Influence of body size and alternate prey abundance on the risk of predation to fish larvae

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ABSTRACT: We investigated the effects of variations in the abundance of microzooplankton (*Artemia* sp. nauplii) and the size of larval fish on the latter's vulnerability to predation by a vertebrate, the three-spine stickleback *Gasterosteus aculeatus*. We used capelin *Mallotus villosus*, cod *Gadus morhua* and winter flounder *Pleuronectes americanus* larvae as our prey species. Analysis of covariance indicated a highly significant effect on mortality rates due to predation caused by the presence of alternate prey ($F_{3,148} = 10.8$, p < 0.001), but a close examination of the results indicates that only levels of alternate prey exceeding 250 nauplii l^{-1} caused a reduction in the impact of sticklebacks on larval fish. Furthermore, the size of the fish larvae also had a significant impact on mortality rates ($F_{1,148} = 6.9$, p < 0.001) in a comparison among species, however, this relationship was not apparent within species. Overall, as the size of larvae increased, mortality rates increased. As the size of the larvae decreased, the ingestion rate of larvae by the predator at low levels of alternate prey (≤25 nauplii l^{-1}) showed a substantial increase relative to the ingestion rate of larvae at high levels of alternate prey (250 nauplii l^{-1}). Results indicate that as the size of larvae approaches the size of the more abundant alternate prey, the likelihood of an attack may decrease due to the presence of alternate prey. Whether the impact of increased microplankton abundance in the field would be greater through enhanced feeding of the larvae or reduced impact of the predator is unclear.

KEY WORDS: Fish larvae · Body size · Predation

INTRODUCTION

When considering the effects of variations in predation pressure on the survival of fish larvae, it is imperative to consider that larvae are a relatively scarce element of the planktonic community, at least in terms of numbers and possibly biomass (Smith & Lasker 1978). Hewitt et al. (1985) and Purcell (1990) presented field evidence that predation is a dominant factor during much of the early larval stage but starvation may become important during the period associated with yolk absorption. However, there is still insufficient evidence to infer the consequences of variations in abundance or composition of either the prey community or predators to larval fish survival, particularly if multispecies interactions are considered.

In aquatic systems, the relative sizes of prey and predators is an important determinant of the former's

vulnerability (*sensu* Greene 1985) to the latter (e.g. Kerr 1974, Hansen et al. 1994). Kerr (1974) and Ware (1978) for example estimated that in pelagic ecosystems, prey are on average 5 to 7% of their predator's body length. However, organisms do not feed on a single prey type or size. Pearre (1986) found a constant niche breadth (i.e. the standard deviation of the log-transformed prey length) with respect to prey size consumed by different species of fish, independent of the predator's size. The values reported by Pearre (1986) imply that within a fish's niche (i.e. 95% confidence interval of prey size), prey weights could range over 2.5 orders of magnitude. Consequently, a predator and its principal prey, as determined by their average sizes (Kerr 1974, Ware 1978, Hansen et al. 1994), may be capable of feeding on the same food resources. For example, animals which consume yolk-sac and early larvae sized prey weighing 20 to 60 µg dry wt (Theilacker & Dorsey 1980) are also capable of feeding on copepod eggs and nauplii and other microzoo-

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plankton weighing between 0.15 and 1.3 µg dry wt (Theilacker & Dorsey 1980). Thus, larval fish may be vulnerable to both predation and competition by the same organism. The consequences of this interaction are 2-fold. If microzooplankton abundance is low, competition and predation by the predator may increase larval fish mortality. If microzooplankton abundance is high, starvation related mortality may not be significant, and predation may be reduced because microzooplankton could serve as an alternate prey for the predator thereby reducing larval mortality (Pepin 1987, Kean-Howie et al. 1988, Marguiles 1990, Gotceitas & Brown 1993).

