly. In my study, cod larvae did not begin to trade-off foraging until week three post-hatch in high food treatments. The only observed change in larval behaviour in response to predation threat was a reduction in flee MAP's, which were replaced with avoidance behaviour after week four. These results indicate that cod larvae possess the ability to assess predation threat and modify their behaviour. As predator-prey size ratios decline over ontogeny, I would expect larval cod to reduce the magnitude of their behavioural trade-offs. This may occur near metamorphosis. Results from the stickleback (Bishop and Brown 1992) and the current studies suggest that both size and developmental state influence the timing and magnitude of foraging/predator avoidance trade-offs in larval fishes.

My experiments showed that larval cod began to reduce foraging behaviour in the presence of predation threat at a standard length of approximately 7.0 mm. The question that can now be posed is - 'What factors are influencing the emergence of this trade-off ?' Many studies have shown that factors other than body size play a role in determining prey vulnerability and responsiveness to predator attack (P.J. Williams unpubl. data, Pepin et al. 1992). For example, the appearance of body pigmentation and increased activity levels often make larval fish more readily detectable to visually feeding predators. In my study, the timing of foraging trade-offs in larval cod appeared to correspond with an increase in body pigmentation and the development of internal organs. A consequence of these developmental changes was increased larval visibility. Fahay (1983) observed the emergence of lateral pigment streaks forming on the tail region of larval cod (6.5 mm total length), which eventually fused and resulted in uniform pigmentation at 8-10 mm. In my study, I observed similar increases in body pigmentation in larval cod at approximately 7 mm. At this stage larval swimming and foraging activity were also observed to increase. The emergence of a foraging-predator avoidance trade-off in larval cod may, therefore, be necessary in order to counter-balance increased visibility due to both body pigmentation and activity levels which are associated with increased growth and development.

In mesocosm experiments, Pepin et al. (1992) investigated the effects of body size on vulnerability to a vertebrate predator in larval caplin (*Mallotus villosus*). They found contrasting patterns in size-dependent vulnerability. When comparing larval mortality rates between experimental trials, an increase in length (i.e. developmental state) resulted in decreasing predation rates. However, an examination of within experimental trials found that larger larvae incurred higher rates of predation. If predation rates are higher on larger and more visible larvae, it may not be necessary for newly-hatched cod larvae to trade-off foraging. They may rely solely on body transparency during early stages of development when reductions in foraging could influence survival. Of course, in the wild, predation by non-visual predators (i.e. jellyfish) will influence mortality at this time. It is evident that many factors influence the relationship between predator and prey. All of these must be considered when examining the costs and benefits, as well as the timing of associated behavioral trade-offs.

4.4 **Conclusions**

The ability to feed while at the same time avoid predation often produces a situation where two necessary but incompatible behaviours conflict. Since starvation and predation are the two major causes of mortality in larval fishes (Blaxter 1986), larvae may often be forced to take risks in one activity in order to gain benefits in another. Because it would be energetically costly to give up foraging opportunities in the presence of non-threatening predators, animals should possess the behavioural flexibility to assess their environment and behave in a manner that maximizes fitness (Lima and Dill 1990, Milinski 1993). A survival advantage should therefore be associated with the ability to respond to a predator in a threat-sensitive manner.

The first objective of my study was to determine if larval cod alter their foraging activity in the presence of a predator. I observed that larval cod reduced foraging and swimming activity in the presence of a predator. These results indicate that larvae have the ability to assess predation risk and trade-off foraging against predator avoidance. To determine the long-term effects of reduced foraging and swimming activity (i.e. behaviours that were traded-off) on larval growth and survival, it would be necessary to expose larvae to predation threat over an extended period of time. In such cases, one would be able to examine how larval fitness was influenced by such trade-offs.

The second and third objectives of my study were to determine the effects of prey density on the timing of foraging/predator avoidance trade-offs, as well as on larval growth and morphological development. Results showed that foraging environment and morphological development were found to influence larval behaviour and the timing of foraging and swimming trade-offs. At medium prey densities, smaller and slower growing larvae reduced foraging and swimming behaviour one week later, and to a lesser extent than larger and faster growing larvae reared at high prey densities. The timing of foraging/predator avoidance trade-offs in larval cod appeared to be size-dependent, demonstrating that growth and development are linked with the emergence of behaviour and a larva's ability to assess risk.

It appears from both my study and work by Bishop and Brown (1992) that larval cod and larval stickleback have the ability to assess predation risk relatively early in development. It would be interesting to examine if this phenonema exists for other larval species hatching at different sizes and stages of development.

Future research into the area of foraging and predator avoidance trade-offs in larval fishes should become increasingly important as scientists strive to obtain a better understanding of the mechanisms larvae employ to survive in the wild. Because the larval period is one of rapid growth and development, examining these behaviours from an ontogenic perspective should prove beneficial.

Table 1:

Operational Definitions of Foraging and Predator Avoidance MAP's in larval cod.

MAP	Definition
Swim	-forward movement of larva through water column accomplished by caudal fin action.
Motionless	-larva remains still.
Orient	-larva stationary and fixes on a prey item.
Attempt	-larva attempts to capture prey with mouth (i.e. bite) -marked by a posterior drive of the tail
Success	-identical to attempt except prey is captured
Pass	- larva orients on a prey item but does not bite,larvae then swims in another direction.
Flee	-continuous rapid swim in a straight line away from a predator attack.

Attack=Attempt + Success

Foraging Activity=Orient + Attack + Pass

Table 2. Results of a 2-way analysis of variance on the foraging activity of larval cod reared at low, medium, and high prey densities and in the absence of a predator (ie. control aquaria).
p significant at < 0.05.

source	df	F-value	p
wk	5	12.11	0.0001*
fl	2	43.79	0.0001*
wk*fl	5	5.49	0.0001*

Table 3. Results of Bonferroni post-hoc comparisons of foraging activity between larvae fed low, medium, and high prey densities in control aquaria.

Week	500 vs 1500 p/l	500 vs 4500 p/l	1500 vs 4500 p/l
1	0.247	0.0086**	0.141
2	0.0001*	0.0001*	0.148
3	----	----	0.004*
4	----	----	0.098
5	----	----	0.0001*

* significant at 0.05 (comparison wise alpha level=0.0055)
** significant at 0.1 (comparison wise alpha level=0.01)

Table 4. Foraging success, (% = success MAP's / attacks) in larval cod reared at low, meduim and high prey densities and in control aquaria.

age (wks)	500 p/l	1500 p/l	4500 p/l
1	7:17 41%	15:23 65%	11:33 33%
2	6:6 100%	25:26 96%	44:44 100%
3	------	29:35 83%	42:44 96%
4	------	18:24 73%	42:48 88%
5	------	11:16 68%	17:18 93%
6	------	------	20:22 92%

Table 5. Multivariate Hotelling-Lawley trace results for the total frequency of active MAP's performed by larval cod in predator, middle, and nonpredator grids of the larval rearing chamber. wk=week, tr=treatment (presence or absence of a predator), fl=food level. p significant at < 0.05 (*).

Source effects	df num	df den	F-value	p
wk	15	4100	6.560	0.0001*
tr	3	1368	16.48	0.0001*
fl	6	2734	8.877	0.0001*
wk*tr	15	4100	2.066	0.009*
wk*fl	18	4100	3.952	0.0001*
tr*fl	6	2734	0.445	0.849
wk*tr*fl	15	4100	0.647	0.837

Table 6. Univariate results for the total frequency of active MAP's performed by larval cod in predator, middle, and non-predator grids. wk=week, tr=treatment (presence or absence of a predator), fl=food level. p significant at < 0.05 (*).

