PREDATION ON PLANKTONIC MARINE INVERTEBRATE LARVAE

by

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A DISSERTATION

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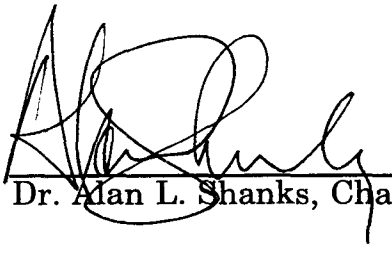

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CHAPTER I

GENERAL INTRODUCTION

Many marine and estuarine invertebrates have complex life cycles and produce planktonic larvae which reside in the water column for hours to months (Levin and Bridges, 1995). Larvae may develop from free-spawned ova or be released from adults or egg cases after a period of brooding or encapsulation. A single adult invertebrate can produce vast numbers of these planktonic propagules. For example, during a single spawning season one female sand dollar (*Dendraster excentricus*) can spawn 3.8 x 10^5 eggs (Morris et al., 1980), one female dungeness crab (*Cancer magister*) can release 2.5 x 10^6 larvae (Morris et al., 1980), a female oyster (*Crassostrea gigas*) can spawn 55.8 x 10^6 ova (Galtsoff, 1964), and the sunflower star *Pycnopodia helianthoides* may release as many as 160 x 10^6 eggs (Chia and Walker,1991). These larvae then develop in the plankton until competent for settlement and metamorphosis. The numbers of competent larvae present in local plankton correlates with recruitment to benthic communities (Connell, 1985; Gaines et al., 1985; Roughgarden et al., 1991). These studies of supply-side ecology have investigated the important relationship between planktonic larval supply and benthic community composition. Recruitment to benthic populations can be

determined by the supply of larvae available in the plankton (Roughgarden et al., 1984; Connell, 1985; Gaines et al., 1985; Roughgarden et al., 1991).

The number of new recruits to the benthic adult assemblages can be high—the barnacle *Semibalanus balanoides* was observed to settle in densities reaching 215 individuals cm^{-2} (Connell, 1985). When compared to the area's estimated propagule production, however, these newly metamorphosed juveniles are few. Some studies attempt to estimate mortality rates by contrasting propagule production with benthic recruitment (see Rumrill, 1990 for review). These studies have estimated mortality rates to be from 0.03 day^{-1} in the cone snail *Conus quercinus* (Perron, 1986) to 0.80 day^{-1} in the clam *Mya arenaria* (Ayers, 1956), but cannot distinguish between larval and early juvenile mortality. Many planktonic mortality studies suffer from the drawbacks and potential biases of anecdotal information and indirect evidence (Strathmann, 1985), limiting available reliable knowledge of the sources and importance of mortality. High mortality rates are expected, however, because invertebrate populations are generally stable over time, and mortality must occur between spawning or release and recruitment. Possible sources of planktonic mortality include fertilization failure, starvation, lethal temperatures, the absence of the proper settlement substratum, transport away from suitable settlement sites, predation on embryos and larvae, and pathogens and genetic abnormalities (Thorson, 1946, 1950, 1966; Rumrill, 1990). Only pathogens and genetic abnormalities have not been investigated.

Fertilization failure is potentially responsible for 0% (Sewell and Levitan, 1992) to 100% (Babcock et al., 1992; Brazeau and Lasker, 1992) of propagule loss. Many organisms, however, exhibit behaviors or other adaptations to help overcome potential low fertilization. Some of these include synchronous spawning, aggregated spawning, increased egg size, and spawning in shallows or pools (reviewed in Levitan, 1995). Field studies have shown that it is possible to have nearly 100% fertilization of ova released into subtidal marine systems (Sewell and Levitan, 1992). Even when fertilization is relatively low (such as 10% fertilization success observed for the sea cucumber *Holothuria coluber,* Babcock et al., 1992), a million eggs produced by a single spawning female would produce 1.0×10^5 planktonic larvae.

Successfully fertilized eggs may develop into larvae which subsequently starve in the plankton. Most invertebrate larvae are planktotrophic (= plankton-feeding) and require external nutrients to complete metamorphosis. The role of starvation as a source of mortality has been investigated for many invertebrate larvae (see reviews by Olson and Olson, 1989; Boidron-Métairon, 1995). An additional factor that may be important in assessing the threat of starvation is the ability of many larvae to uptake dissolved organic matter (Pavillon, 1976; De Burgh and Burke, 1983; Lucas et al., 1986; Jaeckle and Manahan, 1988, 1989). Substantial fractions of nutrients needed for metabolism and development can be obtained by DOM uptake (Manahan and Wright, 1991; Manahan, 1983) and offset nutritional stress when particulate food is unavailable (Boidron-

Métairon, 1995). Nutritional resources in the field, whether dissolved or particulate, are usually sufficient to prevent starvation (Olson, 1985, Olson, 1987; Strathmann, 1987; Gallager, 1988; Boidron-Métairon, 1995).

Many larvae are sensitive or intolerant of extremes or fluctuations in temperature (Pechenik, 1987). Sensitivity and intolerance may take the form of changes in behavioral or physiological activity, changes in developmental rates, or actual mortality (Pechenik, 1987). In general, lower temperatures depress developmental rates (Bayne, 1965; Scheltema, 1967; Lima and Pechenik, 1985; Harms, 1984), but extreme increases in temperature can also slow growth (Scheltema, 1967; Kingston, 1974; Leighton, 1974). The effects of changes in temperature have not been widely studied, but some evidence suggests that depressed developmental rates at lower temperatures may not fully recover when larvae experience an increase in temperature (Beaumont and Budd, 1982). Little evidence of direct mortality from natural temperature extremes or fluctuations is available. Temperature's influence on larval mortality, whether by direct or indirect means, is potentially important and continues to receive attention from investigators.

Offshore transport can potentially displace entire populations of planktonic larvae and remove them from the proximity of suitable coastal settlement sites. Evidence of transport-dependent recruitment includes pulses of barnacle settlement that are correlated with the migration of an upwelling front onto the shore (Farrell et al., 1991; Roughgarden et al., 1991) and the occurrence of shoreward-propagating internal waves (Shanks

and Wright, 1987). When larvae are transported away from suitable settlement sites, mortality results from finite planktonic life-spans or other agents of mortality (temperature, starvation, or predation) which may affect larvae to different extents as their duration in the plankton is prolonged. Many larvae can delay metamorphosis for weeks or months in the absence of a suitable place to settle. In one extreme laboratory study, veligers of the snail *Fusitriton oregonensis* remained planktonic larvae for 4 years in the absence of the proper settlement cue (M. Strathmann, pers. communication). Assuming that the potential time for larval persistence in the plankton is finite, transport away from a proper site may force metamorphosis and settlement at a site where the juvenile cannot survive or the resulting adult cannot effectively reproduce (Jackson and Strathmann, 1981). If agents other than transport itself are responsible for mortality, then a prolonged planktonic period due to the unavailability of sites will result in mortality by other means. This is an active area of research and promises to reveal much about larval ecology, the importance of larval supply, and the potential influence of physical oceanography on the biology of marine invertebrates (Jackson and Strathmann, 1981).

Planktonic invertebrate larvae can be consumed either by benthic suspension-feeders or planktonic predators. Planktonic embryos and larvae may encounter benthic suspension-feeding predators shortly after release, incidentally during their planktonic life, or as they attempt to settle and test the benthos for a suitable substratum. Benthic predators may form a "wall of mouths" (Emery, 1973) and can make the acquisition of a

settlement site a hazardous undertaking. Organisms associated with coral reefs may consume as much as 60% of passing zooplankton, which included the larvae of crustaceans, polychaetes, cnidarians, molluscs, and echinoderms (Glynn, 1973). Suspension-feeding barnacles also inhibited recruitment of colonial ascidians and bryozoans in field experiments conducted by Young and Gotelli (1988). The anthozoans *Alcyonium siderium* and *Metridium senile* captured and consumed planktonic invertebrate larvae (Sebens and Koehl, 1984). Not all suspension-feeders, however, consume invertebrate larvae. For instance, Bingham and Walters (1989) found that settling larvae escaped predation by suspension-feeding ascidians and Rumrill (1987) calculated the risk of predation, by 2 species of benthic suspension-feeders consuming *Asterina miniata* brachiolaria larvae, to be 1.2% per saltation event (i.e., settlement or re-suspension). Additional evidence of low predation by ascidians includes their lack of effect on larval recruitment in a study by Young (1989). Mortality of settling larvae by benthic suspension-feeders is clearly variable, but much more investigation is necessary to determine the overall risk of predation presented by benthic suspension-feeders.

Planktonic predators of invertebrate larvae have been studied in the laboratory, in the field through correlation of high predator abundance and larval decline, and by gut content analysis of field-caught predators. Laboratory experiments have investigated the following factors and their effect on larval predation rates: antipredator defenses (Pennington and Chia, 1984; Morgan 1987, 1989), developmental stage and post-contact

behavioral responses (Rumrill et al., 1985; Pennington et al., 1986), larval size (Pennington and Chia, 1984; Rumrill et al., 1985; Rumrill, 1987), container size (Toonen and Chia, 1993), prey density (Rumrill et al., 1985; Pennington et al., 1986; Johnson and Shanks, 1997, Johnson and Brink, 1998), and background plankton presence (Johnson and Shanks, 1997; Johnson and Brink, 1998). In a review on larval mortality, however, Rumrill points out a caution with regard to laboratory experiments on predation:

> An important limitation is that the majority of laboratory experiments have been conducted in small containers at prey densities that are 2 to 3 orders of magnitude greater than natural densities of larvae in the plankton. Direct extrapolation of mortality rates from laboratory studies is unwarranted because rates of predation in the laboratory are strongly dependent upon the size of the experimental container. (Rumrill, 1990, p. 173)

In order for laboratory experiments to provide information that is directly applicable to estimates of natural mortality, much more information must first be collected about specific natural predator-prey relationships with confirmation that the containers employed do not create artifacts.