The possible significance of variations in a predator's feeding on several trophic levels on the survival of larval fish has been considered by few researchers (Brownell 1985, Pepin 1987, Kean-Howie et al. 1988, Bailey & Houde 1989, Marguiles 1990, Gotceitas & Brown 1993). Although predator and food abundance are both recognized as important factors which influence the survival of larval fish (Shepherd & Cushing 1981, Hewitt et al. 1985, Purcell 1990), the general concept is that larval fish feed on small zooplankton and predators feed on larval fish and other similar sized prey, which assumes a linear food chain, but there are some exceptions (e.g. Suthers & Frank 1990). Because of the potential for marine organisms to feed on a wide range of prey sizes (Pearre 1986) rather than prey which are a constant proportion of predator size, ecological studies of larval fish need to consider how size-dependent vulnerability to predators changes as the abundance of alternate prey varies.

In this study, we present the results of experiments designed to investigate the effect of variations in the abundance of microzooplankton and the size of larval fish on the latter's vulnerability to predation by a vertebrate. We used the threespine stickleback *Gasterosteus aculeatus* as our predator because it is known to prey on fish eggs and larvae in both marine and freshwater systems (Rogers 1968, Lemmetyinen & Mankki 1975, Manzer 1976, Ohman 1986, Williams & Delbeek 1989). Sticklebacks are visual particulate feeders (Wooton 1976). We used capelin *Mallotus villosus*, cod *Gadus morhua* and winter flounder *Pleuronectes americanus* larvae to provide a wide range of prey lengths and morphologies, thus allowing a contrast of the influence of body size on vulnerability to predation among species (Pepin et al. 1987, Miller et al. 1988, Bailey & Houde 1989, Pepin & Miller 1993). *Artemia* sp. nauplii were used as alternate prey because they represent organisms of the appropriate size for larval fish feeding. Furthermore, the response of sticklebacks to adult *Artemia* sp. suggested that this species may represent an adequate substitute for wild zooplankters (Gotceitas & Brown 1993).

MATERIALS AND METHODS

Eggs were obtained from laboratory-held brood stocks (cod, winter flounder) or from natural spawning (capelin). Eggs were retained in flow-through containers (8°C) lined with 333 µm mesh nitex. For each species, egg production and hatching occurred over a 3 to 6 wk period. Hatching was monitored daily and emerging larvae were placed in 20 l black plexiglass containers maintained at approximately 10°C. Larvae were fed a mixture of rotifers (3 to 5 ml^{-1}) and *Artemia* sp. nauplii (0.5 to 1 ml^{-1}). We kept track of cohort age because of the possible significance of this factor on vulnerability to predation (Litvak & Leggett 1992).

Sticklebacks were obtained from a salt water inlet (28 to 30‰) using a beach seine with 7 mm mesh. The sticklebacks were acclimated to laboratory conditions in 280 l fibreglass containers with running sea water for at least 6 mo prior to the experiments. Sticklebacks were fed *Artemia* sp. adult and nauplii, and ground fish. Approximately 1 mo prior to the start of experiments, individual sticklebacks between 35 and 40 mm standard length were isolated in 1 l aquaria to habituate them to feeding as solitary predators. Prior to the start of experimental trials, each predator was presented larval fish prey of varying species and sizes at least 5 times to ensure a degree of experience to the prey type. This procedure was designed to reduce the variability in experience at the onset of the experiments. Individuals which did not respond and prey on larval fish in these pre-experiment trials were not used in the experiments.

For each experimental trial, the protocol consisted of placing 30 fish larvae of a single species into each of 8 aquaria. Experiments were conducted in 40 l glass aquaria (51 × 30 × 27 cm) at 10 to 12°C. Larvae were counted using a wide-bore pasteur pipette and placed into the aquaria for 30 min to allow acclimation. Two aquaria contained only fish larvae. The remaining 6 aquaria were divided into 3 pairs, each of which received approximately 100 (2.5 l^{-1}), 1000 (25 l^{-1}) or 10 000 (250 l^{-1}) *Artemia* sp. nauplii. After acclimation, a single stickleback was added as a predator in each aquaria. To provide a constant initial hunger level, predators were deprived of food for 24 h before experimental trials. Predators were chosen at random from the bank of approximately 20 animals. Each experimental trial lasted 30 min after the onset of the first feeding bout on the part of the predator. Predators were then removed and measured for standard length. Each aquarium was thoroughly rinsed to gather the contents using a 150 µm mesh sieve for preservation in 2% buffered formaldehyde. The number of larvae recovered from each tank was determined. We conducted 19 experimental trials.