Grid	source	df	F-value	p
Predator grid	wk	5	2.31	0.042*
	tr	1	14.5	0.0001*
	fl	2	1.16	0.312
	wk*tr	5	1.75	0.120
	wk*fl	6	1.12	0.351
	tr*fl	2	0.35	0.703
	wk*tr*fl	5	0.64	0.669
Middle grid	wk	5	1.28	0.271
	tr	1	0.05	0.820
	fl	2	3.01	0.049
	wk*tr	5	0.18	0.969
	wk*fl	6	0.83	0.549
	tr*fl	2	0.24	0.788
	wk*tr*fl	5	0.49	0.785
Non-predator grid	wk	5	1.45	0.202
	tr	1	1.05	0.305
	fl	2	1.57	0.209
	wk*tr	5	0.21	0.959
	wk*fl	6	0.87	0.516
	tr*fl	2	0.77	0.465
	wk*tr*fl	5	0.23	0.951

Table 7. Results of Bonferroni post-hoc comparisons examining weekly mean differences in the total frequency of active MAP's performed by larval cod in the predator grid of control and predator treatments.

food level	week 1	week 2	week 3	week 4	week 5	week 6
500	0.796	0.889	-----	-----	----	----
1500	0.619	0.415	0.501	0.145	0.341	----
4500	0.825	0.851	0.056	0.004**	0.0004*	0.019

* significant at 0.05 (comparison wise alpha rate = 0.004)
** significant at 0.1 (comparison wise alpha rate = 0.008)

Table 8. Multivariate Hotelling-Lawley trace results for total foraging activity and swimming duration by larval cod reared at low, medium and high prey densities in control and predator treatments. wk=week, tr=treatment, fl=food level. p significant at <0.05 (*).

Source	df num	df den	F-value	p
wk	10	2736	16.448	0.0001*
tr	2	1369	37.690	0.0001*
fl	4	2736	22.569	0.0001*
wk*tr	10	2736	5.403	0.0001*
wk*fl	12	2736	4.404	0.0001*
tr*fl	4	2736	0.313	0.869
wk*tr*fl	10	2736	1.229	0.266

Table 9. Multivariate Hotelling-Lawley trace results for total feeding MAP's (i.e. orient, attack and pass) and swimming duration by larvae reared at low, medium and high prey densities in control and predator treatments. wk=week, tr=treatment, fl=food level. p significant at <0.05 (*).

Source effect	df num	df den	F-value	p
wk	20	5462	10.805	0.0001*
tr	4	1367	19.528	0.0001*
fl	8	2732	11.553	0.0001*
wk*tr	20	5462	3.001	0.0001*
wk*fl	24	5462	2.709	0.0001*
tr*fl	8	2732	0.409	0.916
wk*tr*fl	20	5462	1.517	0.065

Table 10. Univariate results for total foraging activity, feeding MAP's and swimming duration by larvae reared at low, medium and high prey densities in control and predator treatments. wk=week, tr=treatment, fl=food level. p significant at < 0.05 (*).

Behaviour	Source	df num	F-value	p
forage	wk	5	14.37	0.0001*
	tr	1	55.74	0.0001*
	fl	2	44.64	0.0001*
	wk*tr	5	6.58	0.0001*
	wk*fl	6	7.58	0.0001*
	tr*fl	2	0.34	0.714
	wk*tr*fl	5	1.07	0.373
orient	wk	5	14.08	0.0001*
	tr	1	54.83	0.0001*
	fl	2	44.54	0.0001*
	wk*tr	5	6.26	0.0001*
	wk*fl	6	7.57	0.0001*
	tr*fl	2	0.45	0.640
	wk*tr*fl	5	1.44	0.208
attack	wk	5	6.88	0.0001*
	tr	1	5.49	0.0192*
	fl	2	8.99	0.0001*
	wk*tr	5	2.63	0.0223*
	wk*fl	6	2.58	0.0172*
	tr*fl	2	0.32	0.726
	wk*tr*fl	5	0.79	0.555
pass	wk	5	16.81	0.0001*
	tr	1	53.96	0.0001*
	fl	2	34.94	0.0001*
	wk*tr	5	4.92	0.0002*
	wk*fl	6	6.31	0.0001*
	tr*fl	2	0.64	0.526
	wk*tr*fl	5	1.86	0.099
swim	wk	5	17.72	0.0001*
	tr	1	34.69	0.0001*
	fl	2	4.43	0.0121*
	wk*tr	5	6.23	0.0001*
	wk*fl	6	2.23	0.0382*
	tr*fl	2	0.41	0.662
	wk*tr*fl	5	1.22	0.299

Table 11. Results of Bonferroni post-hoc comparisons examining weekly mean differences in total foraging activity, feeding MAP's and swimming duration performed by larvae reared at low, medium and high prey densities in control and predator treatments. forage (act)=foraging activity.

Activity /MAPs	wk 1	wk 2	wk 3	wk 4	wk 5	wk 6
forage (act)						
500	0.729	0.888	-	-	-	-
1500	0.377	0.195	0.016	0.0007*	0.032	-
4500	0.300	0.696	0.0001*	0.0003*	0.0001*	0.0001*
orient						
500	0.687	0.892	-	-	-	-
1500	0.243	0.141	0.022	0.0007*	0.037	-
4500	0.203	0.700	0.0001*	0.0005*	0.0001*	0.0001*
attack						
500	0.900	0.976	-	-	-	-
1500	0.211	0.334	0.113	0.225	0.062	-
4500	0.802	0.328	0.169	0.006**	0.947	0.434
pass						
500	0.671	0.846	-	-	-	-
1500	0.871	0.049	0.055	0.002*	0.171	-
4500	0.445	0.845	0.0005*	0.007**	0.0001*	0.0001*
swim						
500	0.196	0.740	-	-	-	-
1500	0.808	0.656	0.0008*	0.298	0.002*	-
4500	0.888	0.501	0.0003*	0.0001*	0.0001*	0.002*

* significant at $p<0.05$ (comparison alpha level=0.004)

** significant at $p<0.1$ (comparison alpha level=0.008)

Table 12. Multivariate Hotelling-Lawley trace results for foraging activity and swimming by larvae in the middle grid. wk=week, tr=treatment, fl=food level.
p significant at < 0.05 (*).

Source effects	df num	df den	F-value	p
wk	10	2736	4.003	0.0001*
tr	2	1369	1.630	0.496
fl	4	2736	4.482	0.0013*
wk*tr	10	2735	0.484	0.902
wk*fl	12	2736	1.201	0.276
tr*fl	4	2736	0.523	0.719
wk*tr*fl	10	2736	0.429	0.933

Table 13. Multivariate Hotelling-Lawley trace results for swimming and feeding MAP's (i.e. orient, attack and pass) performed by laval cod in the middle grid. wk=week, tr=treatment, fl=food level. p significant at < 0.05 (*).

Source effects	df num	df den	F-value	p
wk	20	5462	3.064	0.0001*
tr	4	1367	2.013	0.090
fl	8	2732	2.462	0.012*
wk*tr	20	5462	0.449	0.983
wk*fl	24	5462	1.034	0.416
tr*fl	8	2732	0.372	0.936
wk*tr*fl	20	5462	0.804	0.711

Table 14. Univariate results of foraging activity, feeding MAP's and swimming performed by larvae in the middle grid. wk=week, tr=treatment, fl=food level.
p significant at < 0.05 (*)

Activity/ MAP	Source	df num	F-value	p
foraging activity	wk	5	2.75	0.018*
	tr	1	2.68	0.102
	fl	2	8.57	0.0002*
	wk*tr	5	0.82	0.534
	wk*fl	6	1.85	0.086
	tr*fl	2	0.00	0.997
	wk*tr*fl	5	0.47	0.799
orient	wk	5	2.86	0.014*
	tr	1	2.99	0.084
	fl	2	8.87	0.0001*
	wk*tr	5	0.86	0.510
	wk*fl	6	1.92	0.074
	tr*fl	2	0.00	0.996
	wk*tr*fl	5	0.54	0.747
attack	wk	5	1.67	0.138
	tr	1	0.00	0.968
	fl	2	3.91	0.020*
	wk*tr	5	0.57	0.72
	wk*fl	6	1.26	0.275
	tr*fl	2	0.08	0.924
	wk*tr*fl	5	0.61	0.692
pass	wk	5	3.36	0.003*
	tr	1	3.95	0.047
	fl	2	6.46	0.002*
	wk*tr	5	0.7	0.621
	wk*fl	6	1.28	0.262
	tr*fl	2	0.02	0.981
	wk*tr*fl	5	0.41	0.843
swim	wk	5	2.19	0.053
	tr	1	0.23	0.633
	fl	2	2.3	0.100
	wk*tr	5	0.5	0.779
	wk*fl	6	0.46	0.841
	tr*fl	2	0.55	0.575
	wk*tr*fl	5	0.26	0.935

Table 15. Multivariate Hotelling-Lawley trace results for swimming and foraging activity performed by larvae in the non-predator grid. wk=week, tr=treatment, fl=food level.
p significant at < 0.05 (*)

Source effects	df (num)	df (den)	F-value	p
wk	10	2736	4.317	0.0001*
tr	2	1369	2.849	0.058
fl	4	2736	5.207	0.0004*
wk*tr	10	2736	0.883	0.545
wk*fl	12	2736	1.155	0.309
tr*fl	4	2736	0.458	0.766
wk*tr*fl	10	2736	1.157	0.327

Table 16. Mulitvariate Hotelling-Lawley trace results for swimming and feeding MAP's performed by larvae in the non-predator grid. wk=week, tr=treatment, fl=food level.
p significant at < 0.05 (*)

Source effects	df (num)	df (den)	F-value	p
wk	20	5462	3.183	0.0001*
tr	4	1367	2.233	0.063
fl	8	2732	2.913	0.003*
wk*tr	20	5462	0.745	0.782
wk*fl	24	5462	1.129	0.299
tr*fl	8	2732	0.387	0.928
wk*tr*fl	20	5462	0.891	0.599

Table 17. Univariate results for foraging activity, feeding MAP's and swimming performed by larvae in the non-predator grid. wk=week, tr=treatment, fl=food level.
p significant at < 0.05 (*).