Predation on planktonic larvae can be studied in the field by identifying pelagic predators whose abundance is inversely correlated with that of larvae. One example of this is the predatory ctenophore *Mnemiopsis leidyi*, whose abundance has been negatively correlated with larval abundance and recruitment of crustaceans and fish (Nelson, 1925; Burrell and Van Engel, 1976; Cowan et al., 1994). This method requires, however, the fortuitous monitoring of key predators and the need to assume that

larval decline in the plankton is due, in whole or part, to predation by these predators.

Another method of monitoring predation on planktonic invertebrate larvae is by gut content analysis of potential predators. Indeed, predators have been identified based upon their gut contents. Examples of invertebrate larval predators identified in this manner include the ctenophore *Mnemiopsis leidyi* (Nelson, 1925; Burrell and Van Engel, 1976), the hydromedusa *Phialidium* sp. (McCormick, 1969), decapod larvae (Lebour, 1922), and salmon fry (Bailey et al., 1975). Unfortunately, some of these predators may have consumed larvae in cod-end plankton buckets and predation may be an artifact of collection. For example, chaetognaths are known to feed unnaturally or at increased rates on plankton in collection reservoirs (Feigenbaum and Maris, 1984).

Because predation in the plankton may be determined by opportunity, or encounters between predators and prey (see laboratory evidence of density-dependent predation— Rumrill et al., 1985; Pennington et al., 1986; Johnson and Shanks, 1997, Johnson and Brink, 1998), many predators may feed unnaturally when concentrated with potential prey in plankton samples. Even if it is assumed, however, that the presence of larvae in predator guts is not an artifact of collection, predator gut analysis has not been an effective method for evaluating the impact of predation on larval populations. When gut content studies have identified predators, the focus has often been on the composition of the predator's diet. Invertebrate larvae are a minor part of predator diets. However, the relative importance of

predation has not yet been determined for an individual larva throughout the duration of larval life. Since data on the concurrent density of planktonic prey is rarely offered, little can be said about the importance of particular predators in the ecology of larval invertebrates. For example, Bailey et al. (1975) observed that salmon fry had preyed upon decapod larvae. Only 9% of salmon fry guts sampled, however, contained decapod larvae. Decapods only represented 1% of the diet by volume. Decapod larvae are not likely to be an important component of young salmon diets and nothing is known of the potential impact on decapod populations by salmon predators. Some hydromedusae of *Phialidium* sp. consume invertebrate larvae, but less than 10% of predators sampled contained larvae and, in those, larvae comprised less than 3% of identified prey (McCormick, 1969). As with decapod larvae and salmon fry, these larvae are not likely to be an important component of *Phialidium* sp. diets and nothing is known of the potential impact on larval populations by this predator. Because this data focuses on predator diets rather than larval risk, important questions still remain. How important is planktonic predation over a larva's planktonic life? What is the daily risk of predation for an individual larva from *all* potential predators?

It is possible to evaluate predation risk using gut contents in combination with known digestion rates and field densities of predators and prey. This has been done to evaluate predation on adult copepods by larval fish (Purcell, 1990) and on copepods, fish eggs, and fish larvae by coelenterates (Purcell et al., 1994; Chandy and Greene, 1995). These results

cannot be extrapolated to predation on invertebrate larvae because these predators may preferentially consume copepods, larval fish, or eggs, and digestion times vary with prey type and size (Purcell, 1982; Chandy and Greene, 1995). According to Purcell (1982), this combination approach to evaluating *in situ* predation requires accuracy in measurements of digestion times for particular prey, identification of digested prey, converting size to dry weight and carbon, and determining predator and prey densities from plankton tows. We would add that predator digestion times for particular food types can vary tremendously depending on the total amount of food in the gut. For instance, trochophore larvae of the scaleworm *Arctonöe vittata* will pass bivalve veligers within 3 to 4 hours when several veligers have been consumed and more are available. A lone veliger in the gut of *A. vittata*, however, may remain in the gut for as long as a day (K. Johnson, pers. obs.). In spite of the potentially inaccurate assumptions, estimates using gut contents, digestion times, and densities may more accurately estimate field mortality than estimates based upon laboratory predation studies (Purcell, 1982). Laboratory studies of predation are potentially fraught with behavioral artifacts (Reeve 1977, 1980), but it is unknown whether indirect field studies or laboratory experiments provide the best estimate of field mortality.

This doctoral dissertation investigates planktonic predation on invertebrate larvae both in the laboratory and the field . Laboratory experiments examine the hypotheses that 1) changes in prey density can influence the proportion of prey consumed and 2) natural background

plankton (i.e., the natural suite of diverse plankton in whole, unfiltered seawater) reduces or eliminates predation. The bulk of laboratory experiments are described in chapters II and III. In chapter II, three species were examined in the laboratory as predators on echinoid and cirriped embryos or larvae. In chapter III, five larval polychaete species representing 4 families were investigated as predators on bivalve larvae. In both studies a general pattern emerged: predation was dramatically reduced when prey were presented at natural prey densities and with background plankton.

Chapter IV investigates the importance of predator encounter radius and prey swimming speed in a planktonic predator-prey encounter model. Encounter estimates of a simple predator with its prey are compared to actual observations of predation. The predators and prey selected to examine the model are the trochophore larvae of the scaleworm *Arctonöe vittata* and the veliger larvae of the oyster *Crassostrea gigas*.

Chapter V details field studies and related laboratory investigations of predation on invertebrate larvae. Most field studies were designed to simply observe predation, expose predator identities, and determine predation rates under near-natural conditions. These observational field studies test the hypothesis that populations of invertebrate larvae suffer significant predation in near-natural plankton assemblages. To examine factors affecting predation rates, additional field and laboratory studies test the hypotheses that 1) proportion of predation on a larval population changes with prey density and 2) natural background plankton reduces

predation rates. Field experiments used natural assemblages, including a diverse suite of potential predators, enabling me to directly determine the predation risk for experimental larval populations. Corrals were inoculated with marked and enumerated invertebrate larvae at the start of 24 h experiments. By marking prey, we could know initial prey densities, retrieve larvae after the experiment, determine the number of survivors, and identify the natural predators. Observations of predation are direct and can be related directly to the potential impact of predation on experimental populations of invertebrate larvae. Corral assemblages also included wild (i.e., randomly caught and unmarked) invertebrate larvae at natural densities. We were able to examine predation risk for captured wild larvae using predator gut content analyses, known wild prey densities, and a planktonic predator-prey encounter model. Finally, corrals were also used to manipulate prey density and "background plankton" presence, examining their effect on predation rates.

Three of the ensuing chapters (II, III, and V) have co-authors. I am the primary author of all chapters. The second author of chapters II and V is Alan L. Shanks, my doctoral advisor. The second author of chapter III is Laura A. Brink, a fellow graduate student at the Oregon Institute of Marine Biology. In chapter V I shared equal responsibility for the development of methods with my co-author. Research, data analysis, and writing for chapter V were primarily my responsibility. In my other co-authored chapters, I was the principal investigator in all aspects of the study.

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CHAPTER II

THE IMPORTANCE OF PREY DENSITIES AND BACKGROUND PLANKTON IN STUDIES OF PREDATION ON INVERTEBRATE LARVAE

In accordance with the regulations and approval of the University of Oregon Graduate School, this chapter is a reproduction of previously published and co-authored material: *Marine Ecology Progress Series* Vol. 158: 293-296, Kevin B. Johnson and Alan L. Shanks, co-authors.

Abstract

Laboratory experiments investigating predation by plankton on meroplanktonic invertebrate larvae often use unnaturally high densities of prey in filtered seawater. Offering prey under these conditions, however, can alter predator behavior and capture success, potentially creating artifactual predator-prey relationships and predation rates. We conducted laboratory experiments investigating the effect of a range of larval invertebrate densities on predation rates. For the four predator-prey combinations examined, there was no predation at natural prey densities in filtered seawater. We then conducted predator-prey experiments in the presence and absence of naturally occurring ambient plankton ("background plankton") at densities where predation had been observed in

filtered seawater. In most experiments, background plankton dramatically decreased or eliminated predation which had been observed with unnaturally high prey densities in filtered seawater.

Introduction

Laboratory experiments investigating predation upon meroplanktonic invertebrate larvae are often conducted using unnaturally high densities of meroplanktonic prey in filtered seawater. Unnaturally high prey densities can alter predator behavior, capture success, and food preference. These density effects have been observed in other predator-prey systems (e.g., Holling 1959, Krebs et al. 1977). To the best of our knowledge, however, this is the first study directly examining the influence of prey densities on predation of invertebrate larvae by planktonic predators.

Using filtered seawater for laboratory predation experiments, like using unnaturally high prey densities, may also induce unnatural predation. Planktonic predators may be generalists, feeding upon all potential prey, including the naturally occurring ambient plankton ("background plankton"). Background plankton, including protists and phytoplankton, are far more abundant than relatively rare meroplanktonic invertebrate larvae. By occupying or satiating the predator, or obscuring larvae from detection, background plankton may reduce larval predation. Alternatively, predators may specialize in feeding on prey other than the type being offered. In either case, predators consuming prey in filtered seawater may not do so in the presence of background plankton.

We conducted predation experiments, observing predation rates, in filtered seawater over a range of prey densities, including near-natural and unnaturally high densities. Using prey densities where predation was observed in filtered seawater, we then conducted predation experiments with and without background plankton.