The initial physical condition of the larvae from each experimental trial was assessed by keeping 30 larvae preserved in 2% buffered formaldehyde. The physical characteristics of larvae (standard length, yolk-sac diameter, eye diameter, depth of pectoral girdle) were measured to the nearest 0.1 mm using an image analysis system for preserved specimens taken at the start and end of the experiments.

The instantaneous mortality rate due to predation (Z, h^{-1}) was calculated as

$$Z = -\left[\frac{\ln\left(\frac{N_t}{N_0}\right)}{t}\right] \quad (1)$$

where t is the time interval in hours, N_0 is the number of larvae at time 0, and N_t is the number of larvae recovered at the end of the experiment. Eq. (1) corrects for depletion of larvae during the experiment in which ingested prey are not replaced (Royama 1971, deLafontaine & Leggett 1988).

Predator ingestion rates (I, larvae predator^{-1} h^{-1}) were calculated as

$$I = N_0(1 - \exp^{-ZP^{-1}}) \quad (2)$$

where Z is the instantaneous mortality rate due to predation and P is the number of predators; in this case $P = 1$.

An analysis of covariance was used to determine the effects of alternate prey abundance and larval size, or species, on mortality rates. Alternate prey abundance was incorporated as a classification variable because we had no a priori expectation of the functional

response of the predator to this variable. Larval length was included as a linear covariate.

RESULTS

The physical attributes of reared larvae used in our experiments varied substantially among species. Average daily growth rates ($\Delta L/\Delta t$) of capelin and winter flounder were 0.16 and 0.08 mm d^{-1} (Fig. 1), respectively. These are comparable to those obtained in other rearing studies of these species (Frank & Leggett 1986, Chambers et al. 1988). The growth rate of cod larvae was 0.05 mm d^{-1}, which is relatively low in comparison with other studies (e.g. Gamble & Houde 1984) and may indicate that the condition of these larvae was not optimal during our experiments.

There was a highly significant effect on mortality rates due to the presence of alternate prey ($F_{3,148} = 10.8$, p < 0.001) (Fig. 2), but a close examination of the results indicates that only levels of alternate prey of 250 nauplii l^{-1} caused a reduction in the impact of sticklebacks on larval fish. Furthermore, the size of the fish larvae also had a significant impact on mortality rates ($F_{1,148} = 6.9$, p < 0.001) (Fig. 3). Overall, as the size of larvae increased, mortality rates increased. The analysis of covariance also revealed that size rather than age ($F_{1,148} = 0.6$, p > 0.4) was the principle correlate of vulnerability to predation in these experiments.

The pattern of size-selection within experimental trials also showed a pattern in which mortality rates appeared to be higher on larger individuals within trials (Fig. 4). The average size of survivors revealed that predation within experiments with high levels of alter-
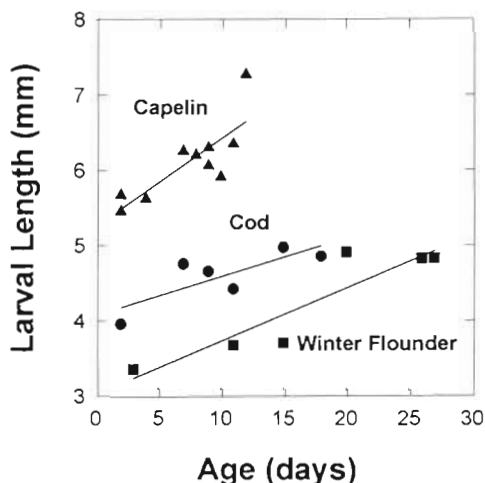

Fig. 1. Length at age relationships for capelin (▲), cod (●), and winter flounder (■) larvae reared in the laboratory. Age is measured in days post-hatch. Each point represents the average from a sample of 30 larvae used in experimental trials. Average growth rates were estimated using least-squares regressions for individual species. The r^2 for capelin, cod, and winter flounder are 0.66, 0.48, and 0.84, respectively
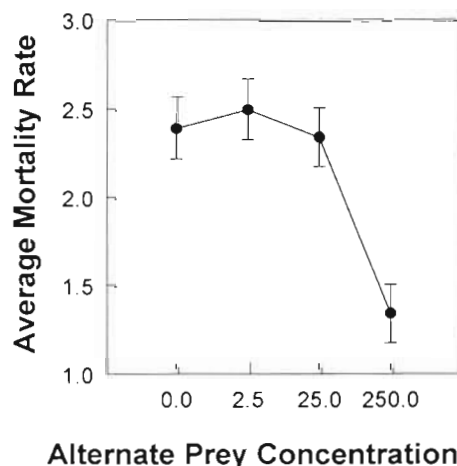