Activity/ MAP's	Source	df	F-value	p
foraging activity	wk	5	2.17	0.055
	tr	1	5.14	0.024
	fl	2	7.06	0.0009*
	wk*tr	5	0.9	0.477
	wk*fl	6	1.36	0.228
	tr*fl	2	0.74	0.479
	wk*tr*fl	5	0.23	0.950
orient	wk	5	1.98	0.079
	tr	1	4.55	0.033
	fl	2	7.33	0.0007*
	wk*tr	5	0.92	0.467
	wk*fl	6	1.32	0.246
	tr*fl	2	0.64	0.525
	wk*tr*fl	5	0.36	0.874
attack	wk	5	1.74	0.122
	tr	1	1.20	0.274
	fl	2	1.67	0.188
	wk*tr	5	0.85	0.514
	wk*fl	6	1.15	0.334
	tr*fl	2	0.60	0.550
	wk*tr*fl	5	0.81	0.543
pass	wk	5	3.36	0.005*
	tr	1	7.12	0.008
	fl	2	6.72	0.001*
	wk*tr	5	0.72	0.605
	wk*fl	6	1.73	0.109
	tr*fl	2	0.49	0.615
	wk*tr*fl	5	0.30	0.911
swim	wk	5	3.74	0.002*
	tr	1	1.00	0.317
	fl	2	0.25	0.781
	wl*tr	5	0.89	0.487
	wk*fl	6	0.56	0.765
	tr*fl	2	0.11	0.896
	wk*tr*fl	5	0.28	0.922

Table 18. Multivariate Hotelling-Lawley trace results for swimming and foraging activity by larvae in the predator grid. p significant at < 0.05 (*)

Source effect	df (num)	df (den)	F-value	p
wk	10	2736	4.182	0.0001*
tr	2	1369	15.32	0.0001*
fl	4	2736	5.331	0.0003*
wk*tr	10	2736	1.952	0.036*
wk*fl	12	2736	1.004	0.443
tr*fl	4	2736	1.813	0.124
wk*tr*fl	10	2736	1.066	0.385

Table 19. Multivariate Hotelling-Lawley trace results for swimming and feeding MAP's performed by larvae in the predator grid. wk=week, tr=treatment, fl=food level. p significant at < 0.05 (*).

Source effect	df (num)	df (den)	F-value	p
wk	20	5462	3.138	0.0001*
tr	4	1367	8.063	0.0001*
fl	8	2732	2.802	0.004*
wk*tr	20	5462	1.367	0.127
wk*fl	24	5462	1.002	0.459
tr*fl	8	2732	1.126	0.342
wk*tr*fl	20	1370	0.973	0.492

Table 20. Univariate results for foraging activity, feeding MAP's and swimming performed by larvae in the predator grid. wk=week, tr=treatment, fl=food level.
p significant at < 0.05 (*).

Activity/ MAP's	Source	df	F-value	p
foraging activity	wk	5	3.00	0.012*
	tr	1	27.11	0.0001*
	fl	2	6.61	0.001*
	wk*tr	5	3.49	0.004*
	wk*fl	6	1.35	0.230
	tr*fl	2	2.84	0.059
	wk*tr*fl	5	1.44	0.208
orient	wk	5	2.91	0.013*
	tr	1	28.03	0.0001*
	fl	2	6.52	0.002*
	wk*tr	5	3.44	0.004*
	wk*fl	6	1.20	0.304
	tr*fl	2	2.97	0.052
	wk*tr*fl	5	1.50	0.186
attack	wk	5	3.06	0.009*
	tr	1	9.23	0.002*
	fl	2	2.25	0.105
	wk*tr	5	2.27	0.045*
	wk*fl	6	1.22	0.296
	tr*fl	2	0.67	0.511
	wk*tr*fl	5	0.55	0.742
pass	wk	5	3.12	0.008*
	tr	1	23.54	0.0001*
	fl	2	6.25	0.002*
	wk*tr	5	3.13	0.008*
	wk*fl	6	1.20	0.304
	tr*fl	2	2.86	0.058
	wk*tr*fl	5	1.80	0.109
swim	wk	5	2.64	0.022*
	tr	1	22.89	0.0001*
	fl	2	0.01	0.990
	wk*tr	5	2.33	0.041*
	wk*fl	6	0.60	0.734
	tr*fl	2	0.64	0.525
	wk*tr*fl	5	0.57	0.721

Table 21. Results of Bonferroni post-hoc comparisons examining weekly differences in mean foraging activity, feeding MAP's and swimming performed by larvae in the predator grid of control and treatment aquaria. forage (act)=foraging activity

Activity/ MAP's	week 1	week 2	week 3	week 4	week 5	week 6
forage (act)						
500	0.728	0.459	-	-	-	-
1500	0.493	0.514	0.14	0.029	0.791	-
4500	0.361	0.549	0.0001*	0.0001*	0.0001*	0.0002*
orient						
500	0.258	0.439	-	-	-	-
1500	0.472	0.482	0.145	0.028	0.794	-
4500	0.303	0.554	0.0001*	0.0001*	0.0001*	0.0001*
attack						
500	1.000	0.988	-	-	-	-
1500	0.603	0.854	0.599	0.116	0.464	-
4500	0.429	0.516	0.018	0.0001*	0.261	0.331
pass						
500	0.569	0.357	-	-	-	-
1500	0.589	0.378	0.104	0.061	0.939	-
4500	0.569	0.682	0.0001*	0.001*	0.0001*	0.0001*
swim						
500	0.580	0.834	-	-	-	-
1500	0.927	0.589	0.056	0.363	0.211	-
4500	0.566	0.624	0.009	0.0002*	0.002*	0.004**

* significant at $p<0.05$ (comparison alpha level=0.004)

** significant at $p<0.1$ (comparison alpha level=0.008)

Table 22. Results of Duncans post-hoc test performed on foraging activity and swimming duration of larvae in non-predator (np), middle (m) and predator (p) grids of treatment aquaria.

Behaviours	grid	mean	Duncan comparisons
foraging activity	np	1.03	A
	m	1.03	A
	pr	0.65	B
swimming duration (sec)	np	2.57	A
	m	2.59	A
	pr	1.91	B

Table 23. Results of two-way ANOVA for day and food level (fl) effects on larval cod morphometric data. p significant at < 0.05 (*).

Variable	Source	df	F-value	p
dry weight	day	6	121.91	0.0001*
	fl	2	6.65	0.002*
	day*fl	6	1.55	0.163
standard length	day	6	160.97	0.0001*
	fl	2	6.29	0.002*
	day*fl	6	3.32	0.004*
eye diameter	day	6	284.82	0.0001*
	fl	2	3.45	0.033*
	day*fl	6	4.61	0.0002*
myotomal height	day	6	144.74	0.0001*
	fl	2	5.52	0.004*
	day*fl	6	3.95	0.001*

Table 24. Results of Bonferroni post-hoc comparisons examining mean differences in morphometric variables between food levels within each sample day. low=500 prey/l, med=1500 prey/l, high=4500 prey/l.