Methods

Three predators (the zoea of the mud shrimp *Upogebia pugettensis*, the leptomedusa *Obelia* sp., and an unidentified leptomedusa) and three prey types (blastulae and plutei of the purple sea urchin *Strongylocentrotus purpuratus*, and barnacle nauplii) were used to create four predator-prey combinations. Some zoeae and hydromedusae are known to be predatory (e.g., Rumrill 1987), but no information is available on the natural prey of our selected predatory species. *S. purpuratus* were spawned and maintained using standard techniques (Strathmann 1987). Blastulae were approximately 120 mm long and plutei were 4-arm stage and approximately 200 mm in length. Barnacle nauplii (body length 200 to 250 mm) and all predators were collected at high tide from near the mouth of Coos Bay, Oregon (43°21'10" N, 124°19'50" W) by slowly towing a plankton net equipped with a large blind cod-end (after Reeve 1981). Experiments began within 24 hours of predator collection and were conducted on a roller table (Omori & Ikeda 1984, Larson & Shanks 1996), which rolled 3-liter cylindrical tanks at 1 rpm and prevented plankton from settling. Though enclosed, plankton do not suffer oxygen depletion during the experimental time frame (Larson & Shanks 1996). The roller table was maintained at 12

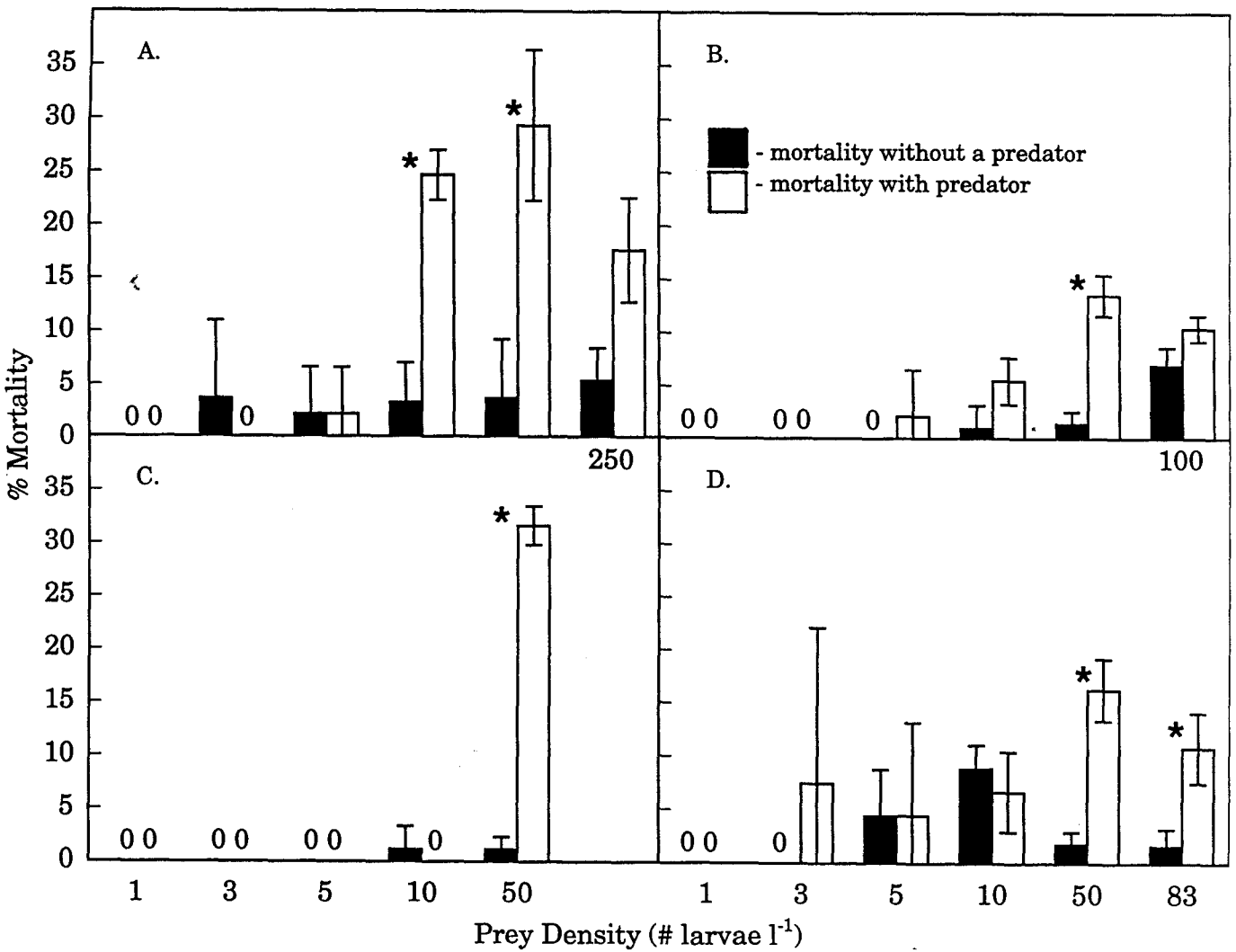
°C in a constant temperature room with a 14:10 Light:Dark cycle for 24 hours. Observations of predators and prey in roller tanks revealed them to stay suspended in the water column and exhibit apparently normal behavior. At the end of each experiment, predators and remaining prey were collected, fixed, and counts of surviving larvae made using a compound microscope. "Mortality" is based upon the lack of retrieval of whole, unconsumed larvae and the difference in mortality between treatments with and without predators is attributed to predation.

When treatments are stated to be different, we refer to $\alpha = 0.05$ with the Games & Howell (G&H) mean significant difference method of *a posteriori* pairwise comparison of means (Sokal & Rohlf 1995), performed after a significant Kruskal-Wallis ANOVA (K-W ANOVA). The G&H method of comparing means is appropriate for heterogeneous variances and small sample sizes.

Prey Density Experiments

Experiments investigating the effect of variation in prey density on predation were conducted in 1 mm-filtered seawater with four different predator-prey combinations: mud shrimp zoea preying upon plutei, mud shrimp zoea preying upon blastulae, unidentified leptomedusa preying upon barnacle nauplii, and *Obelia* sp. medusa preying upon blastulae. Predator density was 1 tank^{-1}. Three replicate treatments (predators present) and controls (predators absent) were run for each prey density.

FIGURE 1. Predator-induced mortality as a function of prey density. A. Mud shrimp zoea preying upon purple urchin plutei. B. Mud shrimp zoea preying upon purple urchin blastulae. C. Unidentified leptomedusa preying upon barnacle nauplii. D. *Obelia* sp. medusa preying upon purple urchin blastulae. Columns with zero mean and variance are indicated by a "0". Error bars represent the 95% confidence interval. Predator treatments that are significantly different from their predator-less controls at α=.05 are marked with a star.

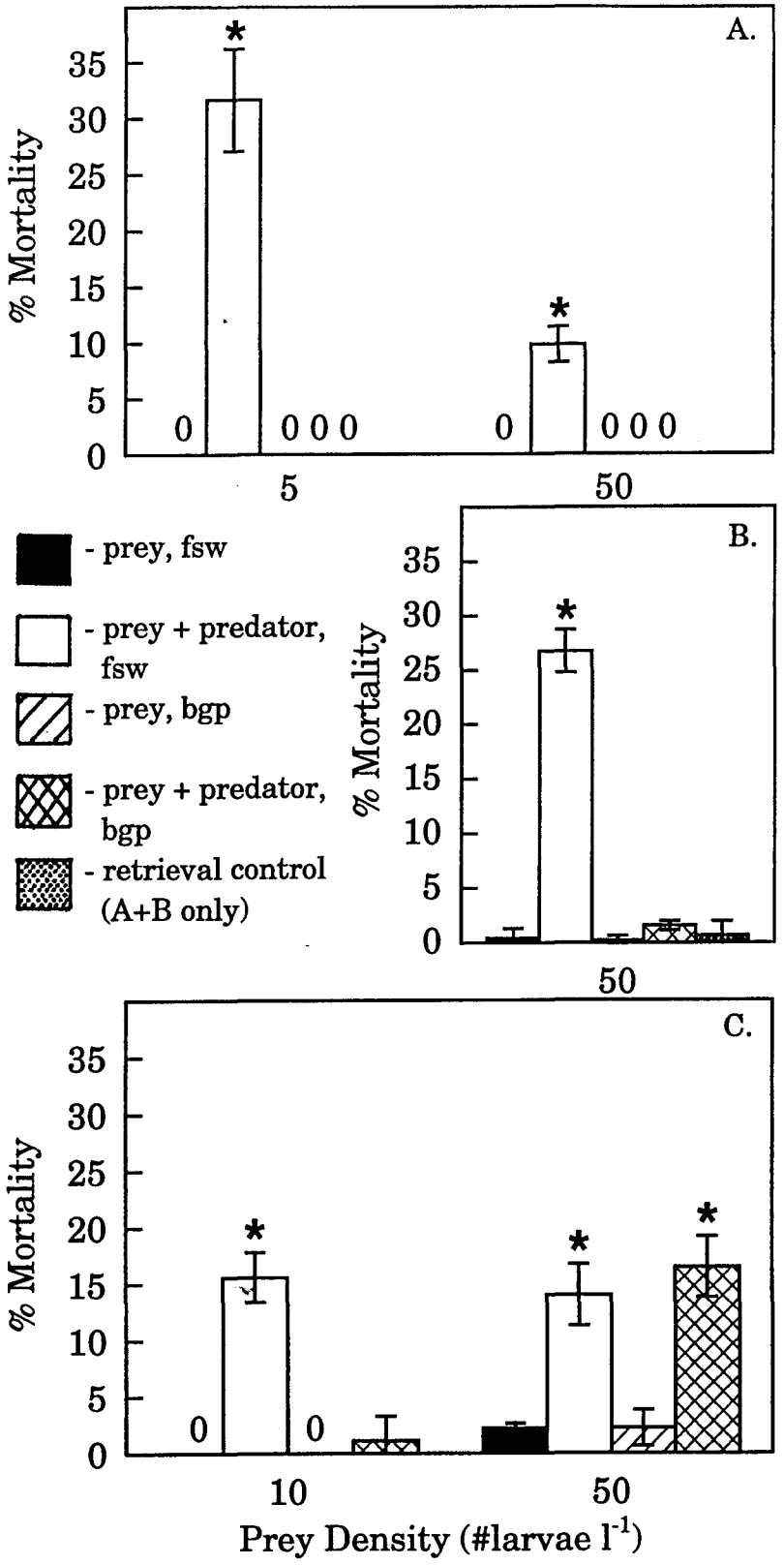

A.
B.
C.
D.
- mortality without a predator
- mortality with predator
% Mortality
0 5 10 15 20 25 30 35
0 0
0
0 0
0 0
0
0 0
0 0
0 0
0
0 0
0
250
100
1 3 5 10 50
1 3 5 10 50 83
Prey Density (# larvae l-1)

