

Size-Specific Predation on Marine Invertebrate Larvae

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Abstract. Predation on planktonic larval stages is frequently a major source of mortality for the offspring of benthic marine invertebrates. Mortality rate likely varies with larval size and developmental stage, but few experiments have measured how these factors affect predation rates. I used experimental reductions in egg size to test how variation in larval size affects the likelihood of predation during planktonic development. Blastomeres of the sand dollar *Dendraster excentricus* were separated at the two-cell stage to produce half-sized zygotes. Larvae resulting from this manipulation were tested for their susceptibility to predation relative to whole-sized siblings at four ages. Individuals from each size class were simultaneously presented as prey items to five predators (crab zoeae, crab megalopae, chaetognaths, solitary tunicates, and postlarval fish) in the laboratory. Four predators consumed significantly more half-sized larvae than whole-sized larvae, but one predator type (postlarval fish) consumed more whole-sized larvae. Predators that consumed more half-sized larvae also preferentially consumed younger larvae. In contrast, postlarval fish showed no significant prey preference based on larval age. These results suggest that assumptions of constant mortality rates during development should be modified to account for the effects of larval size and age.

Introduction

Most benthic marine invertebrates release gametes in numbers that far exceed the number of juvenile recruits. Thorson (1950) hypothesized that this “wastage” of eggs, embryos, and larvae can be primarily attributed to planktonic predation. More recent reviews of field and laboratory data confirm that predation is a significant source of mortality for the eggs, embryos, and larvae of marine invertebrates (Young and Chia, 1987; Rumrill, 1990; Morgan, 1995). These data suggest that larval mortality rates can be

substantial and also highly variable, ranging from 2% to 100% of the population lost per day (Lough, 1976; Allan *et al.*, 1976, cited in Rumrill, 1990). Although there is a consensus that larval mortality due to predation is a significant factor limiting recruitment in marine invertebrates, little evidence is available to explain the wide variation in estimates of larval mortality rates. One possible explanation is that the size and age of larval prey, as well as the composition of the predator community that larvae encounter, determines the likelihood of larval mortality due to predation.

Size- or age-specific predation is a common feature of predator-prey interactions (*e.g.*, Law, 1979; Reznick and Endler, 1982; Wellborn, 1994; Day *et al.*, 2002), yet the way in which changes in size or age affect predation rates for marine invertebrate larvae is poorly understood. In freshwater zooplankton communities, size-specific predation can select for either increased (Dodson, 1974) or decreased (Brooks and Dodson, 1965) prey size, depending on the types of predator species present. Similarly, for marine invertebrate larvae, available data suggest that age-specific predation may be important in predator-prey interactions and that larval predation rates may vary with predator type (Rumrill and Chia, 1984; Rumrill *et al.*, 1985; Pennington *et al.*, 1986). However, no studies have explicitly examined the effects of the interaction between larval size and larval age on predation rates in a rigorous fashion.

Despite the evidence that predation rates can vary with offspring age, most models of life-history evolution in benthic marine invertebrates make the simplifying assumption that offspring mortality rates are constant during development (*e.g.*, Vance, 1973; Jackson and Strathmann, 1981; Roughgarden, 1989; Havenhand, 1993; McEdward, 1997), with few exceptions (*e.g.*, Christiansen and Fenchel, 1979; Levitan, 2000). Even models of “mixed” life histories, which account for mortality variation due to encapsulation, assume a constant rate of planktonic mortality (Pechenik, 1979; Caswell, 1981). Data on how rates of predation vary with size and age are crucial to predictions of when species

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with complex life cycles should switch from one habitat to another (Werner and Gilliam, 1984).

In this study, I examine how larval mortality rates vary with egg size in the echinoid echinoderm *Dendraster excentricus* (Eschscholtz, 1831). Echinoids have been used extensively to study egg size, development time, size at metamorphosis, and other characteristics important to models of life-history evolution (e.g., Emler *et al.*, 1987; Hart, 1995; Levitan, 2000). In addition, *D. excentricus* larvae have been the focus of laboratory studies examining how vulnerability to predation varies during the course of development (Rumrill *et al.*, 1985; Pennington *et al.*, 1986), making the data presented here directly comparable to previous work.

