

Size-dependent predation risk in larval fishes: mechanistic inferences and levels of analysis

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In any ecological study, the level of observation, as well as the aggregation and analysis of data, affects the inferences that can be drawn. In fisheries science, many studies, covering a wide range of levels of analysis, have examined size-dependent predation processes, particularly predation, as a primary source of mortality for larval fish (reviewed by Bailey and Houde, 1989; Bertram and Leggett, 1994; Leggett and Deblois, 1994). A general result from those studies is that mortality rate declines as body size increases both across (e.g. Peterson and Wroblewski, 1984) and within species (e.g. van der Veer and Bergman, 1987). However, the use of that general result to forecast survival probabilities at lower levels of aggregation and analysis (e.g. for individual larvae) could lead to erroneous predictions (Pepin and Miller, 1993). Several recent studies have questioned the validity of the generality that increasing larval size reduces predation risk when analyses were conducted at the level of the individual and when the effects of prey size on vulnerability to predation were examined independently of age effects (Litvak and Leggett, 1992; Pepin et al., 1992; Bertram and Leggett, 1994).

The results of Pepin et al. (1992) show that the effect of larval size inversely affects vulnerability to predation, depending on the level at which the information is aggregated and analyzed. Contrasting patterns of larval mortality caused

by predation within and between mesocosmic (2.7 m³ circular tanks) trials were observed in the predation of yolk-sac and first-feeding capelin larvae, *Mallotus villosus*, by threespine sticklebacks, *Gasterosteus aculeatus* (Pepin et al., 1992). Prey age ranged from 1 to 5 d (median post-emergence) and prey size ranged from 5 to 5.8 mm. In each experimental trial, single naive predators were offered a cohort of 500 similar-age prey for 24 h. Comparisons between experiments indicated that greater mean size and age of larvae in the mesocosm reduced mortality due to predation. However, within experiments, larger larvae suffered higher mortality than did smaller individuals of the same age (see also Litvak and Leggett, 1992). Resolving the discrepancy between these results is important because the conclusions differ depending upon the level of observation and analysis. Large size and age were beneficial to larval survival when mean values for each trial were compared over the full range of available prey sizes (i.e. between trial comparisons). Conversely, large size at age was detrimental to larval survival at a lower level of observation and analysis (i.e. within trials) when a reduced range of prey sizes was examined. Patterns and generalizations based on observations from higher levels of aggregation (e.g. cohorts, populations, species) and extended ranges of data, although conceptually appealing, may be

misleading for gaining insights into the mechanistic processes that affect larval survival at the level of the individual, where selection acts (Pepin and Miller, 1993). Moreover, to achieve an understanding of the mechanisms that determine overall survival, information from several levels of observation must be integrated (Crowder et al., 1992; Pepin and Miller, 1993). In this study I use fundamental foraging theory to examine an underlying mechanism that could have produced both of the observed mortality patterns in Pepin et al.'s (1992) results at low and higher levels of analysis, within and between trials, respectively.

Pepin et al. (1992) argued that the within- versus between-trial differences occurred because predators actively selected larger larvae within trials ("because of greater encounter or attack probabilities due to greater activity or longer perception distance [i.e. the distance that larvae were visible to the predator] relative to smaller prey") but as the average size of prey increased between trials, the average predation rate decreased owing to greater avoidance capabilities of the larger, older larvae. In accordance with foraging theory (e.g. Stephens and Krebs, 1986), the predators in Pepin et al.'s (1992) study may also have actively selected larger larvae because of their higher caloric value and hence their profitability to a predator within trials (prey handling time was likely to be size-independent in the study system; energetic costs of attack were also assumed to be independent of prey size). Furthermore, the consistently high profitability

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of large larvae to a predator may have more than compensated for the fact that fewer larvae were captured as prey size increased, between trials.

I evaluated this proposition by estimating the total mass of prey that were consumed by predators in each of the 23 predation trials conducted by Pepin et al. (1992). I estimated the total number of prey ingested for each trial in two ways. First, as an estimate of the maximum number of prey ingested, I used the difference between the number of prey present at the beginning and end of each trial (Pepin, unpubl. data). Second, I calculated an estimate for the minimum number of prey ingested by using Equation 2 from Pepin et al. (1992). For each trial I estimated the total mass of prey consumed by multiplying the number of prey ingested by the mass of a capelin larva whose length was equal to the mean of prey lengths used in that trial. To calculate the mass of larvae of average length, I used a general allometric length-weight relationship for capelin (Pepin, 1995). The results demonstrate that the maximum total number of prey consumed per predator decreased significantly with increasing prey length between trials (Fig. 1A; $F=22.1$, $df=1,21$, $P=0.0001$, for the pooled data set). Moreover, the total maximum mass of prey consumed increased significantly with increasing prey length (Fig. 1B; $F=52.8$, $df=1,21$, $P<<0.001$; see also Fig. 9 in Pepin et al., 1992). The lat-

ter result also held within all three categories of prey and predator length ratios.