Prey densities (Figure 1) ranged from near-natural to unnaturally high densities. Published observations of larval urchin field densities (and, by extrapolation, conservative urchin blastula densities) range from 0.08 to 0.39 l^{-1} (Zimmerman 1972, Cameron & Rumrill 1982, Emlet 1986, Rumrill 1987, Rumrill et al. 1985) and the highest reported density is only 0.74 l^{-1} (Miller 1995). Natural urchin densities are represented in our experiments as a density of 1 l^{-1}. By contrast, densities of echinopluteus larvae used in past laboratory predation experiments has often ranged from 25 to 500 l^{-1} (e.g., Rumrill et al. 1985, Pennington et al. 1986). Natural densities for barnacle nauplii may be as high as 15 l^{-1} (Zimmerman 1972). Natural nauplius densities are represented in our experiments as densities of 1, 3, 5, and 10 l^{-1}. Our high density of 50 l^{-1} exceeds published observations and is intended to be unnaturally high. At the end of each experiment, predators and remaining prey were collected and fixed. Counts of surviving larvae were made using a compound microscope.

Background Plankton Experiments

Predation experiments with and without background plankton were conducted with three of the same predator-prey combinations used in the previous experiments. Experiments were run at prey densities where predation was observed in the above-described prey density experiments (Figure 2). Experiments with the *Obelia* sp. medusa preying upon blastulae and the unidentified leptomedusa preying upon barnacle nauplii consisted of 5

FIGURE 2. For three predator-prey combinations, percent prey mortality at densities selected based upon observed predation in prey density experiments (see Figure 1): A. *Obelia* sp. preying upon blastulae B. Unidentified leptomedusa preying upon barnacle nauplii C. Mud shrimp zoea preying upon plutei. In A and B, the five columns for each prey density are (left to right): 1. prey in filtered seawater (fsw) 2. prey and predator in fsw 3. prey and background plankton (bgp) 4. prey and predator with bgp 5. prey and bgp fixed immediately (retrieval control). The four data columns for each prey density in C represent treatments 1-4 above. Columns with zero mean and variance are indicated by a "0". Error bars represent the 95% confidence interval. Treatments that are significantly different from their respective control at α=.05 are marked with a star.


A.
% Mortality
35
30
25
20
15
10
5
0
*
*
0
0 0 0
0
0 0 0
5
50
- prey, fsw
- prey + predator, fsw
- prey, bgp
- prey + predator, bgp
- retrieval control (A+B only)
B.
% Mortality
35
30
25
20
15
10
5
0
*
50
C.
% Mortality
35
30
25
20
15
10
5
0
*
*
*
0
0
10
50
Prey Density (#larvae l-1)

treatments, three replicates each, at each selected prey density. The five treatments were prey alone in filtered seawater, prey with a predator in filtered seawater, prey alone with background plankton, prey with a predator and background plankton, and larvae and background plankton fixed at the onset of the experiment (a control for retrieval artifacts in the presence of background plankton). The protocol for the experiment with the mud shrimp zoea preying upon plutei was the same as those described above, but lacked the background plankton control. Background plankton were obtained by collecting whole seawater (unfiltered seawater with a natural composition and density of plankton) from near the mouth of Coos Bay at high tide.

Results

Prey Density Experiments

For all predator-prey combinations the percent predation varied with prey density. For the zoea preying upon plutei and blastulae, predation was significant only at prey densities of 10 and 50 l^{-1} (Figure 1A) and 50 l^{-1} (Figure 1B), respectively. With the unidentified leptomedusa as a predator on barnacle nauplii (Figure 1C), significant predation was only observed at a prey density of 50 l^{-1}. Significant predation was observed at prey densities of 50 and 83 l^{-1} with *Obelia* sp. as the predator on blastulae (Figure 1D).

Background Plankton Experiments

When *Obelia* sp. was a predator upon blastulae (Figure 2A), mean mortalities of 31% and 10% were observed in filtered seawater at prey densities of 5 and 50 l^{-1}, respectively. When background plankton was present, however, mortality was completely eliminated at both of these prey densities. The primary components of background plankton in this experiment included four diatom species and the dinoflagellate *Noctiluca scintillans*. Background invertebrate larvae found in relatively low numbers included polychaete metatrochophores (Spionidae) and copepod nauplii. When background plankton and larvae were fixed immediately, the exact number of added blastulae were retrieved in all replicates, suggesting there were no wild blastulae in the background plankton medium. Only one prey density, 50 l^{-1}, was examined for the unknown leptomedusa preying upon barnacle nauplii (Figure 2B). At this prey density, the mean mortality of 27% in filtered seawater was completely eliminated by the addition of background plankton. The primary components of background plankton in this experiment included two diatom species (different from species in the first background plankton experiment) and a variety of moderately abundant dinoflagellates. Pine pollen was also common in this background plankton. The number of barnacle nauplii retrieved when background and larvae were fixed immediately was exactly the number added in two of the replicates. In the third replicate, 98% of added barnacle larvae were recovered. As with blastulae, this suggests that there were no wild barnacle larvae in the size range of those used as prey. For the mud shrimp zoea preying on plutei

(Figure 2C) at a prey density of 10 l^{-1}, the presence of background plankton significantly reduced predation from an average of 16% to 1%. At a prey density of 50 l^{-1}, however, the average predation in filtered seawater was 14% vs. 17% in the presence of background plankton. Background plankton consisted of relatively abundant loricated ciliates, dinoflagellates of the genus *Protoperidinium*, and a wide variety of diatoms. This experiment lacked the treatment where background plankton and larvae were fixed immediately to control for artifacts. Retrieval of larvae with background plankton in the absence of a predator, however, was exactly 100% at 10 l^{-1} and slightly less than 100% at 50 l^{-1}. Once again, this suggests that wild plutei were not added to the experiment by the use of background plankton. In all but this last predator-prey combination, background plankton reduced or eliminated predation.

Discussion

For all predator-prey combinations examined, predator-induced mortality tended to increase with prey density. Predation at natural prey densities was often nonexistent. The fact that predation tended to occur only at unnaturally high densities may be due to altered predator behavior, increased capture success at high densities, or may simply be the result of more frequent encounters with prey. Only in the latter case can predation rates at unnaturally high densities be extrapolated to the lower natural densities. Altered predator behaviors resulting from high densities of prey, such as prey switching and selectivity, and increased capture success (i.e., practice makes perfect) may be artifactually induced when unnaturally

high prey densities are used. The mechanism underlying prey density's effect on predation rates has not been identified for these predator-prey combinations. Natural prey densities should be used to prevent behavioral artifacts from misleading investigators about the existence or strength of predator-prey relationships.

In all but one case, even when prey densities were unnaturally high, background plankton reduced or eliminated predation which had been observed in filtered seawater. Background plankton may serve as alternate food, occupying or satiating generalist predators. Background plankton may also obscure larvae from detection or hinder their capture. Whatever the mechanism, background plankton reduced the likelihood of these predators consuming meroplanktonic invertebrate larvae and embryos. Background plankton, a pervasive component of natural planktonic systems, should be present in laboratory investigations of planktonic predation.

Much of the information on predators of marine invertebrate larvae comes from laboratory experiments which have utilized unnaturally high prey densities and excluded background plankton. These experiments have contributed to the idea that predation in the plankton may be a major cause of larval mortality (Rumrill 1990, Morgan 1995). In this study we included natural prey densities and background plankton in an attempt to make our laboratory experiments more natural. We found that, under more natural conditions, predation was eliminated or greatly reduced. Perhaps previous laboratory experiments have given us a false impression of predation rates in the plankton.

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Bridge

Chapter II describes laboratory experiments which manipulate prey densities and background plankton to study predation on barnacle nauplii echinoid embryos and larvae. Predators examined in chapter II include an anomuran zoea and two hydromedusae. Chapter III describes laboratory experiments which are similar in respect to hypotheses, parameters manipulated, and general method to those presented in chapter II. In chapter III, however, polychaete larvae were examined as predators of bivalve larvae. A long history of anecdotal references in the literature to predation on bivalve veligers by polychaete larvae adds depth and interest to this study. The results of experiments in chapter III agree with those in chapter II—predation is reduced or eliminated when prey are presented at natural densities with background plankton present.

CHAPTER III

PREDATION ON BIVALVE VELIGERS BY POLYCHAETE LARVAE

In accordance with the regulations and approval of the University of Oregon Graduate School, this chapter is a reproduction of previously published and co-authored material: *Biological Bulletin* Vol. 194: in press, Kevin B. Johnson and Laura A. Brink, co-authors.

Abstract

Polychaete larvae from several families are thought to be natural predators upon planktonic bivalve larvae. However, little direct evidence of interactions between these predators and prey is available. We conducted predator-prey experiments on laboratory roller tables for five putative predatory polychaete larvae, representing four families (metatroch-less larvae of the Polynoidae and metatrochophore larvae of the Spionidae, the Magelonidae, and the Phyllodocidae). D-hinge veliger larvae of the oyster *Crassostrea gigas* were offered as prey. Predation was monitored over a range of prey densities and in the presence and absence of background plankton. "Background plankton" are any naturally occurring plankton assemblages found in whole, unfiltered seawater at ambient concentrations. For all polychaete larvae examined, when natural *C. gigas* densities *and* background plankton were used, no predation was observed.