Blastomere separations are a simple embryological tool that can be used to address questions of how changes in egg size affect development rate and larval size, shape, and mortality (Sinervo and McEdward, 1988; Bernardo, 1991; McEdward, 1996; Allen, 2005; Allen *et al.*, 2006). Using this technique, I tested the hypothesis that larvae developing from larger eggs experience lower rates of predation than larvae developing from smaller eggs. I used blastomere separations to generate two size classes of sibling larvae and then, in the laboratory, tested their susceptibility at four ages to predation by five predators common to the waters surrounding San Juan Island, Washington. Since the specific identity of predators on the larvae of marine invertebrates is largely unknown, the predators used in these experiments were chosen to represent broad categories of predator types likely to be encountered by planktonic larvae (Young and Chia, 1987). However, the individual predator species used may or may not prey on the larvae of *D. excentricus* in natural situations.

Materials and Methods

Adult collection and spawning methods

Adults of *Dendraster excentricus* were collected from a large population in East Sound, Orcas Island, Washington, and transported by boat to the Friday Harbor Laboratories (Friday Harbor, WA), where they were maintained in a flow-through seawater system at 12–15 °C. Gametes were obtained from ripe adults of *D. excentricus* by intracoelomic injection of 1 ml of 0.5 mol l⁻¹ KCl, and eggs were fertilized using standard methods described in Strathmann (1987). Unfertilized eggs were 128.0 ± 1.3 μm (mean ± SE) in diameter (*n* = 4 females; 10 eggs measured per female).

Blastomere separations

About 5 min after fertilization, zygotes were poured through a 100-μm Nitex mesh to mechanically remove the fertilization envelope (FE) before it hardened. Approximately 50% of FEs were removed by this treatment. Em-

bryos with and without the FE were washed three times in calcium-free seawater (Ca-FSW) to dissolve the hyaline layer. Treated embryos remained in Ca-FSW for about 45 min, until first cleavage was complete. After first cleavage, embryos were again poured through a 100-μm Nitex mesh. Embryos that had retained the FE after the first mesh treatment also retained the FE after the second passage through the mesh, producing whole-sized (W) embryos. Embryos that had lost the FE and had their hyaline layer dissolved in Ca-FSW were separated at the two-cell stage by the second passage through the mesh, producing half-sized (H) embryos.

After treatment, W and H embryos were placed in containers of FSW and kept at ambient seawater temperatures. After 24 h, when the treated embryos were at the swimming blastula stage, they were placed under a dissecting microscope and a mouth pipette was used to sort them by size. The two size classes (W and H) could be readily distinguished at this stage of development. W and H embryos were placed, at densities of 1 ml⁻¹, in culture containers with 1 liter of filtered seawater. Embryos were kept suspended in culture containers by using a motorized (7 rpm) stirring rack (Strathmann, 1987). Cultures were fed the unicellular alga *Dunaliella tertiolecta* at a concentration of 5 cells ml⁻¹ every other day. On feeding days, the culture containers were cleaned by filtering seawater through a beaker with a 75-μm-mesh bottom (allowing larvae to remain in the container) and then adding fresh FSW to the original volume.

Predator collection

Predation trials were run using five separate predators: (1) zoeae of *Cancer magister*, (2) megalopae of *Cancer magister*, (3) adults of *Sagitta elegans*, (4) adults of *Boltenia villosa*, and (5) postlarvae of *Ammodytes hexapterus*. All five predator types were collected near the Friday Harbor Laboratories (FHL), San Juan Island, Washington. Predators were chosen on the basis of their abundance in surface waters surrounding FHL, their diversity of feeding strategies, and previous work showing that they prey readily upon the larvae of *D. excentricus* in the laboratory (Rumrill *et al.*, 1985; Pennington *et al.*, 1986). Chaetognaths (*Sagitta elegans*) and sand lance (*Ammodytes hexapterus*) were collected at night from the FHL floating breakwater near a submerged light. Zoal and megalopal stages of the Dungeness crab, *Cancer magister*, were collected near the surface of the same location during the day and at night, using dip nets. Individuals of the solitary tunicate *Boltenia villosa* were collected from floating docks in the town of Friday Harbor, along with a small portion of the foam float to which they were attached. The piece of float allowed the tunicates to be suspended in a consistent orientation (siphons down) during trials. Before use in feeding trials, all predators were kept in FSW at ambient seawater tempera-

tures for 24 h to allow for clearance of the gut and to ensure that they were hungry.

