Effects of body size on probability of predation for juvenile summer and winter flounder based on laboratory experiments

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Predation by brown shrimp (*Crangon crangon*) has been hypothesized to impose significant mortality on settling juvenile plaice (*Pleuronectes platessa*) in European waters (Edwards and Steele, 1968; Lockwood, 1980; Veer and Bergman, 1987; Pihl, 1990). Laboratory experiments found that predation rate was dependent upon prey density and that predation, estimated by gut content analysis, could be the source of previously unexplained density-dependent mortality of early juvenile plaice in the Wadden Sea (Veer, 1986; Veer and Bergman, 1987). An important finding of this work is that predator and prey body size may have profound effects upon rate of predation and that recently settled plaice (under 30 mm) are much more vulnerable to predation than are larger fish. We were prompted to investigate the role of the sevenspine bay shrimp (*Crangon septemspinosa*) as a predator on metamorphosing and small juvenile summer (*Paralichthys dentatus*) and winter (*Pleuronectes americanus*) flounder because 1) all of these species are abundant components of New Jersey estuaries, 2) they all co-occur temporally, 3) the sevenspine bay shrimp is morphologically similar to the European brown shrimp, and 4) fish scales were present in the guts of this shrimp (Wilcox and Jeffries, 1974). We conducted laboratory experiments to determine the size range over which juveniles of these fish species may be susceptible to predation by sevenspine bay shrimp.

Methods

We used small cylindrical glass bowls, 197 mm diameter, containing 2 cm of washed sand (sufficient for both predators and prey to burrow in), filled with seawater to a depth of 50 mm. We conducted all experiments at prevailing ambient water temperatures (Table 1) by immersing the bowls in a flow-through seawater bath.

We collected transforming and juvenile winter flounder in May–July, 1990 and summer flounder in January–February 1990, with nightlights, plankton nets, and seines. Adult sevenspine bay shrimp were collected (January–July) by using a seine. All collections were made in the Great Bay-Little Egg Harbor estuarine system (New Jersey). In the laboratory, we fed experimental animals in excess (shrimp-chopped fish and shrimp; flounder-live brine shrimp nauplii), and then starved them for 24 hours before the start of each experiment. After anesthetization ($25\,\mathrm{mg \cdot l^{-1}}$ MS–222) we measured body sizes (Table 1) of flounder (in mm, standard length [SL]) and shrimp (in mm, total length [TL], from the tip of the antennal scale to the end of the uropod, Price, 1962).

At the start of each trial, we placed one flounder into each container and allowed it to acclimate for 24 hours. We then introduced one shrimp into each container at approximately 1500 hours. All containers were covered with perforated clear plastic sheets and were left undisturbed for 18 hours. We ran the experiments under a natural light cycle (11 hours dark, 13 hours light, lights out at 1800) using fluorescent lighting. Because sevenspine bay shrimp are unlikely to forage during the day (Haefner, 1979), we introduced the shrimp three hours before darkness in order to reduce the likelihood of predation immediately following their introduction. We recorded water temperature at the start and end of each trial. For each experiment, we set up several control containers (prey present, predator absent) and observed no flounder mortality in these controls (n=15 for summer flounder, n=12 for winter flounder). At the termination of each trial we scored predation as plus or minus based on the presence or absence of a live flounder.

We repeated trials for winter and summer flounder and varied shrimp and flounder size (Table 1). Because settlement in summer flounder occurs earlier than winter flounder, experiments involving summer flounder were conducted during late winter and winter flounder experiments were conducted in the spring, resulting in different ambient water temperatures (Table 1). In trials involving winter flounder, we

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Table 1

Sample sizes and body sizes of sevenspine bay shrimp and flounder prey for laboratory experiments. Sample size refers to the number of individual predator-prey trials. Pearson correlation coefficients (*r*) are given for correlations of predator size with prey size to indicate random allocation of predator and prey sizes.

Prey	Temperature (°C)	Sample size	Size range (C.V.)		*r*	*P*
			Predator (TL)	Prey (SL)		
Pleuronectes americanus	18	60	51–59 mm (4.2%)	9–46 mm (37.4%)	0.15	0.24
Paralichthys dentatus	9–12	135	27–65 mm (17.5%)	11–16 mm (7.1%)	0.03	0.70

used large shrimp to minimize the predator size effect, thereby concentrating on prey size to determine if there was a size refuge for winter flounder. In trials involving summer flounder, we used a large range of predator sizes, but a narrow range of flounder sizes (those in the last stage of eye migration) because of the greater availability of the latter. This combination of predator and prey sizes was used to establish the relationship between shrimp size and their ability to successfully prey upon small summer flounder. In all trials, we randomly allocated predators and prey to the bowls to avoid deliberate or inadvertent size biases.