Magelonids and phyllodocids did not consume any *C. gigas* larvae, regardless of conditions. Polynoid and spionid trochophores consumed *C. gigas* veligers at both the "natural" and unnaturally high prey densities in filtered seawater. The addition of background plankton eliminated the predation at all natural prey densities and significantly reduced the predation observed at high prey densities.

Introduction

Predation in the plankton is a source of mortality which may control the presence and abundance of the planktonic larvae of benthic marine invertebrates (Thorson, 1950). Observations of predation upon meroplanktonic invertebrate larvae are recorded from as far back as the 1920s. For example, Lebour (1922) noted bivalve veliger larvae in the guts of the larval polychaete *Magelona papillicornis* (Magelonidae). Other biologists have also observed bivalve veligers within the guts of field-caught *Magelona* sp. larvae (Thorson, 1946; Smidt, 1951; Kühl, 1974; Wilson, 1982). Lebour (1922), Smidt (1951), and Kühl (1974) recorded only bivalve larvae as prey for magelonids, but Thorson (1946) and Wilson (1982) observed that *M. papillicornis* also consumed other planktonic organisms. In spite of these many observations and the general impression that larval polychaetes of the genus *Magelona* are specialist predators of bivalve veligers (e.g., Todd et al., 1996), a natural predator-prey relationship between larval polychaetes and bivalve larvae has yet to be definitively shown. There are problems also with the anecdotal nature of some past observations on wild-caught

plankton: when planktonic predators and prey are concentrated in the cod-end of a plankton net for several minutes or more, as is usually the case when plankton samples are being collected, it is not possible to differentiate natural predation from that occurring in the cod-end under very abnormal conditions, which we refer to as "artifactual predation".

Predation upon bivalve veligers by polychaete trochophores (metatroch-less trochophores and metatrochophores) has also been observed for representatives of other polychaete families, including the Polynoidae (Yokouchi, 1991), the Nephtyidae (Mileikovski, 1959; Yokouchi, 1991), the Phyllodocidae (Yokouchi, 1991), and the Spionidae (Daro and Polk, 1973; K.B. Johnson, unpubl. data). These observations of predation are remarkable in two ways. First, it is very seldom that a larva has been observed to be the primary food consumed by a planktonic suspension-feeding predator that consumes its prey one individual at a time. Unlike cases in which predators (e.g., some scyphozoans and clupeid fish) indiscriminately feed on many planktonic prey, consistent observations of a given prey item in the gut of such a "single-particle predator" may indicate a strongly specific predator-prey relationship and provide insight into predator behavior. Second, bivalve veligers consumed by polychaete larvae are often surprisingly large relative to the predator's body diameter and apparent mouth size (see Fig. 1).

Examining the mechanism underlying particle ingestion by polychaete larvae, Phillips and Pernet (1996) fed larvae of the polychaetes *Serpula vermicularis* (Serpulidae) and *Arctonöe vittata* (Polynoidae)

polystyrene beads and plankton at a range of sizes. *S. vermicularis* larvae were apparently not equipped to handle food particles greater than 12 μm in diameter (Phillips and Pernet, 1996). *A. vittata* larvae less than 100 μm in diameter were observed to ingest large particles (polystyrene beads and phytoplankton) up to 60 μm in diameter, a common size for small bivalve larvae. The larvae of *A. vittata,* a scaleworm, likely include relatively large particles in their natural diet. Does this diet include larval bivalves? Bivalve veligers have been observed in the guts of field-caught polynoid larvae (Yokouchi, 1991). Like the larvae of *Magelona* sp., the larvae of polynoids and several other polychaete families may be natural predators upon bivalve veligers.

We examined the potential predator-prey relationship between several larval polychaetes and bivalve veliger larvae. The relationship was examined using a combination of field observations (plankton samples) and laboratory experiments. In plankton samples, trochophores representing several families were observed with bivalve veligers in their guts. More important for this study, however, field samples helped determine densities used in laboratory experiments. Densities of predators and prey reflected field densities from samples where predation was observed. Laboratory experiments used five types of larval polychaetes as predators: *A. vittata* (metatroch-less trochophore, Polynoidae), *Magelona* sp. (metatrochophore, Magelonidae), and unidentified species from the families Polynoidae (metatroch-less trochophore), Spionidae (metatrochophore) and Phyllodocidae (metatrochophore). D-hinge veliger larvae of the oyster

Crassostrea gigas were offered as prey. Experiments were conducted at two prey densities and in the presence or absence of background plankton. The presence of background plankton [by which we mean naturally occurring phyto- and zooplankton ever-present in the field but often excluded in laboratory experiments] is potentially important because it may act as a substitute food for predators or obscure prey from detection (Johnson and Shanks, 1997).

Materials and Methods

Field Observations

During August 1994, plankton samples were collected from within 10 km of the shore of Duck, North Carolina. Using a 100-μm-mesh plankton net and an on-board electric centrifugal pump, samples were collected for 3 minutes at 227.1 l minute^{-1}, for a final sample volume of approximately 680 liters. Between 3 and 5 sampling depths were chosen at each station, depending upon the station depth. After pumping was complete, samples were rinsed from the cod-ends and preserved with 10% $CaCO_3$-buffered formalin for later sorting. Plankton samples were sorted under a dissection microscope with polarized light to aid in locating bivalves. For a more detailed description of collection and sorting methods, see Brink (1997).

Bivalve veligers were tallied when observed in the guts of predatory polychaete larvae. The total density of bivalve larvae and polychaete larvae

was determined for each sample in which bivalve predation was observed. These densities were considered when deciding upon predator and prey densities to be used in the laboratory experiments described below.

Culture of Predators and Prey

Adult specimens of the scaleworm *Arctonöe vittata*, commensal with the keyhole limpet *Diodora aspera*, were collected with their host from the west shore rocky intertidal of San Juan Island, Washington. Individuals of *A. vittata* were spawned and larvae were cultured using the methods described by Phillips and Pernet (1996) with the addition of *Coscinodiscus radiatus* (CCMP 310) as a food source. Fertilized eggs were cultured in 600-ml beakers at densities of ~500 l^{-1}. Larvae approximately 21 days old were used as predators in experiments.

All other larval polychaetes used as predators were collected at high tide near the mouth of Coos Bay, Oregon, by slowly towing a 150-µm-mesh plankton net equipped with a large, blind cod-end (Reeve, 1981). Pipettes (3-mm-bore) were used to immediately remove predators from the plankton sample and isolate them in 250 ml of filtered seawater. Experiments began within 6 hours of predator collection.

D-hinge veligers of the oyster *Crassostrea gigas*, 5 to 10 days old (greatest linear dimension 70-90 µm), were used as prey in all laboratory experiments. The oyster larvae were obtained from Whiskey Creek Oyster Farms, Tillamook, Oregon, and maintained in 1-gallon jars on a diet of *Isochrysis galbana* and *Rhodomonas* sp.

Roller Table Experiments

One laboratory experiment, with four treatments, was conducted for each of the five species of larval polychaete (Table I). Two densities of prey were used. The first prey density (treatments A and B) was designed to approximate natural field concentrations and was set at 33 bivalve larvae l^{-1} on the basis of the highest value we found in the literature (Carriker, 1951). The second prey density (treatments C and D) was chosen to represent an unnaturally high concentration (1000 l^{-1}) and thus increase the likelihood that the prey would be encountered and ingested by predators. Each prey density was presented to predators in either filtered seawater (treatments A and C) or with background plankton (treatments B and D). Background plankton was collected by filling buckets with whole, unfiltered seawater at the high tide immediately preceding the start of an experiment. To fill background treatment tanks, the seawater in buckets was stirred gently, suspending settled plankton, and then poured into tanks.

For each experiment, all treatments and replicates were conducted simultaneously. Cylindrical 3-liter tanks (19 cm dia. x 10.5 cm ht.) were placed on a roller table (Omori and Ikeda, 1984; Larson and Shanks, 1996) maintained at 12 ∞C in a constant temperature room with a 14:10 light:dark cycle. The slow (1 rpm) rotation of the tanks kept the plankton from settling, and the experiments were of short duration (24 h) to prevent oxygen depletion (Larson and Shanks, 1996). At the close of the experiments, the water in the roller table tanks was filtered through a

partially submerged 20-μm-mesh Nitex filter, and each tank was rinsed twice to ensure that all polychaete larvae were retrieved. Within 2.5 minutes of filtration, polychaetes were located and isolated in filtered seawater. Consumed bivalve larvae, visible through the polychaete larva's transparent body, were then counted.

The experiment using *Arctonöe vittata* larvae as predators was conducted at Friday Harbor Laboratories (Friday Harbor, Washington). A predator density of 2 l^{-1} (6 $tank^{-1}$) was chosen based upon the upper range of polychaete trochophore densities from our field samples in which predation upon bivalve larvae had been observed. Each tank was replicated three times. Thus, a total of 18 polychaete larvae were used as predators for each treatment.

All other experiments were conducted at the Oregon Institute of Marine Biology (Coos Bay, Oregon). The four species of larval polychaetes used as predators were *Magelona* sp. (metatrochophores) and three unidentified species representing the families Polynoidae (metatroch-less trochophores), Spionidae (metatrochophores), and Phyllodocidae (metatrochophores). The unidentified genera will be referred to as polynoid A, spionid A, and phyllodocid A, respectively. All predator densities in Coos Bay experiments were 1 l^{-1} (3 $tank^{-1}$) and, for each experiment, tanks were replicated four times.