Experimental design

Replicate predation trials were performed on separate days for each of the five predators: four replicate days for *C. magister* zoeae, five replicate days for *C. magister* megalopae, and three replicate days each for *S. elegans*, *B. villosa*, and *A. hexapterus*. For each trial, predation rates on four age classes (2-day-old, 6-day-old, 10-day-old, 14-day-old) of larval *D. excentricus* were measured. Age was used to distinguish categories of prey rather than developmental stage. Over the 14-day period measured, larval stage ranged from 2-arm plutei to 8-arm plutei, depending on egg size treatment and larval age. Comparisons of larval predation rates for equivalent ages of prey were more straightforward than comparisons of prey at equivalent developmental stages because of variation within and among treatments in developmental stage. Equivalent developmental stages of whole- and half-sized prey items do not necessarily occur on the same day, and therefore stage differences may be confounded with age differences. Each age class used on a given day was derived from a separate spawning event, using a unique male-female pair (COHORT). For each age class, 25 larvae of each size class (W and H) were added to four 1-liter glass jars filled with FSW for a final density of 50 larvae l^{-1} . One of the jars contained no predators and was used as a control to measure background loss. The remaining three jars were experimental replicates that contained predators. For each trial, only a single predator type was used, and the number of predators added per jar varied by species: seven *C. magister* zoeae or megalopae, five *S. elegans*, and one *B. villosa* or *A. hexapterus*. All 16 of the jars (4 jars \times 4 age classes) were then placed horizontally onto a rotating cylindrical plankton wheel (1.5 rpm) in a cold room at 12 °C. The plankton wheel was used to keep both predators and prey suspended during the course of the trial and was similar in design to wheels used in previous laboratory studies of planktonic predation (Rumrill *et al.*, 1985; Pennington *et al.*, 1986). For trials using *C. magister* and *A. hexapterus* as predators, jars were left on the plankton wheel for 24 h using a light/dark cycle of 12 h:12 h. Trials with *S. elegans* as the predator were also run for 24 h, but were conducted in the dark because chaetognaths feed only at night (Feigenbaum, 1991). Trials run using chaetognaths in the light resulted in mortality levels similar to those in jars with no predators. Trials using *B. villosa* as the predator were run for 3 h and only in the light owing to the high clearance rates for this predator. At the end of each trial, predators were removed, their size was measured, and the water in each jar was filtered through 75- μ m Nitex mesh to concentrate the remaining larvae into a small volume of water. This water was transferred to a Bogorov tray, and the

remaining larvae of each size class were counted under a dissecting microscope.

Predator and prey morphometrics

In chaetognaths, body size is related to the size of prey that adults are capable of consuming (Pearre, 1980). Therefore, body size in *S. elegans* and prey size in *D. excentricus* were measured and used to estimate whether the prey sizes in the current study were appropriate for consumption by chaetognaths. Body lengths of *S. elegans* were measured under a compound microscope from the tip of the head to the tip of the tail as soon as they were removed from experimental jars.

The larvae of *D. excentricus* from a single cohort were also measured using two characteristic lengths: arm length is the distance from the posterior end of the body to the tip of the post-oral arms, and body length is the distance from the posterior end of the body to the middle of the soft tissue connecting the two anterolateral arm rods. Prior to measurement, larvae were fixed in 70% EtOH.