It is worth noting that the group of triangles below the regression lines (Fig. 1, A and B) represent five trials from an experiment that employed the smallest predators (mean=38.4 mm vs. 50.6 mm for all 18 trials in other experiments; $t=3.5$, $df=21$, $P=0.002$) and the lowest temperatures (mean=11.6°C vs. 13.2°C for all other trials; $t=2.6$, $df=21$, $P=0.016$). It is likely that the low number of prey consumed during those trials (mean=393 vs. 474 for all other trials; $t=7.9$, $df=21$, $P<<0.001$) resulted from the small predator size and low temperature, because smaller predators consume fewer prey (Pepin et al., 1992) and activity and ingestion rates are generally reduced at low temperatures.

The minimum total number of prey consumed also decreased significantly with increasing prey length between trials ($F=20.8$, $df=1,21$, $P=0.0002$, for the pooled data set). The mass of prey consumed also increased with prey length within each prey and predator length category when the minimum number of prey consumed were used. When the results from each prey and predator length category were pooled, the relationship between prey consumption and prey length was not significant owing to the low prey consumption values for the five trials with anomalous temperatures and predator lengths (see above). There was a highly

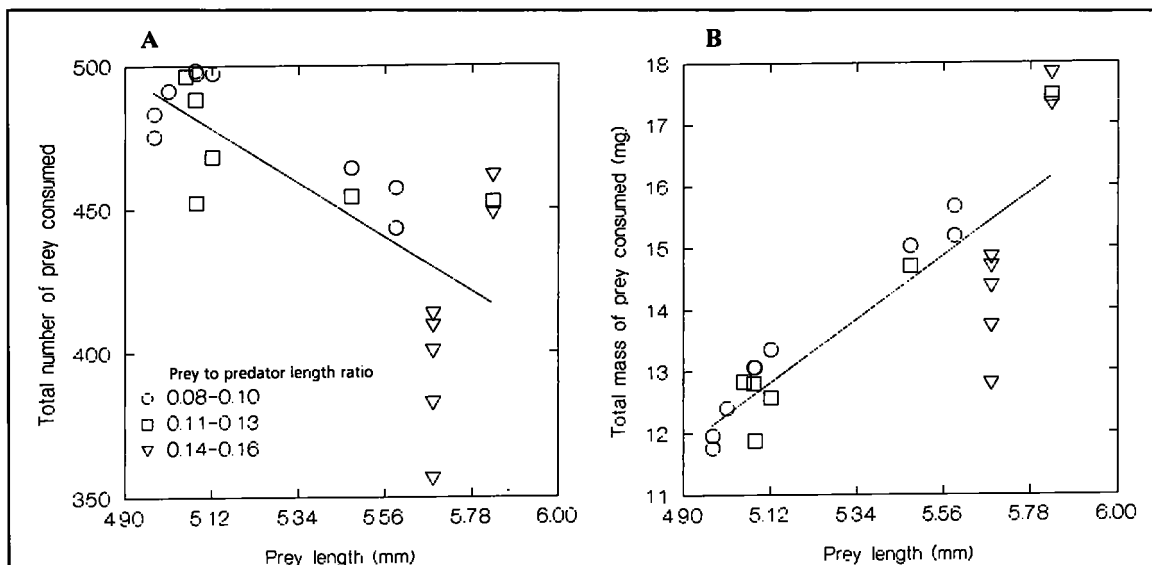


Figure 1

The total mass and number of larval capelin, *Mallotus villosus*, consumed by threespine stickleback, *Gasterosteus aculeatus*. Estimates of the maximum total number (A) ($y=918-85.9x$) and mass (B) ($y=-11.1+4.7x$) of prey consumed by sticklebacks versus the mean length of capelin larvae from 23 predation trials conducted by Pepin et al. (1992). The categories of prey and predator length ratio were assigned arbitrarily (on the basis of unpubl. data from P. Pepin). Regression equations were based on the pooled data set.

significant positive relationship between the minimum mass of prey consumed and prey length when those five trials were excluded from the analysis ($F=43.9$, $df=1,16$, $P<<0.001$). Thus, both estimates of prey consumption indicate a positive relationship between prey length and total mass of prey consumed.

My analysis is consistent with the interpretation that predators actively select the largest, most profitable prey to maximize both the mass of prey consumed and the caloric gain from an attack, as predicted by foraging theory. Because of this pattern of prey selection, predators consumed significantly more biomass as prey size increased, between trials, despite a decline in average predation mortality. More generally, the result confirms that larger larvae may be subject to higher rates of predation notwithstanding that their overall vulnerability to predation is inversely related to length. A future challenge will be to incorporate this result from several levels of analysis into longitudinal studies that examine the effects of mortality caused by predation on the size structure of cohorts of growing prey.

The above arguments on prey profitability are consistent with the interpretation of Pepin et al. (1992) that predators actively select larger prey because of greater encounter or attack probabilities that result from greater activity or a longer perception distance (i.e. the distance that a larva is visible to a predator) relative to smaller prey. Indeed predators may have selected larger prey because of the combined effects of higher profitabilities and encounter rates for larger prey. It is noteworthy, however, that prey encounter rates and profitability may not always increase in unison with increasing prey size because encounter rates will be dependent on prey behavior and the perception capabilities and size of the predator. Separating the general effects of prey encounter rate and profitability on predator size-selectivity (see also Juanes and Conover, 1994) will require mechanistic studies and modelling efforts that address prey behavior, profitability of the prey to a predator, as well as encounter, attack, and capture rates, all of which will require corresponding information on predator foraging technique and perception capabilities over a broad range of prey sizes and prey-to-predator size ratios.

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