Results

Field Observations

Of 150 samples, 18 had at least one polychaete larva that had preyed upon a bivalve veliger. A total of 30 bivalves were observed in the guts of 25 polychaete larvae (20 trochophores and 5 metatrochophores). The number of bivalves consumed by each of the 20 metatroch-less trochophores was variable: 1 trochophore larva had 3 bivalves, 2 trochophore larvae had 2 bivalves each, and 17 trochophore larvae had 1 bivalve each. Trochophores were typically large (mean body length = 237 μm, sd = 35 μm) and robust in form (for examples of body shape, see illustrations of polynoids, phyllodocids, or nephtyids in Bhaud and Cazaux, 1987). Detailed identification of these metatroch-less trochophores was often not possible, but the following families may have been represented: Phyllodocidae, Hesionidae, early Nephtyidae, Polynoidae, and Chrysopetalidae. Of those metatrochophores which had bivalves, 3 were *Magelona* sp. with 1 bivalve each. The last 2 metatrochophores were likely either phyllodocids or hesionids; one (380 μm in length) had 2 bivalves in its gut, while the other (368 μm in length) had 1 bivalve. In addition, a single metatroch-less polychaete larva was observed with a gastropod veliger in its gut.

For the 18 samples in which bivalves were observed in polychaete larva guts, densities ranged from 42 to 1193 polychaete larvae sample^{-1} ($\bar{x}$ = 277.2, sd = 324.3). The range of larval bivalve densities in these same

samples was from 419 to 1949 larvae sample^{-1} ($\bar{x}$ = 1217.6, sd = 494.2). Therefore, at least 42 trochophores and 419 bivalve larvae were concentrated together in the cod-end bucket (approximately 200 ml of seawater) when a sample was complete.

Roller Table Experiments

Table 1 summarizes the results of the roller table experiments. For the larvae of *Magelona* sp. and phyllodocid A, predation on bivalve veligers was not observed in the laboratory under any conditions. The larvae of *Arctonöe vittata*, polynoid A, and spionid A, however, did consume *Crassostrea gigas* veligers (Fig. 1). These three polychaetes exhibited low levels of predation when veliger larvae were presented at near-natural densities and in filtered seawater (Table 1, Treatment A). When background plankton was used with this same near-natural prey density, predation was always absent (Table 1, Treatment B). Predation was most frequent when densities of *C. gigas* were high in filtered seawater (Table 1, Treatment C). Notably, the polynoid larvae, *A. vittata* and polynoid A, consumed the greatest numbers of veligers in Treatment C. The most extreme was polynoid A, averaging 6.17 bivalve veligers gut^{-1} with two of the individuals consuming 8 veligers each. Presenting prey at high densities in the presence of background plankton (Table 1, Treatment D) reduced, but did not eliminate, the predation observed at the same densities in Treatment C.

FIGURE 1. Veliger predation. (A) D-hinge veliger of the oyster *Crassostrea gigas*. (B) Trochophore larva of the polynoid *Arctonöe vittata* with a veliger of the oyster *C. gigas* in its gut. (C) Metatrochophore larva of spionid A with a *C. gigas* veliger in its gut. (D) Trochophore larva of polynoid A. with two *C. gigas* veligers in its gut. A, C, and D are viewed with cross-polarized light. Scale bar = 100 μm.

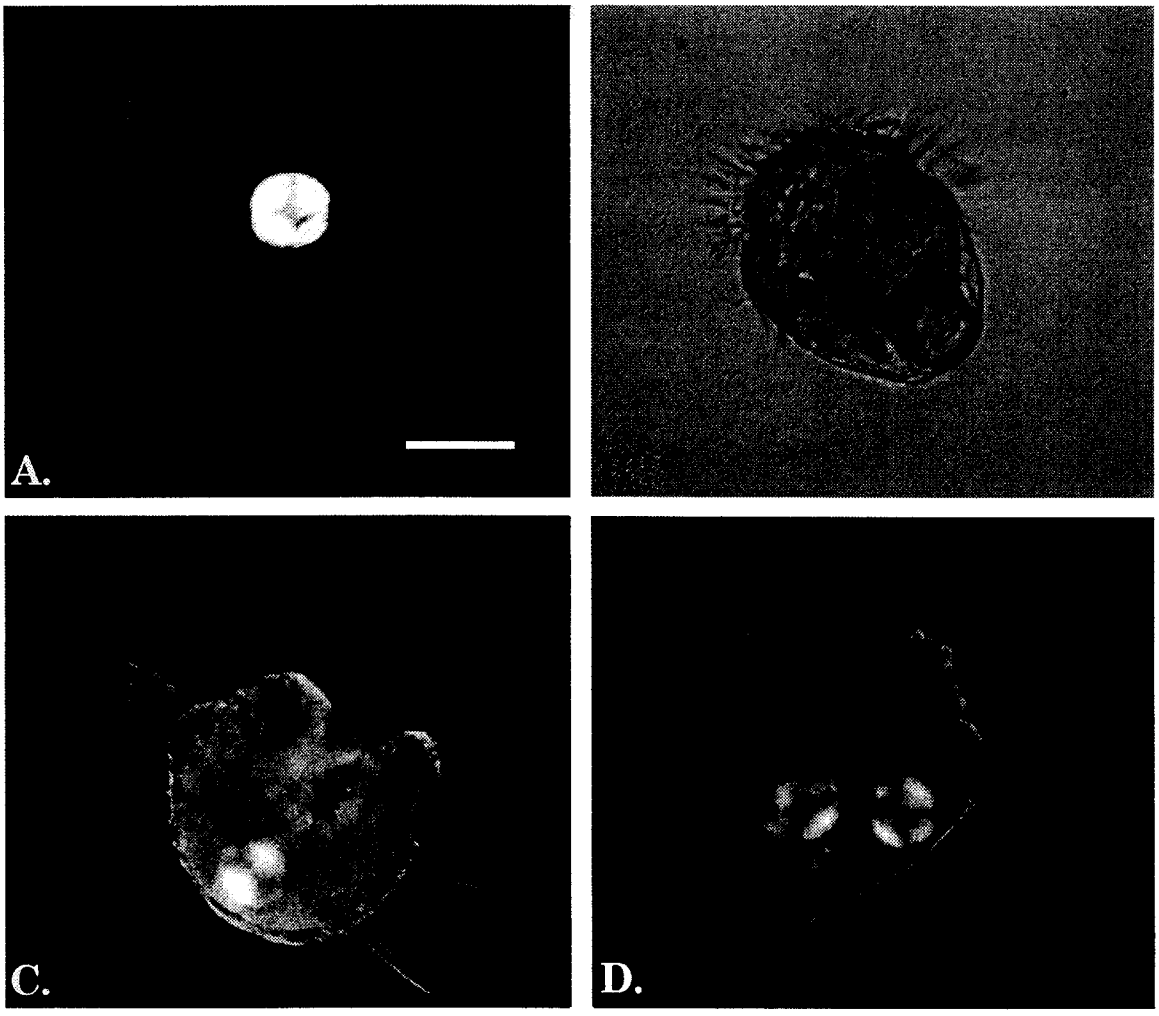
A.
C.
D.

TABLE 1. Mean number of *Crassostrea gigas* veliger larvae in individual guts of predatory larval polychaetes according to treatment (prey density and the presence or absence of background plankton) ± the 95% CI.

	Treatment			
	Near natural prey density (33 prey l^{-1})		High prey density (1000 prey l^{-1})	
Larval polychaete (length)	Filtered seawater A	Background plankton B	Filtered seawater C	Background plankton D
Magelona sp. (2-3 mm)	0	0	0	0
Phyllodocid A (300-360 µm)	0	0	0	0
A. vittata (260-290 µm)	1.05 ± 0.37	0	4.17 ± 0.64	0.72 ± 0.38
Polynoid A (280-310 µm)	0.83 ± 0.41	0	6.17 ± 0.79	1.33 ± 0.44
Spionid A (400-500 µm)	0.08 ± 0.16	0	1.33 ± 0.37	0.50 ± 0.38

Polynoid trochophores, which consumed numerous veligers in Treatment C, voided their gut contents through a large posterior rupture. This rupture quickly heals and the unburdened trochophore suffers no obvious permanent damage. Veliger valves sometimes remain attached at the hinge after passage through the gut. Intact veligers which passed through the guts of larval polychaetes were isolated in filtered seawater, but no consumed veligers revived. Thus, while trochophore digestion can be incomplete, predation does appear to result in mortality for bivalve larvae.

Discussion

None of the larval polychaete species we tested consumed any bivalve larvae when laboratory conditions were the closest to natural (i.e., near-natural prey density with background plankton present; Table 1, Treatment B). We did observe predation in the treatments which used unnatural prey density or filtered seawater. One explanation for the lack of predation in Treatment B could be that larval polychaetes are not natural predators of bivalve veliger larvae. In that case, previously published observations of bivalve veligers in the guts of larval polychaetes might be an artifact of the concentration of predators and prey in cod-end buckets during plankton tows. Such artificial conditions can alter the behavior of predators and prey and increase the probability of encounters between them, resulting in unnatural ingestion. Cod-end predation is well documented for other planktonic predators, such as chaetognaths (Feigenbaum and Maris, 1984), and may mislead observers about predator-prey relationships.