Statistical analysis

Statistical analyses were carried out using the generalized linear mixed-effects models (glme) procedure of S-Plus ver. 7.0 (Insightful Corp.) using a binomial probability distribution and a logit link function. The dependent variable was the proportion of larvae of each size class that survived. Two independent variables were modeled as fixed effects: larval size class (SIZE) and larval age (AGE). The interaction between SIZE and AGE was also modeled as a fixed effect. Three variables were modeled as random effects: the male-female pair from which larvae were derived (COHORT), the day on which the experiment took place (DAY), and the jar in which replicate experiments were contained (JAR). For each analysis, JAR was nested within DAY, which was itself nested within COHORT. Models using all three random terms were then compared to models using all possible subsets of these terms, and the model providing the best fit to the data was determined using Akaike's information criterion (AIC) (Akaike, 1978). Models containing all three random effects best fit the data when analyzing control runs of *C. magister* zoeae and experimental runs of *C. magister* megalopae and *A. hexapterus*. Models including the random effects of DAY and JAR best fit the data when analyzing control runs of *C. magister* megalopae and experimental runs of *C. magister* zoeae. Models containing only the random effect of JAR best fit the data for control runs of *S. elegans* and *A. hexapterus* and for experimental runs of *B. villosa* and *S. elegans*. For control runs of *B. villosa*, all models containing random effects failed to converge, and therefore these runs were analyzed using only fixed effects. For all analyses when AGE was a significant factor, *post hoc* tests were carried out to compare

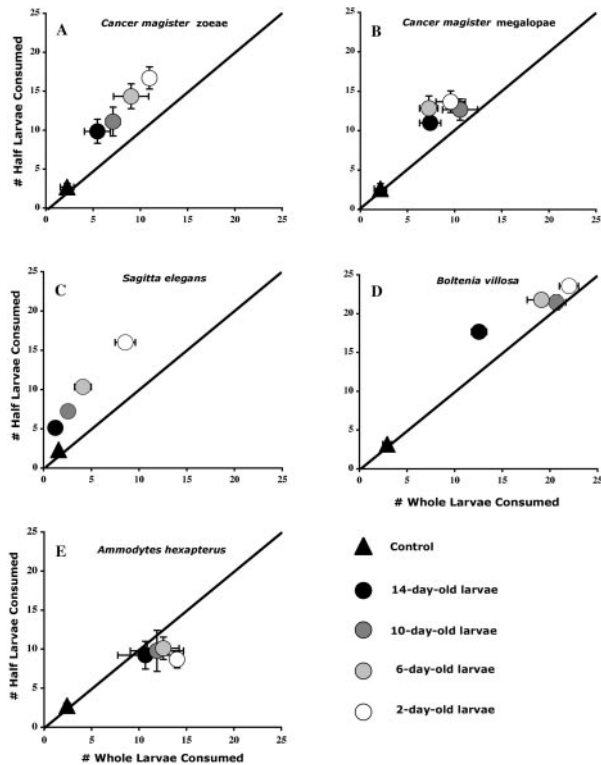


Figure 1. Mean numbers of prey (\pm standard error) consumed for all trials. *Cancer magister* zoeae (A), *C. magister* megalopae (B), *Sagitta elegans* (C), *Boltenia villosa* (D), *Ammodytes hexapterus* (E). Black triangles represent control jars with no predators present. Black circles represent 14-day-old larvae, dark gray circles 10-day-old larvae, light gray circles 6-day-old larvae, and white circles 2-day-old larvae. Diagonal lines represent a one-to-one relationship between the number of half-sized larvae and whole-sized larvae consumed. In cases where no error bars are visible, the symbol used was larger than the measured error.

age classes, using the multiple comparisons (multicomp; Bonferroni method) procedure in S-Plus.

Results

Four predators consumed significantly more half-sized larvae than whole-sized larvae (Fig. 1A–D; Table 1A–D); the remaining predator, *Ammodytes hexapterus*, consumed significantly more whole-sized larvae than half-sized larvae (Fig. 1E; Table 1E). Larval size did not have a significant effect on mortality rates in any of the control jars (Fig. 1; Table 1).