We used logistic regression analysis (SAS/STAT Users guide, Release 6.03 Edition 1988), which uses maximum likelihood analysis of the natural logarithm of the ratio of these response frequencies (logits) to estimate parameters of a linear model. Because the response is a frequency response rather than a continuous response, a chi-square value is calculated to test for the significance of the treatment variables. Once parameter estimates of the linear model have been made, expected logits can be generated. Expected probabilities of mortality can then be calculated using the following relationship:

$$m = \frac{e^L}{1+e^L}$$

where m is the probability of mortality from predation, e is the root of natural logarithm and L is the logit predicted by the linear model. This relationship is obtained by solving the following simultaneous equations for m:

$$m+s=1$$

and

$$\ln\left(\frac{m}{s}\right) = L$$

where s is the probability of survival.

Results

Sevenspine bay shrimp consumed both flounder species under laboratory conditions, and size effects were important in all interactions. In summer flounder trials, both prey and predator size significantly affected the outcome of prey-predator interactions (predator size $\chi^2=24.07$, $P<0.0001$, prey size $\chi^2=7.75$, $P<0.01$). Summer flounder matched with larger shrimp experienced generally greater mortality than those matched with smaller shrimp (Fig. 1A). Logistic regression of these data produced a positive relationship between probability of predation and shrimp size (Fig. 1B) which was stronger when the effect of flounder size was controlled using linear regression and the residuals were plotted against predator size (Fig 1C). Smaller summer flounder experienced higher mortality (Fig. 2A); however, probabilities from logistic regression show no clear pattern (Fig. 2B) because of the confounding effect of predator size. When we controlled the predator-size effect, a clear negative relationship was revealed between summer flounder size and probability of predation (Fig. 2C).

For winter flounder, the effect of flounder size on the probability of predation was significant ($\chi^2=4.03$, $P<0.05$), but no significant predator size effect occurred ($\chi^2=0.04$, $P>0.8$) presumably because we deliberately selected large shrimp in these trials in order to minimize this effect. Only the smallest individuals (<17 mm SL) were preyed upon (Fig. 3A). Logistic regression analysis demonstrated that the highest probability of predation was on the smallest individuals (>60% for 9 mm SL). This probability declined to zero at flounder lengths of approximately ≥17 mm SL (Fig. 3B). Parameter estimates of the prey size effect for both summer and winter flounder were similar (–0.4 ± 0.2 for winter and –0.6 ± 0.2 for summer), implying a similar size relationship for both species.