Variable	comparison of food level (prey/l)	day 1	day 6	day 11	day 21	day 31
standard length	500 v 1500	0.799	0.394	0.169	------	------
	500 v 4500	0.811	0.861	0.015	------	------
	1500 v 4500	0.622	0.305	0.285	0.019	0.0001
eye diameter	500 v 1500	0.106	0.376	0.196	------	------
	500 v 4500	0.052	0.875	0.068	------	------
	1500 v 4500	0.744	0.465	0.595	0.089	0.0001*
myotomal height	500 v 1500	0.738	0.059	0.275	------	------
	500 v 4500	0.655	0.795	0.005**	------	------
	1500 v 4500	0.910	0.103	0.083	0.013	0.0001*

* significant at $p<0.05$ (comparison alpha level=0.004)

** significant at $p<0.1$ (comparison alpha level=0.008)

Fig. 1. A conceptualization of the recruitment process in fishes (from Houde 1987).

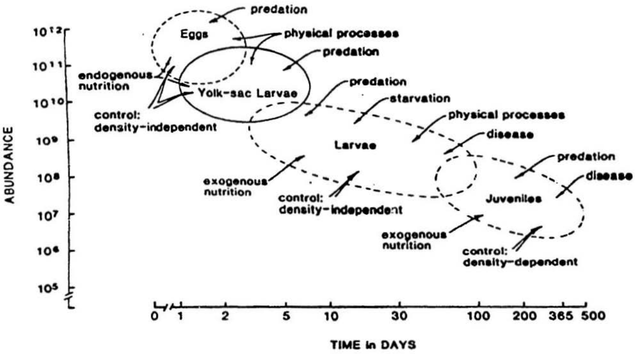

ABUNDANCE
10^{12}
10^{11}
10^{10}
10^{9}
10^{8}
10^{7}
10^{6}
10^{5}
Eggs
predation
physical processes
predation
endogenous nutrition
Yolk-sac Larvae
control: density-independent
predation
starvation
physical processes
disease
Larvae
exogenous nutrition
control: density-independent
predation
disease
Juveniles
exogenous nutrition
control: density-dependent
0
1
2
5
10
30
100
200
365
500
TIME in DAYS

Fig. 2. Side view of an experimental aquarium. (a) predator chamber, (b) larval rearing chamber, (c) transparent non-removable partition, (d) opaque removable partition, "p" = grid adjacent to predators, "predator grid", "m" = grid in the middle, "middle grid", "np" = grid furthest from predator, "non-predator grid".

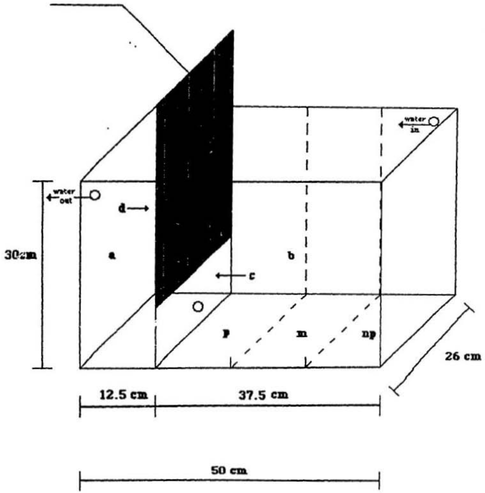

water in
water out
d
a
c
b
p
m
np
30cm
12.5 cm
37.5 cm
26 cm
50 cm

Fig. 3. Larval cod illustrating gross morphometric characteristics. ED=eye diameter, MH=myotomal height, SL=standard length.

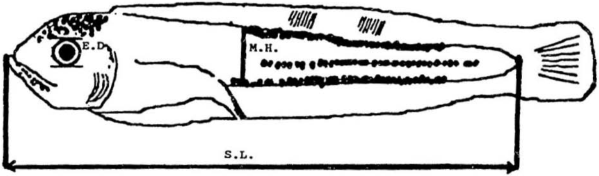

E.D.
M.H.
S.L.

Fig. 4. Weekly mean (+1 SE) foraging activity of larval cod reared in control aquaria and fed at low (500 prey/l), medium (1500 prey/l), and high (4500 prey/l) prey densities. Vertical bar = standard error. n=20 larvae per treatment per week.

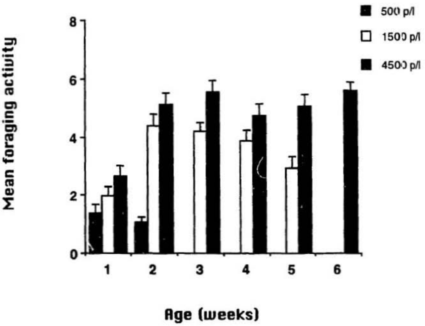

Mean foraging activity
0
2
4
6
8
1
2
3
4
5
6
Age (weeks)
■ 500 p/l
□ 1500 p/l
■ 4500 p/l

Fig. 5. Mean (± 1 SE) proportion of food observed in the guts of larvae reared in control aquaria and fed at low (500 prey/l) medium (1500 prey/l) and high (4500 prey/l) prey densities over the study period. Vertical bar = standard error. n=10 larvae per treatment per week.

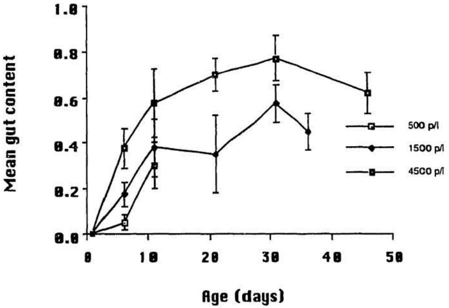

Mean gut content
1.0
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
50
Age (days)
500 p/l
1500 p/l
4500 p/l

Fig. 6. Mean (+ 1 SE) duration of time (seconds) spent each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the non-predator grid of control and predator aquaria. Vertical bar = standard error.

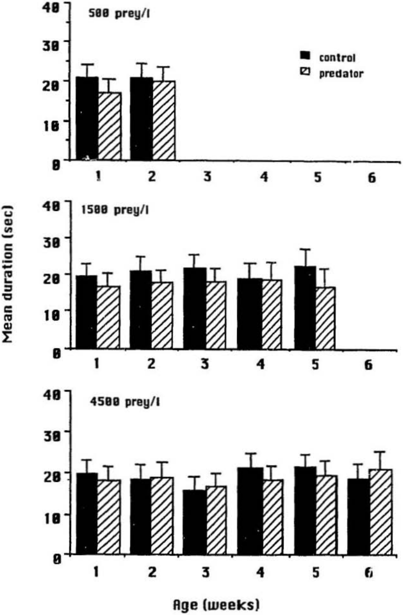
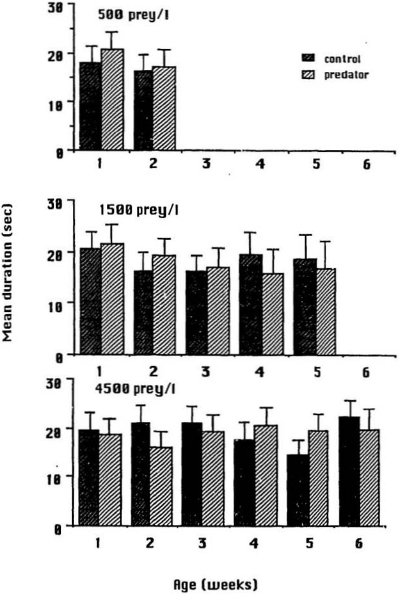

Mean duration (sec)
40
30
20
10
0
500 prey/l
■ control
▨ predator
1
2
3
4
5
6
1500 prey/l
4500 prey/l
Age (weeks)

Fig. 7. Mean (+ 1 SE) duration of time (seconds) spent each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the middle grid of control and predator aquaria. Vertical bar = standard error.



500 prey/l
control
predator
1500 prey/l
4500 prey/l
Mean duration (sec)
0
10
20
30
1
2
3
4
5
6
Age (weeks)

Fig. 8. Mean (+ 1 SE) duration of time (seconds) spent each week by larvae reared at low (500 prey/l),medium (1500 prey/l) and high (4500 prey/l) prey densities in the predator grid of control and predator aquaria.
Vertical bar = standard error.