Larval age had a significant effect on mortality rates for four of the five predators tested (Fig. 1A–D; Table 1A–D). In all four cases, younger larvae were more susceptible to predators. *Post hoc* tests revealed that zoeae of *Cancer magister* consumed significantly more 2-day-old larvae than 14-day-old larvae and significantly more 6-day-old larvae than 14-day-old larvae (Bonferroni’s test, $P < 0.05$). Similarly, *C. magister* megalopae consumed significantly more 2-day-old larvae than 14-day-old larvae (Bonferroni’s test, $P < 0.05$). *Sagitta elegans* consumed greater numbers of 2-day old larvae than 6-, 10-, or 14-day-old larvae and greater numbers of 6-day-old larvae than 14-day-old larvae (Bonferroni’s test, $P < 0.05$). *Boltenia villosa* consumed greater numbers of 2-day-old larvae than 14-day-old larvae, greater numbers of 6-day-old larvae than 14-day-old larvae, and greater numbers of 10-day-old larvae than 14-day-old larvae (Bonferroni’s test, $P > 0.05$). There was no detectable effect of larval age on the mortality rates when *A. hexapterus* was used as a predator (Table 1E). Larval age

Table 1

Analysis of variance table for the proportion of larvae surviving in control and experimental jars for each of the predators used: *Cancer magister* zoeae (A), *C. magister* megalopae (B), *Sagitta elegans* (C), *Boltenia villosa* (D), *Ammodytes hexapterus* (E)

Fixed Effects	Control			Experimental		
	DF	F	P	DF	F	P
(A) SIZE	1, 15	1.687	0.214	1, 42	111.607	<0.001
AGE	3, 15	0.424	0.739	3, 42	6.505	0.001
SIZE*AGE	3, 15	0.401	0.755	3, 42	0.419	0.740
(B) SIZE	1, 14	1.947	0.185	1, 50	74.829	<0.001
AGE	3, 10	4.175	0.037	3, 46	4.563	0.007
SIZE*AGE	3, 14	1.674	0.218	3, 50	2.961	0.041
(C) SIZE	1, 7	1.739	0.229	1, 49	58.213	<0.001
AGE	3, 7	0.957	0.464	3, 49	34.555	<0.001
SIZE*AGE	3, 7	1.654	0.262	3, 49	0.236	0.871
(D) SIZE	1, 16	0.008	0.929	1, 49	14.302	<0.001
AGE	3, 16	0.084	0.968	3, 49	8.380	<0.001
SIZE*AGE	3, 16	0.053	0.984	3, 49	0.718	0.546
(E) SIZE	1, 7	0.373	0.561	1, 32	30.732	<0.001
AGE	3, 7	1.731	0.247	3, 32	0.137	0.931
SIZE*AGE	3, 7	1.774	0.239	3, 32	2.270	0.099

The combination of COHORT, DAY, and JAR that yielded the best fit to the data (based on the lowest Akaike information criterion) were included as random effects in each model. Significant effects ($P < 0.05$) are in bold.

did not have a significant effect on mortality rates in control jars except for trials with *C. magister* megalopae (Table 1B). *Post hoc* tests for control trials with *C. magister* megalopae showed that significantly more 2-day-old larvae were lost than 14-day-old larvae (Bonferroni's test, $P < 0.05$).

The interaction between SIZE and AGE was significant only for trials using *C. magister* megalopae as predators (Table 1B). There was no significant effect of this interaction in trials using any other predators or in any of the control jars (Table 1).

Predator and prey sizes

To calculate the size of prey items that chaetognaths were capable of consuming, body length was measured in all trials. The chaetognaths used in predation trials had a mean body length of 14.5 ± 0.2 mm.

To examine changes in the relative sizes of whole- and half-sized larvae over the course of development, ratios of the arm lengths and body lengths of whole-sized to half-sized larvae were calculated on several days (Fig. 2). The

ratios of both arm length and body length declined dramatically between day 2 and day 4 and then remained relatively constant between day 4 and day 15.