Low encounter rates might also explain the absence of predation under the most natural laboratory conditions used in this study. Predators and prey may simply not encounter one another during the experiment. Natural prey densities, which tend to be relatively low, and the presence of background plankton can both decrease the number of encounters between predators and prey (Johnson and Shanks, 1997). For example, lack of encounters may explain the low predation by *Arctonöe vittata* on *Crassostrea gigas* under the most natural conditions (Table 1, Treatment

B). This explanation is supported by comparisons between observed predation by *A. vittata* and encounter model estimates (K.B. Johnson, unpubl. data): the estimates produced by two models (Gerritsen and Strickler, 1977, and a simple clearance rate model) were statistically indistinguishable from the minimum known encounters of *A. vittata* with *C. gigas* (i.e., observed predation events). This bolsters the argument that larval polychaetes naturally prey upon bivalve veligers during relatively infrequent encounters. Indeed, the many published observations of predation (e.g., Thorson, 1946; Smidt, 1951; Kühl, 1974; Wilson, 1982) may reflect relatively rare field encounters rather than artifactual cod-end predation. Predator-prey encounters in these previously published studies can, however, be difficult to estimate. Field densities, swimming speeds, and encounter radiuses, essential components of encounter rate models, are often unknown. Finally, the hypothesis that these polychaetes may, upon infrequent encounters, be natural predators of bivalve larvae is also supported by an observation of a spionid larva with one *C. gigas* veliger in its gut (K.B. Johnson, unpubl. data). This metatrochophore larva was fixed only seconds after being collected in a 120-liter sample of seawater. No plankton net was towed; the water was collected in a plastic bag, then immediately concentrated and fixed. This method allowed little time for artifactual predation.

The true frequency of encounters between predators and prey in the field may, however, be far greater than estimated by models or from laboratory experiments if natural densities are greater than those recorded

by investigators. The effect of plankton patchiness on sampling accuracy has received some attention (Hamner and Carleton, 1979; Omori and Hamner, 1982) and could cause underestimation of field densities. Plankton can be highly concentrated in a localized area—for example, through behavior-related aggregation (e.g., Alldredge and Hamner, 1980; Ueda et al., 1983) or the accumulation of plankton in a front (Stommel, 1949; Bray, 1953; George and Edwards, 1973). A net, towed through such a patch and then towed through a sparsely populated region, would collect a sample with an apparent density lower than the actual density within the front or aggregation. Furthermore, bivalve veligers are known to associate with marine snow (Green and Dagg, 1997; Shanks and Walters, 1997), creating localized high larval densities. Larval polychaetes can also be strongly associated with marine snow (Shanks and del Carmen, 1997) and, as a result, may encounter potential prey items such as bivalve veligers more frequently. Published observations of predation upon bivalve veligers by larval polychaetes may thus reflect natural predation in concentrated patches of predators and prey.

In spite of the fact that we never observed predation on bivalve veligers by *Magelona* larvae in laboratory experiments, published observations of this predator-prey relationship are numerous and should not be summarily dismissed. Wilson (1982) mentions that three species of *Magelona* are known to be carnivorous in later stages and includes descriptions of late stage metatrochophore larvae > 4 mm in length. The *Magelona* metatrochophore larvae used in our experiments were 2-3 mm

long. At a later stage, with larger palps and mouths, these larvae may be more effective at capturing bivalve larvae. It should be noted, however, that a larva of *Magelona papillicornis*, lacking long palps and only 1 mm in length, is depicted by Todd et al. (1996) with a bivalve veliger in its gut. Experiments analogous to ours should be conducted with later stage *Magelona* larvae to clarify the relationship of this predator with potential bivalve prey.

Summary

Certain larval polychaetes may be significant natural predators upon bivalve veligers. This investigation, however, provides laboratory evidence that natural predation on bivalve larvae by polychaete larvae is absent or uncommon, possibly because the predators and prey have few encounters in the field (assuming that published larval bivalve densities accurately reflect natural densities).

Published reports of bivalve veligers in the guts of larval polychaetes suggest a natural predator-prey relationship and are seemingly incongruous with our results. One possible explanation is that polychaete larvae consumed the veligers while in the cod-end of a plankton net, making the predation an artifact of the collection method.

When polychaete larvae consumed bivalve veligers in our laboratory experiments, the use of near-natural prey densities with natural background plankton completely eliminated predation. This lack of predation may be due to a reduction in the number of encounters with prey

(published data indicates that natural densities of bivalve larvae are relatively low) or to the role of background plankton as a substitute food for predators or a screen to obscure prey from detection. In short, our results suggest that a natural predator-prey relationship between polychaete larvae and bivalve veligers may not exist . If a relationship does exist, then the frequency of interaction and its ecological importance may be less than expected based upon published observations.

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Bridge

Chapter III details laboratory experiments with polychaete larvae as predators on bivalve veligers. One of these polychaete larvae, the trochophore of the scaleworm *Arctonöe vittata*, is especially adept at capturing large particles, such as veligers, and has an elaborate tuft of cilia near the mouth which may aid in engulfing large prey. Upon further scrutiny, I found this predator-prey combination ideal for testing various aspects of a widely-used planktonic encounter model.

One important parameter in the encounter model is the encounter radius of the predator, or the distance at which the predator perceives prey. Many planktonic predators detect prey by sight, vibration, or smell. Their encounter radius can be difficult for investigators and modellers to determine. The trochophore of *A. vittata* is a contact predator. It hunts for prey by swimming randomly, at least on a local scale, until it bumps into prey with its anterior episphere. The encounter radius of such a contact predator can be confidently measured as the body radius of the animal. Other helpful attributes of this predator include continuous foraging, relatively constant swimming speed, and a transparent gut for counting prey.

In chapter IV, experiments were conducted with the trochophore of *A. vittata* preying on bivalve veligers. The results of these experiments (i.e., numbers of bivalves consumed) were then compared to predictions based upon encounter estimates. These comparisons allowed examination of the

importance of predator encounter radius and prey swimming speed in calculating encounter predictions.

CHAPTER IV

THE IMPORTANCE OF ENCOUNTER RADIUS AND PREY SWIMMING SPEED IN PLANKTONIC ENCOUNTER MODELS

Abstract

A simple predator-prey system is used to examine the importance of encounter radius and prey swimming speed in a planktonic encounter model. The trochophore of the scaleworm *Arctonoe vittata* is used as a model predator. Comparisons were made between encounter model estimates and actual predation observed in laboratory experiments. *A. vittata* was selected because of its perpetual foraging strategy, quick prey handling time, unambiguous encounter radius, and transparent gut. Encounter models are sensitive to encounter radiuses and I investigate the effects of encounter radius mis-measurements on the accuracy of estimates. Prey swimming speed is often markedly slower than that of cruising predators and I investigate the importance of considering slow prey swimming speed in encounter estimations. Observations of trochophore feeding at sub-saturation food levels are consistent with encounter estimates of two models: one which considers prey swimming speed and another model which neglects it. When the predator swimming speed is approximately one order of magnitude greater than the swimming speed of the prey, the prey's swimming speed can be neglected without

significantly affecting estimates. Because of their simple foraging strategy, planktonic polychaete larvae are a good predator system for testing encounter models. When all parameters are carefully determined, the planktonic encounter model can accurately estimate predator-prey encounter rates.

Introduction

Planktonic encounter models are used to examine predator-prey relationships in a system which is relatively inaccessible to direct observation and experimental manipulation—the microscopic planktonic community. Models can lend ecological meaning to observed predation (i.e., gut contents) and may be used to estimate encounters between planktonic predators and their prey. The first encounter model designed explicitly for planktonic systems was that of Gerritsen and Strickler (1977). Their 3-dimensional model, heretofore referred to as the 'GS model', has had considerable influence on studies of plankton feeding (e.g., Giguere et al., 1982; Bailey and Battey, 1983; Evans, 1989; Rumrill, 1990; Luo et al., 1996). The GS model uses encounter radius R, prey density N_h, and predator and prey swimming speeds, v and u, respectively, to determine the number of encounters Z_p of a single predator with its prey for $v \geq u$:

$$Z_p = \frac{\pi R^2 N_h}{3} \left(\frac{u^2 + 3v^2}{v}\right)$$

Encounter radius can be difficult to measure because predators may employ remote (e.g., visual, chemosensory, mechanical) hunting methods. It is often difficult to measure the radius of a predator's sphere of perception. For example, chaetognaths and some copepods hunt by detecting the distant movements of prey with mechanoreceptors (Horridge and Boulton, 1967; Feigenbaum and Reeve, 1977; Bailey and Yen, 1983; Yen, 1987; Yen and Nicoll, 1990; De Mott and Watson, 1991). Observations of chaetognath feeding may overlook subtle predator responses to remotely-sensed prey. Likewise, visual predators (e.g., Giguere and Northcote, 1987; Giske et al., 1994) may perceive prey at greater distances than determined by observation. Difficulty in determining encounter radius prompts an examination of the sensitivity of the GS model's encounter estimates to variation in the encounter radius.

As a cruising planktonic predator forages, the probability of encountering prey increases if prey are also moving. The GS model incorporates prey speed in estimating encounter rates. A simple alternative model applicable to this model predator, however, can use clearance rate to predict encounters. The clearance concept is analogous to that presented by Rosenthal and Hempel (1970), but assumes a full circumference of predator radius. This clearance rate model is in many respects similar to the GS encounter rate model, but treats prey as passive particles, ignoring their swimming speed. In the 'CR' (=clearance rate) model, total encounters E_p of a predator with prey are estimated using prey

density N_h and the total volume V of water processed (cleared) by the predator.

$$E_p = N_h V$$

For a cruising tactile encounter predator such as the trochophore of *Arctonöe vittata*, the volume of water processed V is the volume of a cylindrical corridor searched by a predator of body radius r, over a time period t, swimming at speed v:

$$V = \pi r^2 v t$$

Encounter predictions of these two models differ primarily in their treatment of prey swimming speed. By comparing encounter predictions of the GS vs. the CR model with actual predator encounters in a controlled system, the importance of prey swimming speed in estimating encounters can be determined.

In this study, I investigate the importance and utility of two encounter model parameters: encounter radius and prey swimming speed. I first investigate the GS model's sensitivity to encounter radius. Using the GS and CR models, I then investigate the importance of prey swimming speed. Comparison of models with actual encounters requires a simple predator-prey system which satisfies basic model assumptions.