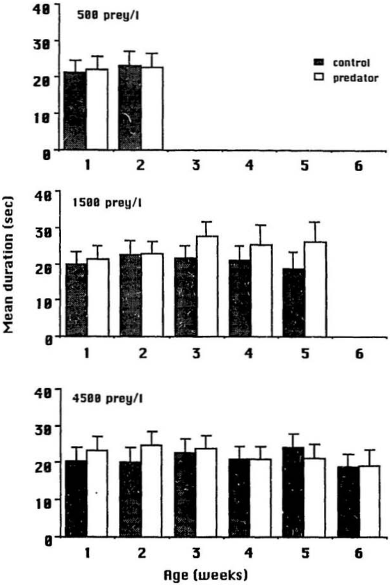
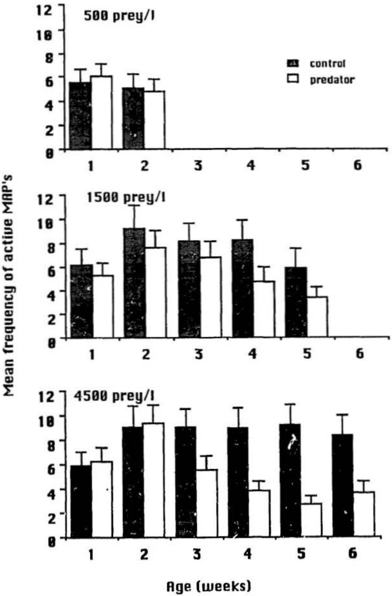

500 prey/l
control
predator
1500 prey/l
4500 prey/l
Mean duration (sec)
0
10
20
30
40
1
2
3
4
5
6
Age (weeks)

Fig. 9. Mean (+ 1 SE) frequency of active MAP's performed each week by larvae in the predator grid in the presence (predator) and absence (control) of a predator and reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities.
Vertical bar = standard error.



Mean frequency of active MAP's
12
10
8
6
4
2
0
500 prey/l
■ control
☐ predator
1
2
3
4
5
6
1500 prey/l
4500 prey/l
Age (weeks)

Fig. 10. Mean (+1 SE) frequency of flee responses performed each week by larvae reared at medium (1500 prey/l) and high (4500 prey/l) prey densities in the predator grid of treatment aquaria. Vertical bar = standard error.

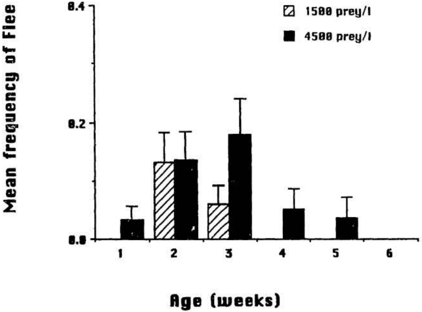

0.4
0.2
0.0
▨ 1500 prey/l
■ 4500 prey/l
Mean frequency of Flee
1
2
3
4
5
6
Age (weeks)

Fig. 11. Mean (+ 1 SE) total foraging activity performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in control and predator aquaria. Vertical bar = standard error. n=60 larvae per treatment per week.

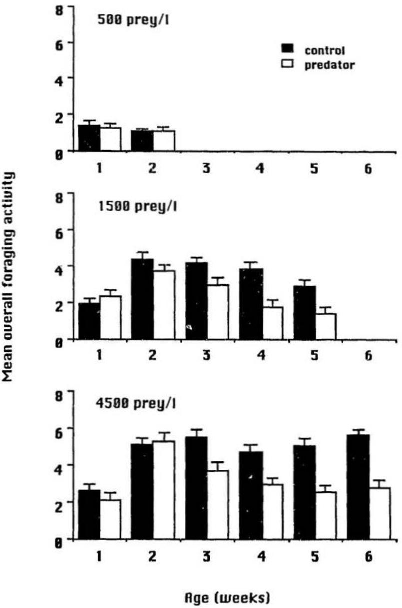

500 prey/l
control
predator
1500 prey/l
4500 prey/l
Mean overall foraging activity
Age (weeks)
0
2
4
6
8
1
2
3
4
5
6

Fig. 12. Mean (+ 1 SE) total frequency of Orient performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in control and predator aquaria. Vertical bar = standard error. n=60 larvae per treatment per week.

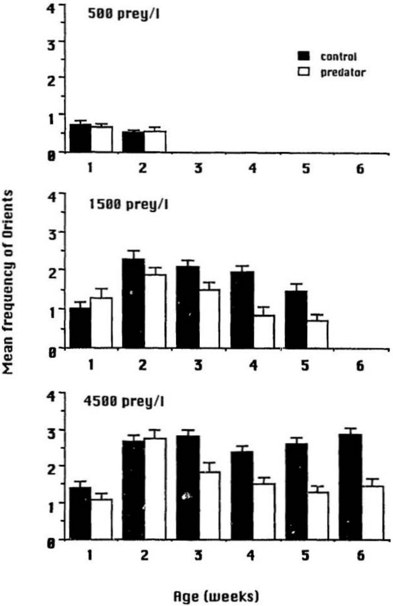

500 prey/l
■ control
□ predator
1500 prey/l
4500 prey/l
Mean frequency of Orients
0
1
2
3
4
1
2
3
4
5
6
Age (weeks)

Fig. 13. Mean (+ 1 SE) total frequency of Attacks performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in control and predator aquaria. Vertical bar = standard error. n=60 larvae per treatment per week.

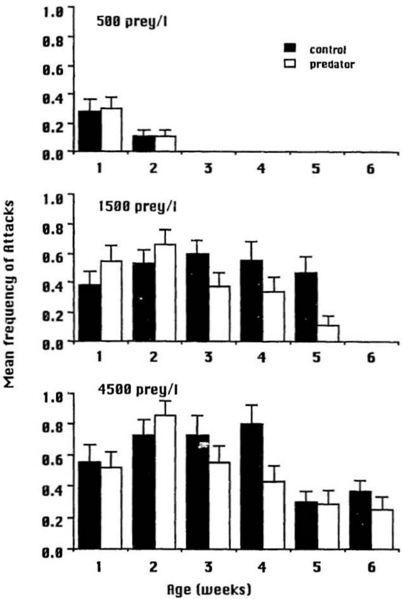

500 prey/l
1500 prey/l
4500 prey/l
■ control
□ predator
Mean frequency of Attacks
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
5
6
Age (weeks)

Fig. 14. Mean (+ 1 SE) total frequency of Pass performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in control and predator aquaria. Vertical bar = standard error. n=60 larvae per treatment per week.

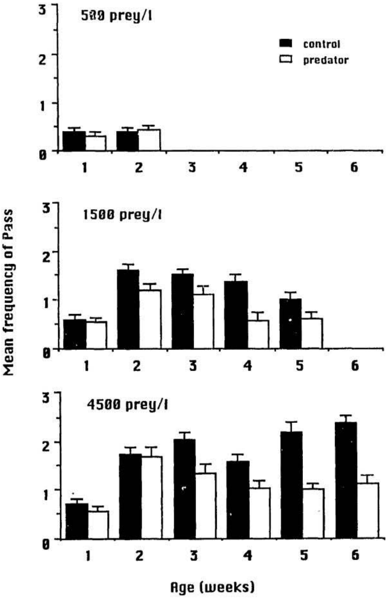
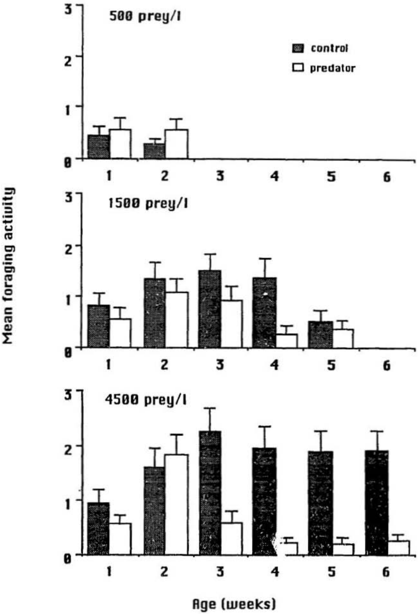

500 prey/l
control
predator
1500 prey/l
4500 prey/l
Mean frequency of Pass
Age (weeks)
0
1
2
3
1
2
3
4
5
6

Fig. 15. Mean (+ 1 SE) foraging activity performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the predator grid of control and predator aquaria. Vertical bar = standard error.