Discussion

Four of the five predators tested (zoeae, megalopae, chaetognaths, and tunicates) consumed greater numbers of half-sized larvae than whole-sized larvae at all four ages. The fifth predator species (the postlarval stage of the sand lance, *A. hexapterus*) showed the opposite pattern, consuming greater numbers of whole-sized larvae than half-sized larvae at all four ages. Whole-sized larvae were larger than half-sized larvae at all ages, but as larvae became older the two size classes converged. In general, the four predators that took more half-sized larvae also consumed greater numbers of younger (and therefore smaller) larvae. The sand lance, *A. hexapterus*, was again the exception, showing no significant preference for larvae on the basis of age. Overall, differences in larval age and size strongly affected the rates of predation on larvae, suggesting that both size- and age-selective predation are important processes structuring marine planktonic communities.

Predation rates on larval *Dendroaster excentricus*

Several previous experiments have used the larvae of *D. excentricus* to measure some aspect of predator-prey interactions in the field or the laboratory. Pennington *et al.* (1986) used 11 different predator species to test predation rates on the embryos and larvae of *D. excentricus*. They found four general patterns of predation: (1) crustacean species ate primarily early embryonic stages, (2) chaetognaths and amphipods ate primarily blastulae and prism larvae, (3) fish species ate plutei and unhatched embryos, and (4) ctenophore species ate few, if any, prey. These results are similar to the current study in that Pennington *et al.* (1986) found stage-dependent predation rates and that invertebrate species generally consumed higher numbers of younger and smaller stages, whereas fish species generally consumed older and larger stages. However, unlike Pennington *et al.* (1986), the current study found that both larval crustaceans and adult chaetognaths were capable of consuming large numbers of pluteus stage larvae.

Rumrill *et al.* (1985) also compared rates of predation on larval *D. excentricus* in the laboratory, using zoeae of the red crab *Cancer productus* as the predator. As in the current study and the study of Pennington *et al.* (1986), Rumrill *et al.* (1985) found stage-dependent predation rates on larval *D. excentricus*. Specifically, in that study, rates of predation were high on early (pre-pluteus) developmental stages and declined at the 4-arm pluteus stage and beyond. These results are in general agreement with the current study, which also found that larval predation rates decline with age when *Cancer* zoeae are present as predators. In addition to stage-dependent predation, Rumrill *et al.* (1985) examined

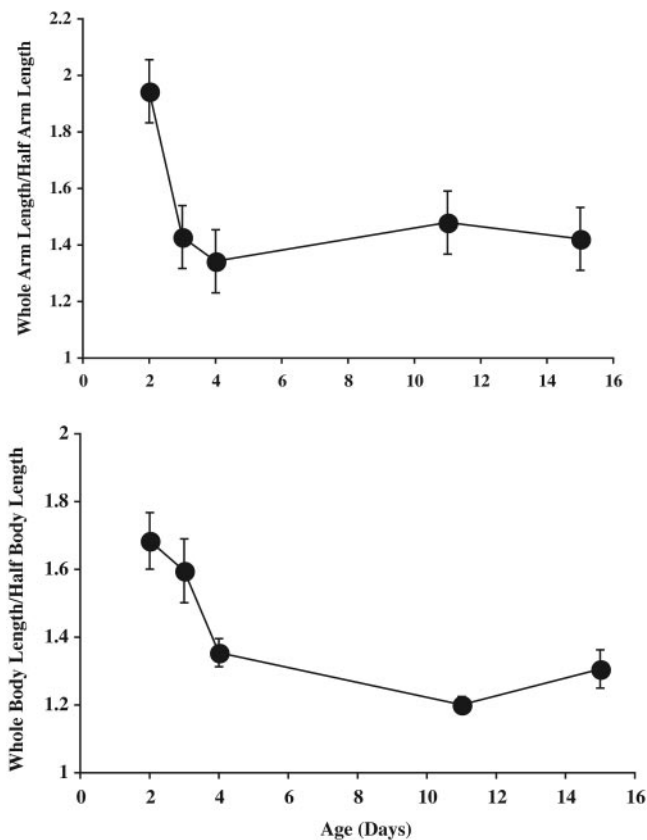


Figure 2. Ratios of the post-oral arm lengths (A) and body lengths (B) of whole-sized larvae to half-sized larvae at each age used in this study. Symbols are means \pm standard error for 10 larvae of each size at each age from a single cohort. In cases where no error bars are visible, the symbol used was larger than the error measured.

size-dependent predation by comparing loss rates of half-sized plutei to those of whole-sized plutei and found no significant difference between the two. This result stands in contrast to the current study's finding that predation rates on half-sized plutei are significantly higher than on whole-sized plutei when *Cancer* zoeae are introduced as predators.