Fig. 2. Average overall mortality rate (h^{-1}) during experimental trials in relation to alternate prey abundance. Average predation rates and SE were estimated after correcting for the effect of variations in size of larvae using an ANCOVA
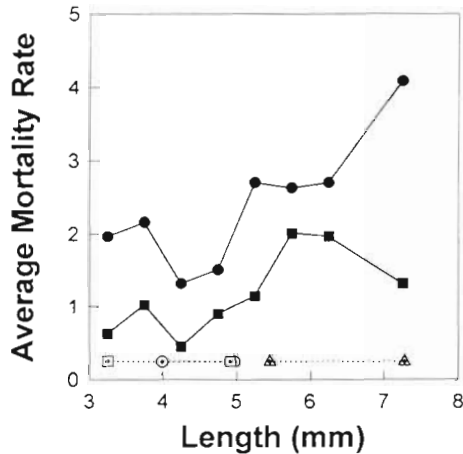
Fig. 3. Average mortality rate (h^{-1}) during experimental trials in relation to initial size of larvae and abundance of alternate prey. Data presented were averaged over 0.5 mm length intervals. (●) Average predation rates for alternate prey levels of 0, 2.5 and 25 nauplii l^{-1}; (■) Average predation rates for alternate prey levels of 250 nauplii l^{-1}; (□), (○) and (△) at the bottom of the graph show the size ranges for winter flounder, cod, and capelin, respectively
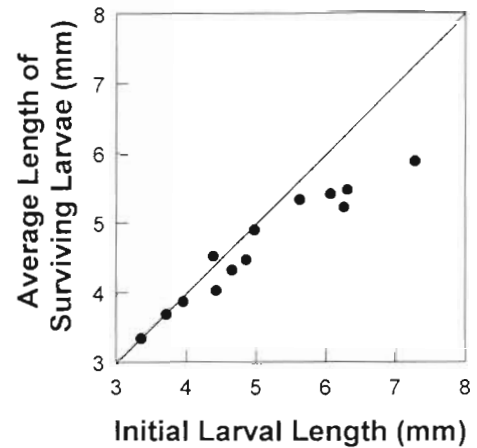

Fig. 4. Average size of larvae surviving each experimental trial in relation to initial average size presented to the predator. The one-to-one line is shown for reference. Low numbers of survivors from some experiments prevented us from including all observations from trials with high levels of alternate prey

nate prey was focused more on larger individuals. The level of size selection within experiments increased with increasing size of larvae. Insufficient numbers of larvae remained in the trials with low alternate prey levels (<250 nauplii l^{-1}) to determine whether this pattern was also apparent under such conditions.

The importance of alternate prey abundance to predation on fish larvae is greater for smaller larvae (Fig. 5). The ingestion rate of larvae by the predator at low levels of alternate prey (≤25 nauplii l^{-1}) relative to the ingestion rate of larvae at high levels of alternate prey (250 nauplii l^{-1}) was greater as the average size of the larvae decreased ($r = -0.43$, $0.1 < p < 0.05$, n = 19). Although the trend was weak, it indicated that as the size of larvae decreased, the likelihood of an attack may have decreased due to the presence of alternate prey.