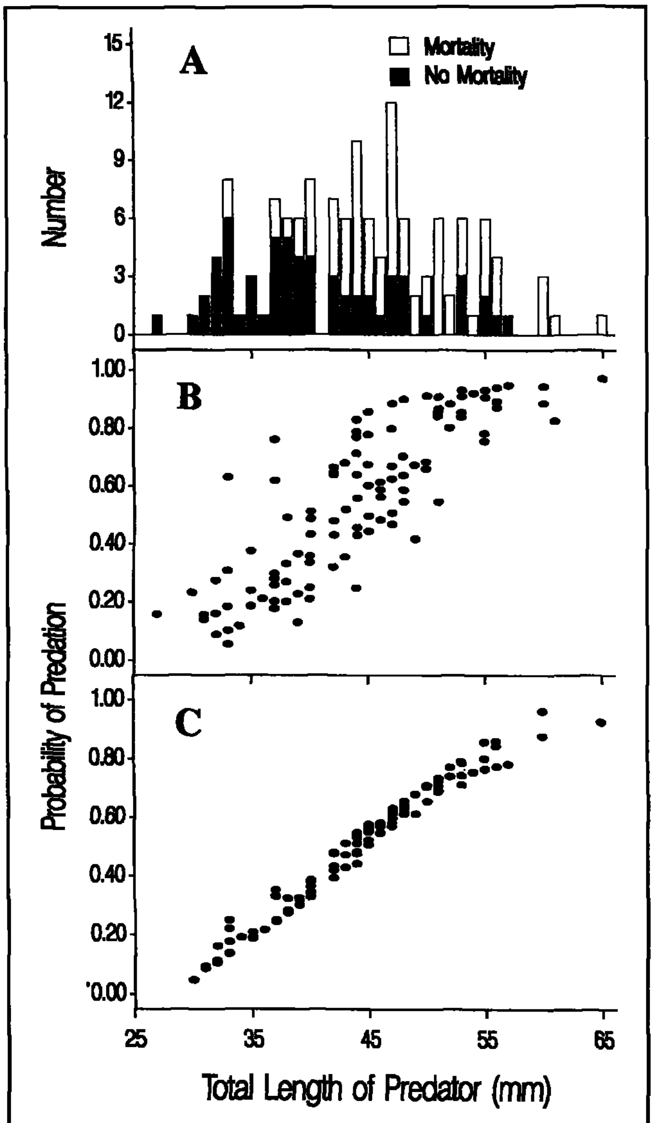

Figure 1

Relationship between size of sevenspine bay shrimp predators and predation on summer flounder prey. Graph presents original data with sample sizes above each bar (A), raw probabilities as predicted by logistic regression (B), and probabilities after being standardized for the effect of prey size (C). These probabilities and those for Figure 2 are based on the equation: Logit = 1.66+(0.15 * predator size)–(0.59 * prey size). See text for discussion of logits.

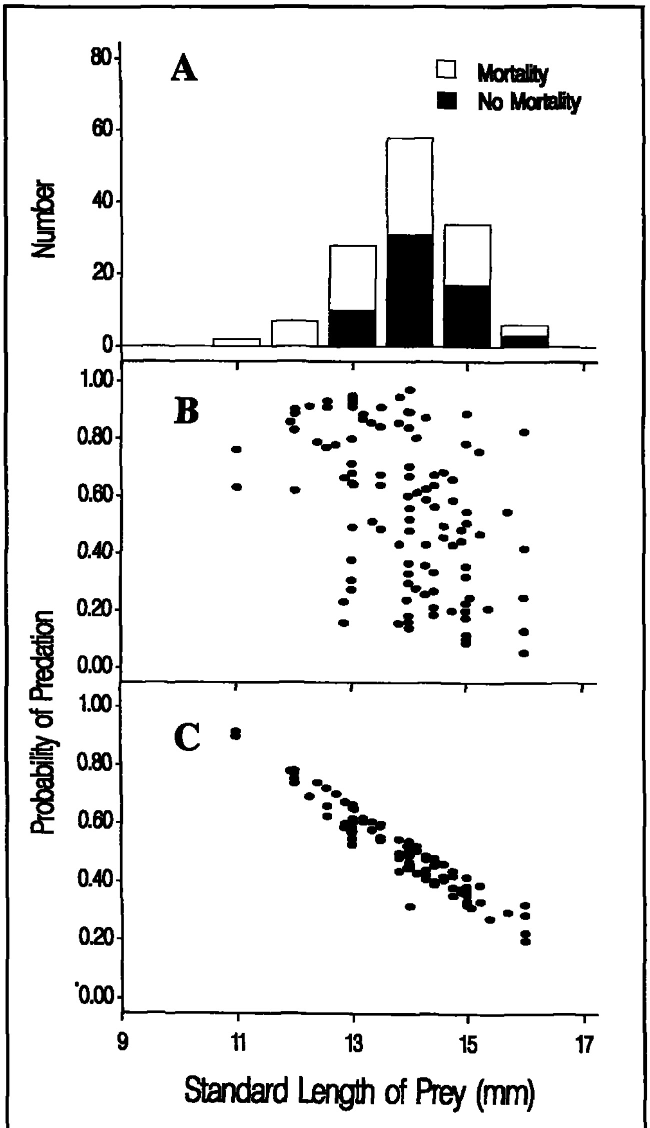

Figure 2

Relationship between prey size and probability of predation on summer flounder by sevenspine bay shrimp. Graph presents original data with sample sizes above each bar (A), raw probabilities as predicted by logistic regression (B), and probabilities after being standardized for the effect of predator size (C).