500 prey/l
▨ control
☐ predator
1500 prey/l
4500 prey/l
Mean foraging activity
0
1
2
3
1
2
3
4
5
6
Age (weeks)

Fig. 16. Mean (+ 1 SE) frequency of Orients performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the predator grid of control and treatment aquaria. Vertical bar = standard error.

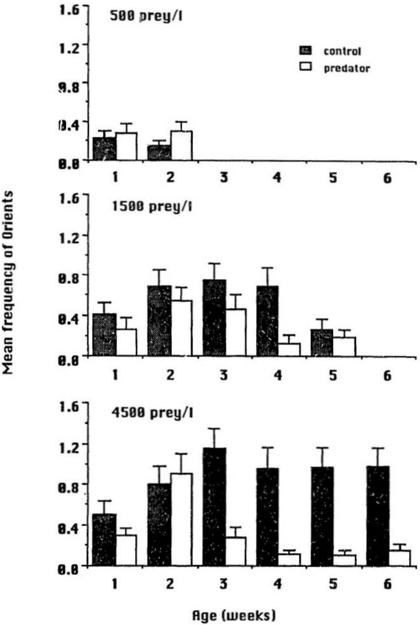

1.6
1.2
0.8
0.4
0.0
500 prey/l
control
predator
1
2
3
4
5
6
1500 prey/l
4500 prey/l
Mean frequency of Orients
Age (weeks)

Fig. 17. Mean (+ 1 SE) frequency of Attacks performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the predator grid of control and predator aquaria. Vertical bar = standard error.

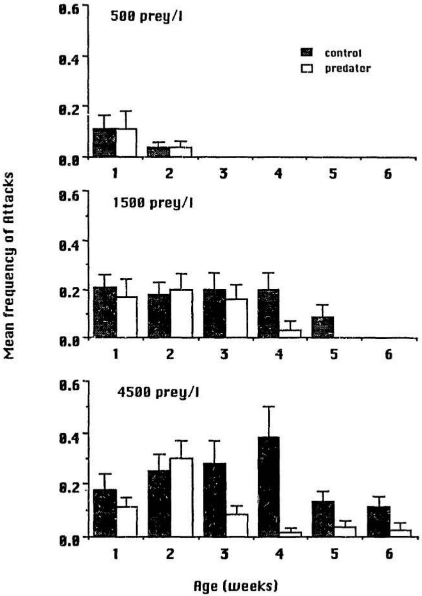

Mean frequency of Attacks
500 prey/l
1500 prey/l
4500 prey/l
control
predater
0.0
0.2
0.4
0.6
1
2
3
4
5
6
Age (weeks)

Fig. 18. Mean (+ 1 SE) frequency of Pass performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the predator grid of control and predator aquaria. Vertical bar = standard error.

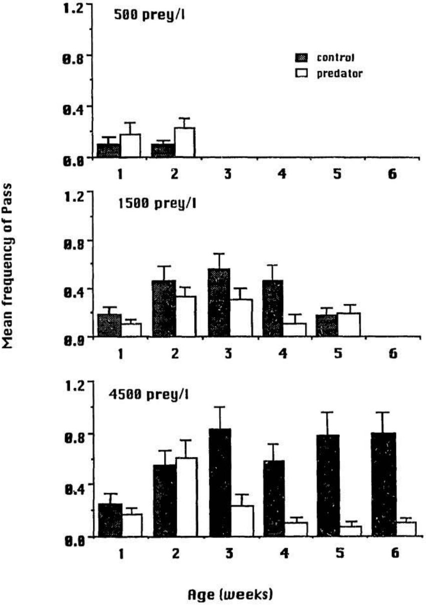

Mean frequency of Pass
500 prey/l
control
predator
1500 prey/l
4500 prey/l
1.2
0.8
0.4
0.0
1
2
3
4
5
6
Age (weeks)

Fig. 19. Mean (+ 1 SE) total swimming duration performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in control and predator aquaria. Vertical bar = standard error.

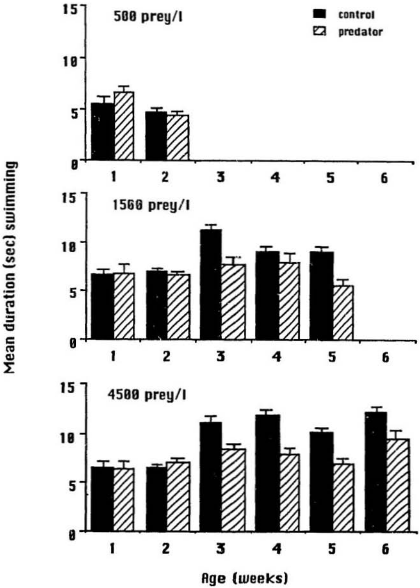

15
10
5
0
500 prey/l
control
predator
1
2
3
4
5
6
1500 prey/l
4500 prey/l
Mean duration (sec) swimming
Age (weeks)

Fig. 20. Mean (+ 1 SE) swimming duration performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the predator grid of control and predator aquaria. Vertical bar = standard error.

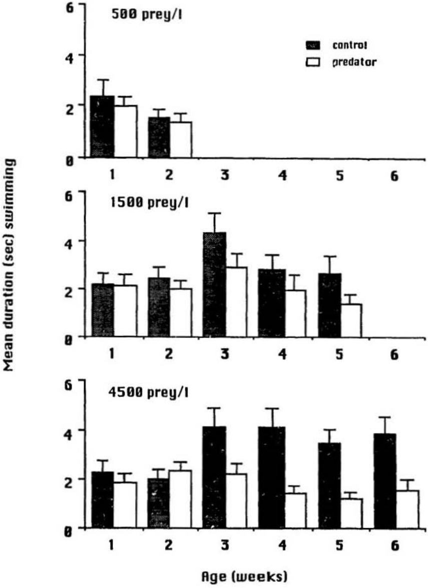
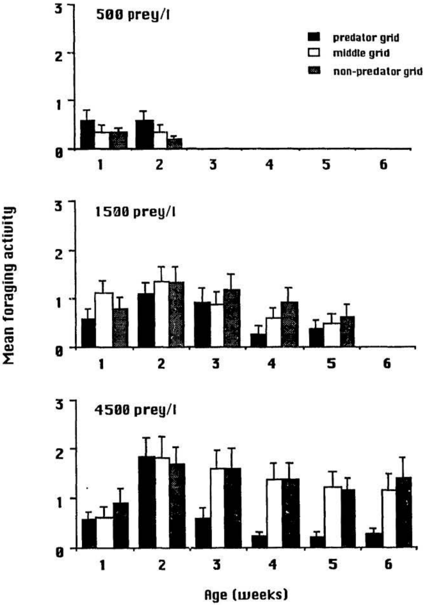

500 prey/l
control
predator
1500 prey/l
4500 prey/l
0
2
4
6
1
2
3
4
5
6
Mean duration (sec) swimming
Age (weeks)

Fig. 21. Mean (+1 SE) foraging activity performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the predator, middle, and non-predator grids of treatment aquaria. Vertical bar = standard error. n=60 larvae per week.



500 prey/l
predator grid
middle grid
non-predator grid
1500 prey/l
4500 prey/l
Mean foraging activity
0
1
2
3
1
2
3
4
5
6
Age (weeks)

Fig. 22. Mean (+1 SE) duration of time (sec) spent swimming each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the predator, middle, and non-predator grids of treatment aquaria. Vertical bar = standard error. n=60 larvae per week.