To this point, the analysis only considered general trends without taking into account difference among species. Because each species used in these experiments represented a different range of sizes (Fig. 1), incorporating taxa as a categorical variable in the analysis of covariance had a significant impact on the results. Although the effect of alternate prey abundance remained highly significant ($F_{3,148} = 10.5$, p < 0.001), neither age ($F_{1,148} = 3.0$, $0.1 > p > 0.05$) nor length ($F_{1,148} = 1.3$, p > 0.2) had a significant impact on predation rates after considering the effects of taxonomy ($F_{2,148} = 4.0$, p < 0.05). This was also confirmed within species where length of larvae did not have a significant impact on predation rates of capelin ($F_{1,56} = 0.2$, p > 0.5), cod ($F_{1,45} = 1.2$, p > 0.2), or winter flounder
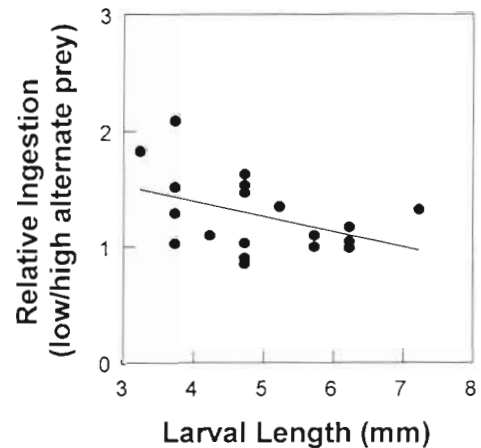

Fig. 5. Relative ingestion rate from experiments with low (0, 2.5, 25 nauplii l^{-1}) in contrast to high (250 nauplii l^{-1}) levels of alternate prey in relation to the initial size of larvae. Solid line represents the least-squares regression

($F_{1,45} = 2.9$, p > 0.1). However, in all instances, the effect of alternate prey abundance on predation was significant and consistent with the general analysis.

DISCUSSION

The presence of alternate prey had a significant impact on the vulnerability of larval fish to a vertebrate predator but the effect was not one of simple dilution. Kean-Howie et al. (1988) noted that the impact of sticklebacks on larval hake and mackerel decreased with increased alternate prey abundance, but that rel-

ative selection by the predator for fish larvae increased. These authors suggested the predator has to spend more time searching for the preferred prey, possibly due to interference or confusion caused by other prey types thus reducing the numbers of larvae caught. Our results appeared to show a similar pattern. The effect of increased abundance of small alternate prey resulted in an abrupt and significant reduction in vulnerability at levels between 25 and 250 nauplii l^{-1}. However, ingestion of larvae by the predator did not decrease by an order of magnitude suggested that the predator did not switch its feeding proportionately to the abundance of alternate prey. Such a behaviour pattern suggests that larger prey items, which in this instance were larval fish, are a highly preferred prey of particulate feeding vertebrate predators. Kean-Howie et al. (1988) referred to this behaviour pattern as counter switching. Pepin et al. (1987) also noted that schooling mackerel showed a strong selection for larval fish relative to other available prey. As with other facultative filter feeders, the availability of relatively large prey (e.g. large copepods, fish larvae, medusae) resulted in strong selection for those prey types (O'Connell 1972, O'Connell & Zweifel 1972, Pepin et al. 1987, Runge et al. 1987, Pepin et al. 1988, Gibson & Ezzi 1992). This suggested that switching to smaller alternate prey types by visual vertebrate predators may require fairly high concentrations relative to the abundance of preferred prey types such as larval fish.

As with previous studies on the effect of alternate prey on vulnerability of larval fish to predators, high concentrations of plankton were required to reduce the impact of predators on fish larvae when using small alternate prey (Kean-Howie et al. 1988, Marguiles 1990, Gotceitas & Brown 1993). Because such high concentrations are rare in the field, it might be argued that the effect of alternate prey may not be an important aspect of the ecology of larval fish. However, Cowan & Houde's (1992, 1993) enclosure studies showed a significant effect of alternate prey on the vulnerability of larval goby Gobiosoma bosci to ctenophores Mnemyopsis leidyi and anchovy Anchoa mitchilli. deLafontaine & Leggett (1987), Gamble & Hay (1989) and Cowan & Houde (1993) argued that experimental conditions using in situ enclosures yield predation rates that are comparable to those observed in the sea. Furthermore, there may also be notable reduction in predation rates due to predation on zooplankton which are of a size comparable to that of larval fish (Gotceitas & Brown 1993), an issue seldom considered in most manipulations. It is therefore possible that the abundance and complexity of the zooplankton community with which larval fish co occur may influence their vulnerability to predators as well as their growth rates.