It is unclear why Rumrill *et al.* (1985) did not find a significant difference in size-dependent predation. One possibility is that *C. productus* is not size-selective in the same way that *C. magister* is. This seems unlikely given that both species consumed greater numbers of earlier stages than later stages. Second, it is possible that the results are difficult to compare because of several differences in experimental design. Rumrill *et al.* (1985) did not present whole- and half-sized larvae to predators in the same jar, therefore eliminating any ability of the predators to choose between prey items. They instead compared overall predation rates on whole- and half-sized larvae across jars, which may have increased the variance in predation rates. Also, the number of zoeae added to the jars was 5 l^{-1} in the Rumrill study and 7 l^{-1} in the current study. Both studies used 1-liter glass jars as experimental units. The increased density of predators relative to prey in the current study may have caused a shift in predator behavior. Finally, the number of replicates used in the current study (three replicate jars per age level per day, for four ages on 4 days) represents a substantial increase in sample size over the Rumrill study, which used only three replicate jars for a single stage (4-arm plutei) on a single day. This increased sample size may have increased the likelihood of detecting differences in predation rate between size classes.

Laboratory experiments from the current study and others (Rumrill and Chia, 1984; Rumrill *et al.*, 1985; Pennington *et al.*, 1986) suggest that the larvae of *D. excentricus* are readily consumed by a variety of predators, despite some evidence that they are chemically defended (Cowden *et al.*, 1984). It is also clear that rates of predation depend on the size and stage of the larvae as well as the type of predator. However, field data on predation on *D. excentricus* larvae are unavailable. In the field, it has been shown that *D. excentricus* larvae undertake diel vertical migrations, but these movements are thought to be a response to UV radiation rather than a tactic to avoid predators (Pennington and Emler, 1986). In addition, larvae from the population used in the current study have been shown to persist for less than 2 weeks in the fjord where they originate, after which time they presumably are passively dispersed by currents to other areas (Emler, 1986). Such long-term and widespread dispersal, combined with vertical movement in the water column, makes it difficult to predict specific encounter rates with any given set of predators and therefore the intensity of predation in nature.

One recent study has, however, attempted to measure larval predation rates on *D. excentricus* larvae in a near-natural setting. Johnson and Shanks (2003) placed known

numbers of marked *D. excentricus* plutei into large corrals containing natural planktonic assemblages and a group of introduced predators. When presented at near-natural densities of larvae (0.8 l^{-1}) with background plankton present, *D. excentricus* larvae suffered no predation. Only at larval densities more than 100 times the near-natural levels were predation events on *D. excentricus* larvae recorded. These data suggest that *D. excentricus* larval mortality rates in the plankton can be extraordinarily low at natural densities, contrary to current dogma (see reviews by Young and Chia, 1987; Rumrill, 1990; Morgan, 1995).

Although the larval densities in the current study, 25 of each size class per liter (*i.e.*, a total larval density of 50 l^{-1}), are substantially higher than the near-natural densities reported by Johnson and Shanks (2003), it should be noted that the density of *D. excentricus* larvae released by the population used in the current study varies widely in space and time (Emler, 1986). The densities of early developmental stages of *D. excentricus* after spawning pulses may be significantly higher ($\sim 500 \text{ m}^{-3}$) than for late-stage larvae that have had longer to disperse ($< 1 \text{ m}^{-3}$; Emler, 1986). However, further studies are clearly needed to confirm the actual densities of both predators and prey in the field.