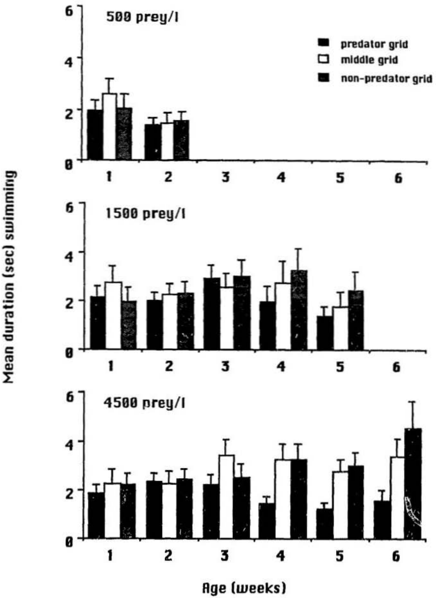
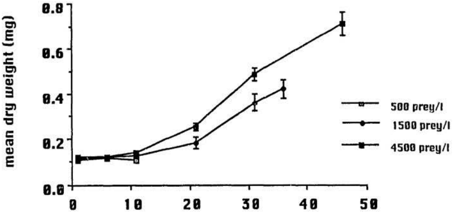

500 prey/l
1500 prey/l
4500 prey/l
predator grid
middle grid
non-predator grid
Mean duration (sec) swimming
Age (weeks)
0
2
4
6
1
2
3
4
5
6

Fig. 23. Weekly mean (± 1 SE) dry weight (mg) and standard length (mm) of larval cod reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities. Vertical bar = standard error. n=20 per treatment per week.


mean dry weight (mg)
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
50
500 prey/l
1500 prey/l
4500 prey/l

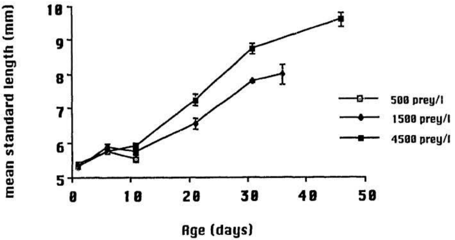

mean standard length (mm)
10
9
8
7
6
5
0
10
20
30
40
50
500 prey/l
1500 prey/l
4500 prey/l
Age (days)

Fig. 24. Weekly mean (± 1 SE) eye diameter (mm) and body depth (mm) of larval cod reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities. Vertical bar = standard error. n=20 per treatment per week.

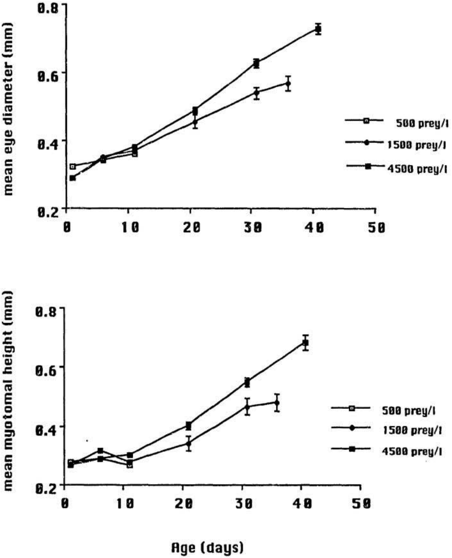

mean eye diameter (mm)
0.8
0.6
0.4
0.2
0
10
20
30
40
50
500 prey/l
1500 prey/l
4500 prey/l
mean myotomal height (mm)
0.8
0.6
0.4
0.2
0
10
20
30
40
50
500 prey/l
1500 prey/l
4500 prey/l
Age (days)

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Fig. 1a. Mean (+ 1 SE) frequency of active MAP's performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the middle grid of control and predator aquaria. Vertical bar = standard error.

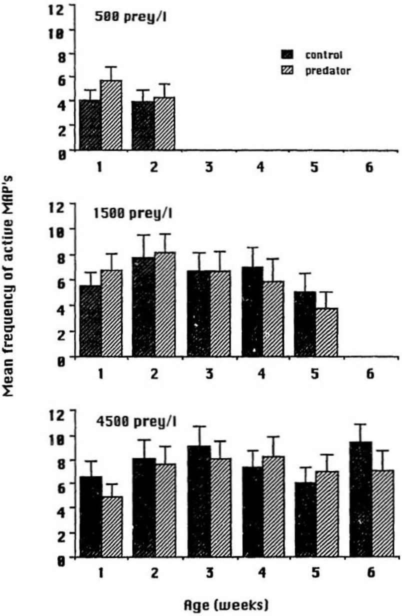

500 prey/l
1500 prey/l
4500 prey/l
control
predator
Mean frequency of active MAP's
Age (weeks)
0
2
4
6
8
10
12
1
2
3
4
5
6

Fig. 2a. Mean (+ 1 SE) frequency of active MAP's performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the non-predator grid of control and predator aquaria. Vertical bar = standard error.

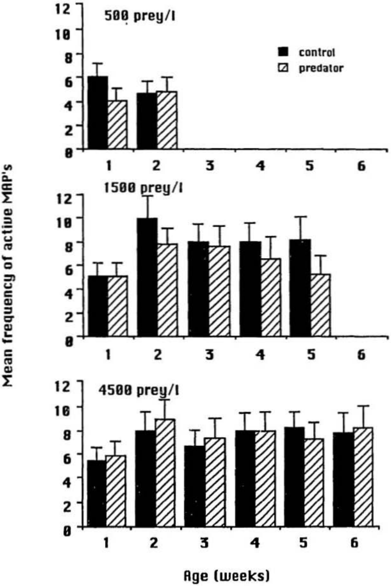

500 prey/l
1500 prey/l
4500 prey/l
control
predator
Mean frequency of active MAP's
Age (weeks)
0
2
4
6
8
10
12
1
2
3
4
5
6

Fig. 3a. Mean (+ 1 SE) foraging activity performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the middle grid of control and predator aquaria. Vertical bar = standard error.

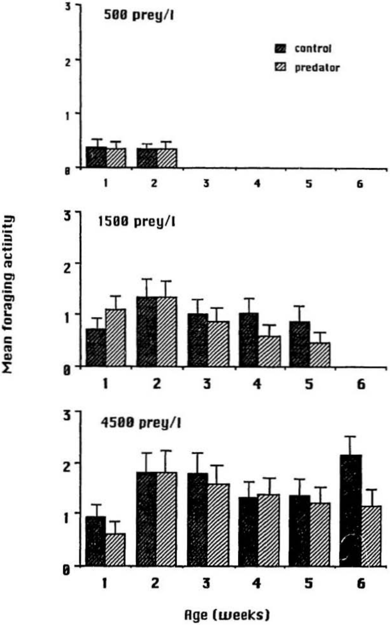

500 prey/l
control
predator
1500 prey/l
4500 prey/l
Mean foraging activity
Age (weeks)
0
1
2
3
1
2
3
4
5
6

Fig. 4a. Mean (+ 1 SE) foraging activity performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the non-predator grid of control and predator aquaria. Vertical bar = standard error.

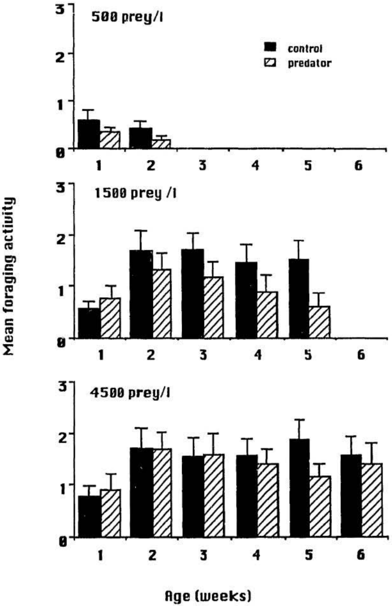

500 prey/l
control
predator
1500 prey /l
4500 prey/l
Mean foraging activity
0
1
2
3
1
2
3
4
5
6
Age (weeks)

Fig. 5a. Mean (+ 1 SE) frequency of Orients performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) densities in the middle grid of control and predator aquaria. Vertical bar = standard error.

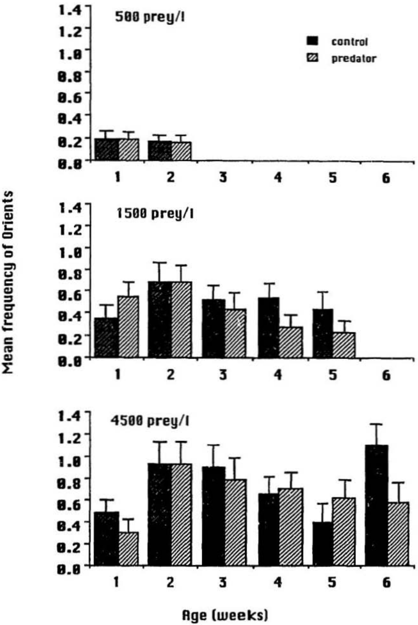

Mean frequency of Orients
500 prey/l
1500 prey/l
4500 prey/l
■ control
▨ predator
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
5
6
Age (weeks)

Fig. 6a. Mean (+ 1 SE) frequency of Orients performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the non-predator grid of control and predator aquaria. Vertical bar = standard error.