The effect of larval size on their vulnerability to predation at high alternate prey concentrations (250 ml^{-1}) appeared to be complex. Vulnerability to predation increased as larval length increased, both within and among experiments, within the limited range of lengths used in this study. However, it appeared that the impact of alternate prey on predation rates may be influenced by the contrast in sizes of the different prey types. As the size of larvae increases relative to the size of alternate prey, the predator may form a stronger search image for the larger prey type. Even within a prey type, the rules governing vulnerability to predators appear to be complex. Although the larger species (i.e. capelin) was more vulnerable to sticklebacks than smaller ones (i.e. cod or flounder), the mean size of individuals within each species had no significant impact on predation rates although there was evidence of size selection by the predators within experimental trials. This contrasted with observations from an earlier study dealing with predation on capelin larvae by sticklebacks (Pepin et al. 1992) which noted a significant effect of prey size over a range comparable to the one used in the current experiments. However, both container volume and experimental duration differed between this and our earlier study. It is possible that the interaction between these factors may influence the probabilities of encounter and attack and thus make comparison among studies or protocols difficult.

deLafontaine & Leggett (1987), Gamble & Hay (1989) and Cowan & Houde (1993) noted a highly significant impact of container volume on the estimated predation rates by gelatinous zooplankton on larval fish. Most experiments dealing with predation on larval fish were conducted in relatively small containers (Bailey & Houde 1989, Paradis & Pepin unpubl. data). Under such circumstances, we know that encounters are artificially inflated relative to natural conditions (deLafontaine & Leggett 1987, Gamble & Hay 1989, Cowan & Houde 1993). Although there is relatively thorough information dealing with the probability of capture in relation to predator and prey sizes (Pepin et al. 1987, Miller et al. 1988), it is essential to recognize that this is only one element of the predation process (O'Brien 1979, Fuiman 1989). By confining predator and prey in relatively small experimental containers, it is possible that the probability of encounter was artificially made size-independent. If correct, and if we assume that the probability of capture decreases with increasing size of prey (Pepin et al. 1987, Miller et al. 1988), this would suggest that the probability of attack would have increased with increasing prey size, over the range used in this study. This contrasted to Brownell's (1985) observations which indicated that the probability of an attack decreased as the size of the larvae increased. However, his conclusions were based on behavioural

observations in which an encounter was assumed to occur if a larvae was within a certain distance of the predator, whereas our statement is based on the assumption that the predator might be able to perceive a prey item within the confines of the aquaria used in our experiments (see Wooton 1976). Size-dependent encounter rates as well as perception of prey and response by the predator (i.e. probability of attack and pursuit) may be significantly influenced by the 3-dimensional nature of the environment in which they are foraging and in which experiments were conducted. We believe these questions point to a strong need to conduct field tests of the many laboratory derived concepts of size-dependent processes in order to gain a better understanding of the factors which influence the survival of larval fish.

Although it is difficult to contrast feeding and predation experiments, it is essential that some effort be made to contrast the effects of nauplii concentration on these 2 processes. A 50% reduction in predation rates by sticklebacks was noted between concentrations of 25 and 250 nauplii l^{-1}. Rearing studies conducted with herring (Werner & Blaxter 1980) and winter flounder (Laurence 1977) found that a similar increase in prey availability for larvae resulted in a 50 to 60% reduction in mortality rates, as well as substantial increases in growth rates. Although it is not possible to extrapolate the absolute magnitude of the changes in mortality rates caused by increased nauplii concentrations to the field, both reduced predation pressure and enhanced feeding/reduced starvation should result in an increase in overall survival. Why then is there relatively little field evidence of a strong link between planktonic prey concentration and the survival or mortality of ichthyoplankton? This may be due partly to inadequate sampling procedures (e.g. Frank & Leggett 1983, 1985, Frank 1988). Furthermore, both predators and prey undergo fluctuations in abundance which can be independent of one another. Pepin (1987) presented evidence that the relative abundance of predators and zooplankton is strongly correlated with the mortality rates of northern anchovy larvae *Engraulis mordax* in the California Current (NE Pacific). Whether this association is due to the enhanced feeding of the larvae or the reduced impact of the predator, or both, is unknown (Pepin 1987). However, it appears that future work should consider larval fish as elements of a complex food web in order to elucidate the relationship between survival and biotic conditions.

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