Evidence for size-selective predation

Size-selective predation is better understood in freshwater planktonic communities than in marine planktonic communities due to the smaller scale of freshwater communities and the lower diversity of freshwater planktonic predators (Greene, 1985). Initial studies of freshwater communities focused on the size-selective feeding behavior of planktivorous fishes that were thought to exhibit "top-down" control of the population dynamics of zooplankton communities by consuming the largest size classes (Brooks and Dodson, 1965; Galbraith, 1967; Brooks, 1968; Dodson, 1970). However, these and subsequent studies concluded that invertebrate predators also exhibited size-selective predation but in the opposite direction, consuming smaller prey in greater numbers (Dodson, 1970, 1974; Kerfoot, 1974; Fedorenko, 1975; Zaret, 1980; Wellborn, 1994). The results of the current study are consistent with the data collected from freshwater communities and suggest that invertebrate and vertebrate predators may exert opposing selective pressures on the size of planktonic prey in marine systems.

Invertebrate predators tend to consume greater numbers of smaller prey in part due to limitations in their ability to consume larger prey items. For example, chaetognaths are gape-limited predators (based on the definition of Zaret, 1980) that are size-selective (Feigenbaum, 1991). As chaetognaths grow larger, the size of the prey that they consume increases according to a known function: $H = aP^b$ (Pearre, 1980). In this equation, H is the body width of the prey, a is a coefficient ranging from 0.27 to 0.86, P is the head width of the chaetognath, and b is a coefficient ranging

from 0.32 to 0.82. The head width, P , of the chaetognath can be estimated from the body length. Using this function and the data on predator and prey sizes presented in the current study, it is possible to calculate the size range of prey items that the chaetognaths in this study could have been consuming. The mean prey size (body width) predicted to be consumed for the mean predator size in this study ranges from 220 to 260 μm . This range of prey sizes corresponds to whole-sized larvae up to 2 days old and half-sized larvae up to 4 days old. This calculation supports the hypothesis that gape limitation is the primary reason for reduced predation rates by chaetognaths on both whole- and half-sized larvae at ages greater than 2 days.

Implications for models of life-history evolution

How should planktonic mortality rates be described when modeling the success of life-history strategies? There are few reliable data on predator-prey interactions in the field, yet it seems clear that predation is a major source of larval mortality and that predation is age- and size-dependent. Most models of life-history evolution in marine invertebrates make the simplifying assumption that planktonic mortality is constant throughout development (Vance, 1973; Pechenik, 1979; Caswell, 1981; Jackson and Strathmann, 1981; Roughgarden, 1989; Havenhand, 1993; McEdward, 1997). Although some models allow mortality rate to vary with larval age (Christiansen and Fenchel, 1979; Ayal and Safriel, 1982) or size (Dekshenieks *et al.*, 1997; Levitan, 2000), few data are available to estimate how these parameters might vary in nature. Other suggestions for dealing with variation in planktonic mortality rates include substituting taxon-specific functions relating egg size, larval size, and mortality rate (Strathmann, 1985) or integrating age-specific mortality rates over several developmental periods (Rumrill, 1990). The data from the current study and others can be used to generate stage- and size-specific mortality rates for *D. excentricus* over a range of ages and for a number of possible predator types. *D. excentricus* is unusual in having this relative abundance of data regarding its life history.

Despite the large number of studies on the larval biology of *D. excentricus*, the frequency with which the larvae of this species are likely to encounter any particular type of predator during the course of their planktonic existence remains unknown. In addition, there is little or no information on the exact identity of the planktonic predators that consume the larvae of *D. excentricus* in natural settings. The current study and several others have shown the larval stages of *D. excentricus* to be palatable and readily consumed both in the laboratory (Rumrill and Chia, 1984; Rumrill *et al.*, 1985; Pennington *et al.*, 1986) and in the field (Allen and McAlister, 2007). However, there is also convincing evidence that the presence of background plankton in laboratory (Johnson and Shanks, 1997) and field (John-

son and Shanks, 2003) experiments can significantly reduce or even eliminate predation on the larval stages of marine invertebrates. Larval behavior may also change in the presence of predators, potentially reducing predation rates in natural settings even further (Metaxas and Burdett-Coutts, 2006). Observations of the suite of natural predators consuming larval *D. excentricus*, combined with future laboratory experiments on larval behavior and predator-prey interactions for these confirmed natural predators, would allow biologists interested in the evolution of life histories to estimate how larval mortality rates may influence selection on traits such as egg size, larval size, and duration of larval development.

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