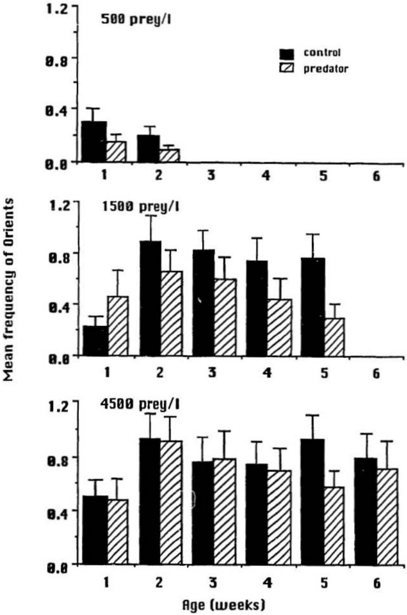

500 prey/l
1500 prey/l
4500 prey/l
control
predator
Mean frequency of Orients
1.2
0.8
0.4
0.0
1
2
3
4
5
6
Age (weeks)

Fig. 7a. Mean (+ 1 SE) frequency of Attacks performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the middle grid of control and predator aquaria. Vertical bar = standard error.

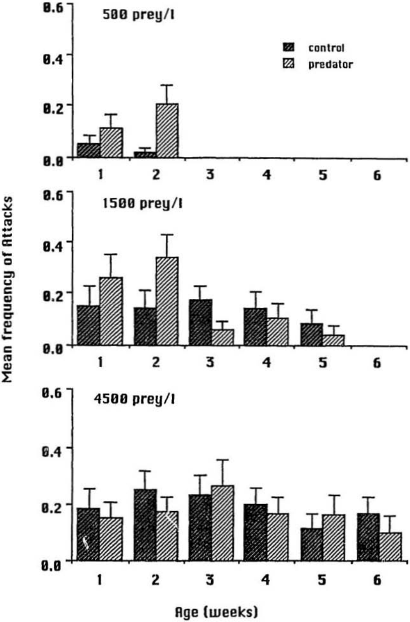

500 prey/l
control
predator
1500 prey/l
4500 prey/l
Mean frequency of Attacks
0.0
0.2
0.4
0.6
1
2
3
4
5
6
Age (weeks)

Fig. 8a. Mean (+ 1 SE) frequency of Attacks performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the non-predator grid of control and predator aquaria. Vertical bar = standard error.

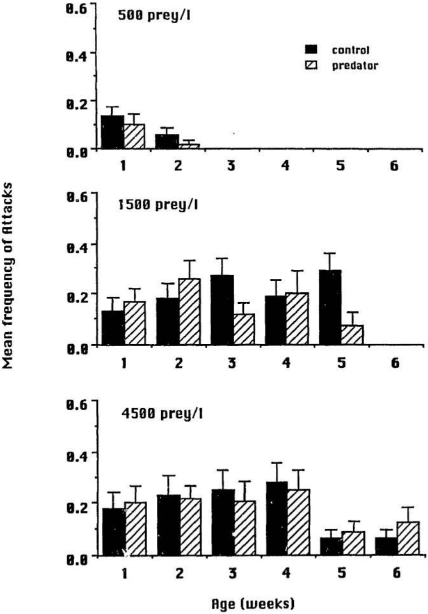

Mean frequency of Attacks
500 prey/l
control
predator
1500 prey/l
4500 prey/l
0.6
0.4
0.2
0.0
1
2
3
4
5
6
Age (weeks)

Fig. 9a. Mean (+ 1 SE) frequency of Pass performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the middle grid in control and predator aquaria. Vertical bar = standard error.

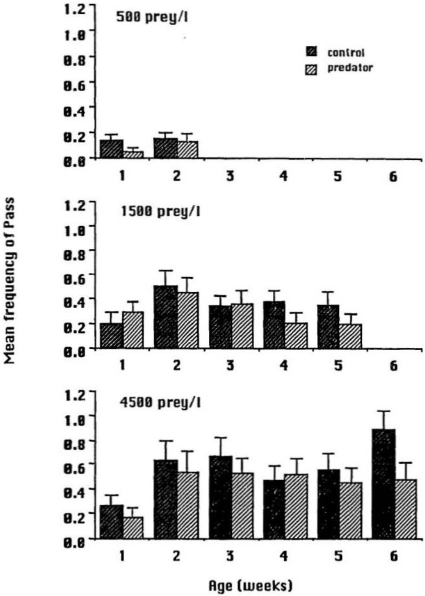

500 prey/l
1500 prey/l
4500 prey/l
control
predator
Mean frequency of Pass
Age (weeks)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
5
6

Fig. 10a. Mean (+ 1 SE) frequency of Pass performed each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the non-predator grid in control and predator aquaria. Vertical bar = standard error.

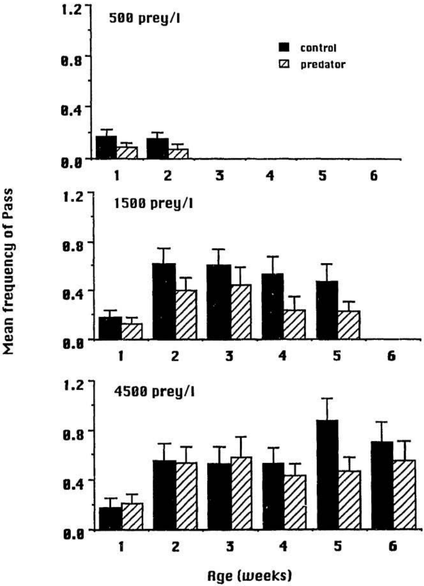

1.2
0.8
0.4
0.0
500 prey/l
■ control
▨ predator
1
2
3
4
5
6
1500 prey/l
4500 prey/l
Mean frequency of Pass
Age (weeks)

Fig. 11a. Mean (+ 1 SE) duration of time (sec) spent swimming each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the middle grid of control and predator aquaria. Vertical bar = standard error. Vertical bar = standard error.

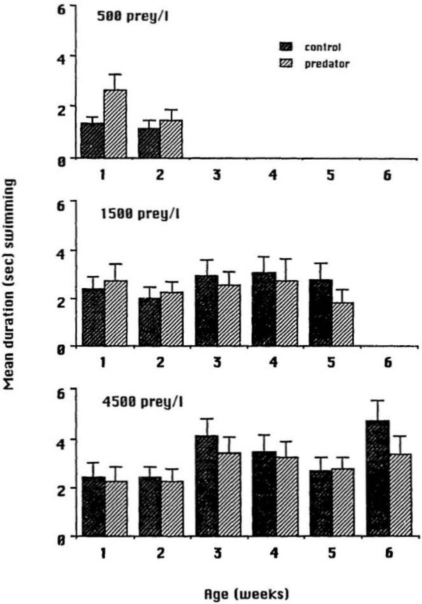
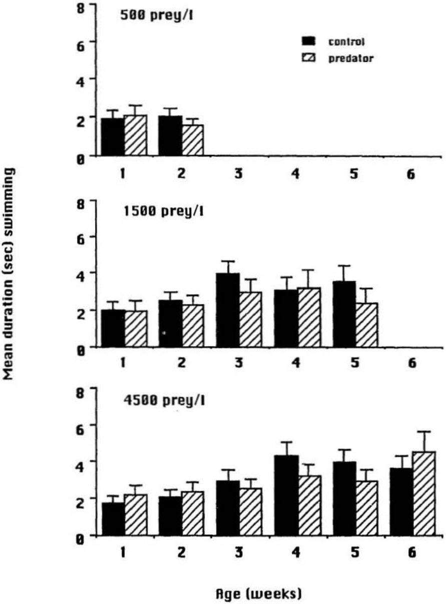

Mean duration (sec) swimming
500 prey/l
1500 prey/l
4500 prey/l
control
predator
6
4
2
0
1
2
3
4
5
6
Age (weeks)

Fig. 12a. Mean (+ 1 SE) duration of time (sec) spent swimming each week by larvae reared at low (500 prey/l), medium (1500 prey/l) and high (4500 prey/l) prey densities in the non-predator grid in control and predator aquaria. Vertical bar = standard error.


500 prey/l
1500 prey/l
4500 prey/l
control
predator
0
2
4
6
8
1
2
3
4
5
6
Mean duration (sec) swimming
Age (weeks)