Discussion

Summer and winter flounder that survive the egg and larval stage and settle to estuarine substrates inhabited by adult sevenspine bay shrimp may be subject to significant predation. Summer flounder of 11–16 mm SL, the size at which they enter the estuary (Szedlmayer et al. 1992, Keefe and Able, 1993), are vulnerable to predation by a large size range of sevenspine bay shrimp. This interaction is likely because these species co-occur under natural conditions. Previous studies indicate that abundance of adult sevenspine bay shrimp, in estuaries to the south and north of the study area (Modlin 1980, Price 1962), begin to increase in the fall and continue to do so until they reach a peak in the spring. This temporal pattern overlaps completely with the period (October–May) that summer flounder enter the estuaries of New Jersey (Able et al. 1990, Szedlmayer et al. 1992). These shrimp range from 10–50 mm TL (Price, 1962). Our data sug-

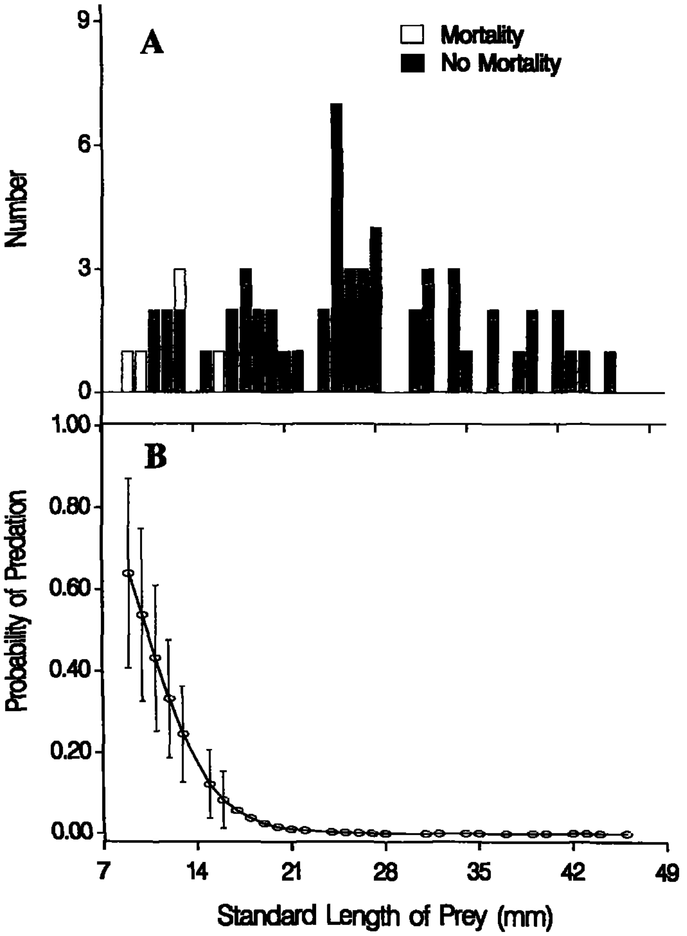

Figure 3

Relationship between size of winter flounder and predation by sevenspine bay shrimp. Figure presents original data with sample sizes above each bar (**A**) and predictions made by logistic regression (**B**). Bars on probabilities reflect one standard error of the estimate. These probabilities are based on the equation: Logit = 4.39–(0.42 * prey size).

gest that small summer flounder are vulnerable to predation over a large fraction of this range, with a 50% chance of mortality when encountering a shrimp of 45 mm TL (Fig. 1).

Winter flounder also settle (April–May) in northeastern U.S. estuaries (Pearcy, 1962) including those in New Jersey (pers. observ.) when adult sevenspine bay shrimp are abundant. Winter flounder settle at a smaller size than summer flounder (7.8 mm SL for winter flounder, Chambers and Leggett, 1987, vs. 13 mm SL for summer flounder, Keefe and Able, In press); however, our data indicate that the relationship between flounder size and vulnerability to predation is similar for the two species. This suggests that winter flounder must approximately double their size (i.e., reach approximately 17 mm) before they achieve a size refuge from predation by large sevenspine bay shrimp (Fig. 3). Both winter and summer flounder appear to exhibit a pronounced decrease in vulnerability to predation between 9 and 20 mm SL.

In summary, the vulnerabilities of both species of flounder were significantly affected by small differences in prey size. The duration of time spent within this size range (i.e., growth rate) can be quite variable depending upon habitat for winter flounder (Sogard, 1992) and temperature effects for summer flounder (Keefe and Able, 1993). Thus slight variation in size at settlement, or growth after settlement, may have important effects upon survival for both species. This scenario suggests that variability in stage duration, not rate of mortality, may be a critical determining factor of year-class strength as has been suggested by a number of authors (Sissenwine, 1984; Chambers and Leggett, 1987; Houde, 1987; Bailey and Houde, 1989).

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