There are several factors to consider when selecting a predator to test encounter models. The predator used in encounter model comparisons should be a true "cruising" predator. The handling time of encountered

particles, prey and non-prey alike, should be negligible. The predator should have an unambiguous encounter radius. It is also helpful if the predators have transparent guts for convenient prey counting. Many potential planktonic predators do not constantly cruise, but vary their speed and even pause. These predators may be saltatory predators (O'Brien et al., 1990), alternating periods of quiescence and movement as they forage. If predator swimming speed is observed over a sufficiently long time, then average overall speed might be used in calculations. Encounter estimates for predators that swim at variable speeds may need to consider the velocity distribution of the predator's varying swimming speeds (Evans, 1989). For simplicity in investigating encounter models, it is best to employ a true cruising predator swimming at a relatively constant speed. Cruising predators may pause in foraging as they encounter both prey and non-prey items (Hansen et al., 1991). For this reason, minimal prey handling time is preferable for meeting the model assumptions. Many predators forage using remote sensory perception such as visual, chemosensory, or mechanical perception. The GS model can be most confidently applied when the encounter radius is unambiguous and directly measurable (e.g., encounter radius = body radius). Finally, many potential predators are relatively small (200-μm to 5-mm) and difficult to dissect. Transparent guts enable scoring of prey items by simple observation. When a predator has these attributes, predation experiments can reveal the strengths and reliability of encounter models.

I used a simple predator with the attributes outlined above to investigate the role of encounter radius and prey speed in planktonic encounter models. The trochophore larva of the marine scaleworm *Arctonoe vittata* was used as a predator upon veliger larvae of the oyster *Crassostrea gigas*. The trochophore of *A. vittata* feeds on suspended prey,

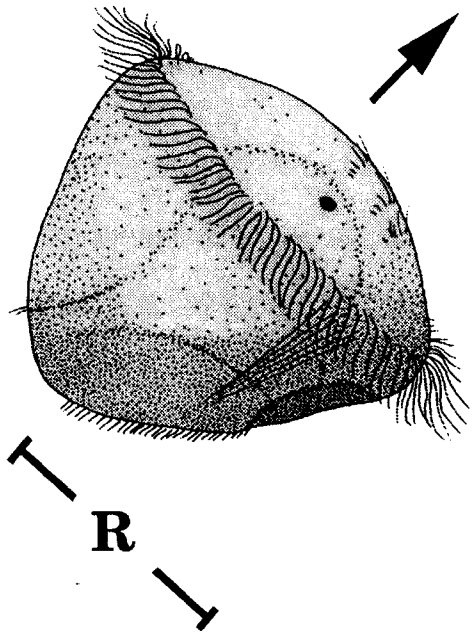

FIGURE 1. Body radius of suspension-feeding trochophore larva of *A. vittata*, synonymous with encounter radius *R*. Arrow indicates swimming direction. (After Phillips and Pernet, 1996).

such as diatoms and bivalve larvae, while constantly swimming. Prey handling time is negligible and a trochophore can likely capture 2 prey items encountered only seconds apart. Trochophore foraging behavior indicates that the animal's encounter radius is equivalent to its body radius: foraging trochophores narrowly missing food particles do not alter

course or behavior. Suspended food particles are apparently not perceived unless they actually bump into the larva's anterior episphere. Encountered (physically contacted) food is promptly captured and ingested. The encounter radius of *A. vittata* trochophores is determined by body radius (Figure 1) and can be measured directly. Lastly, the trochophores of *A. vittata* are transparent and ingested prey can be observed and counted.

Methods

Approximate 21 day-old larvae of the scale worm *Arctonoe vittata* (diameter 294 mm, SD 51 mm) were used as predators and d-hinge veligers of the oyster *Crassostrea gigas*, 5 to 10 days old, were used as prey. Adult specimens of the scaleworm *Arctonoe vittata*, commensal with the keyhole limpet *Diodora aspera*, were collected with their host from the rocky intertidal zone on the west side of San Juan Island, Washington, USA. Female *A. vittata* were spawned, eggs fertilized, and larvae cultured using the methods described by Phillips & Pernet (1996) with the addition of *Coscinodiscus radiatus* (CCMP 310) as a food source. Fertilized eggs were cultured in 600-ml beakers at densities of ~ 500 l^{-1}. Oyster veligers, obtained from Whiskey Creek Oyster Farms (Tillamook, OR), were maintained in 1-gallon jars on a diet of *Isochrysis galbana* and *Rhodomonas* sp.

The 24 hour experiment consisted of three treatments: low, medium, and high prey densities in filtered seawater. Each treatment was replicated four times. One cylindrical 3-liter tank was used for each replicate. The prey densities for the low (L), medium (M), and high (H)

treatments were 3, 33, and 1000 bivalve larvae l^{-1}, respectively. *A. vittata* densities were 2 l^{-1} (6 tank $^{-1}$), a density similar to that in the field when trochophores were observed preying upon bivalve larvae (Johnson and Brink, 1998). To prevent plankton from settling, all treatments and replicates were conducted simultaneously on a roller table (Omori & Ikeda, 1984; Larson & Shanks, 1996) rolling at 1 rpm. The roller table was maintained at 12 °C in a constant temperature room at Friday Harbor Laboratories (Friday Harbor, Washington). Experiments were run with a 14:10 light:dark cycle. Plankton do not suffer oxygen depletion during the experimental time frame (Larson & Shanks, 1996). At the close of the experiment, tank contents were concentrated in a partially submerged 20-µm mesh nitex filter. Trochophores were quickly located and removed to filtered seawater. Consumed bivalve veligers were then counted through the transparent gut of each trochophore.

The number of prey ingested by each predator were then used to examine the sensitivity of the GS model to encounter radius and the importance of prey swimming speed. For the examination of encounter radius, the number of prey ingested was compared to that predicted by the GS model using an encounter radiuses of 210 µm (*A. vittata*'s body radius and actual encounter radius), 420 µm, and 1000 µm. For the investigation of prey swimming speed, prediction curves were generated based on different relative magnitudes of predator and prey swimming speeds. Predator swimming speed used in calculations was 2.56 mm s^{-1} (SD = 0.53, Pernet, unpublished). Prey swimming speed used was 0.30 mm s^{-1},

consistent with observed swimming speeds of *C. gigas* d-hinge veligers (pers. obs.) and published horizontal swimming speeds of d-hinge *Crassostrea virginica* (Hidu and Haskin, 1978). Theoretical curves generated by the model were then compared to the actual data to determine the importance of prey swimming speed in estimating encounter rates.

Results

Encounter Radius Sensitivity

Figure 2 superimposes the mean number of prey gut^{-1} on three encounter probability curves predicted by the GS model, each calculated using different encounter radiuses: 210 μm (*A. vittata's* mean body radius and actual encounter radius), 420 μm, and 1000 μm. Assuming a capture occurs with each encounter, the number of veligers consumed by individual trochophores is consistent with the predictions of the GS model in the Low and Medium prey density treatments. In the High prey density treatment, however, the number of veligers consumed is less than predicted by the models. This is probably a result of predator saturation at high prey densities (see Discussion).

Prey Swimming Speed

The predicted curves from the GS and CR models are plotted in Figure 3. The curves overlap completely, giving the appearance of a single curve. Figure 3 also superimposes predation data on the prediction curves.

Assuming a capture occurs with each encounter, then the number of encounters by the trochophores at the Low and Medium prey densities is

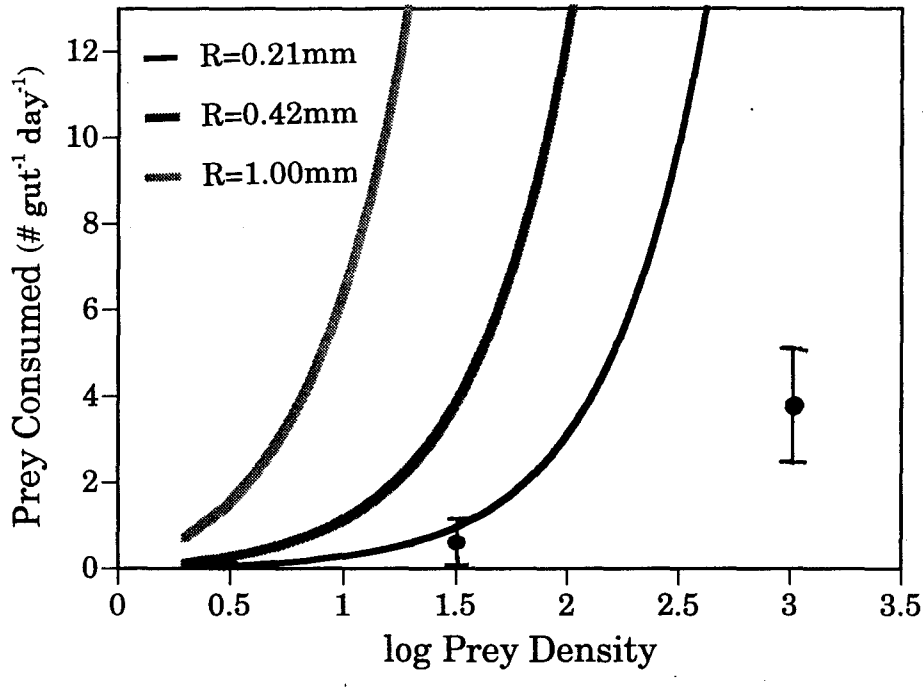

FIGURE 2. The number of captured prey in *Arctonöe vittata* trochophores vs. log prey density. The black curve is the GS prediction using actual encounter radius (=body radius of 210 μm) of the predator *A. vittata*. The checkered curve is the prediction when the radius is 420 μm. The gray curve is the prediction when the radius is 1000 μm. Black dots indicate the mean # of prey gut^{-1} at each prey density (n=24 trochophores for each prey density). Error bars are 95% Confidence Intervals.

consistent with the predictions from both models. In the High prey density treatment, however, the numbers of veliger larvae consumed is less than predicted by the models. As previously mentioned, this may be explained by predator satiation at the highest prey density (see Discussion).

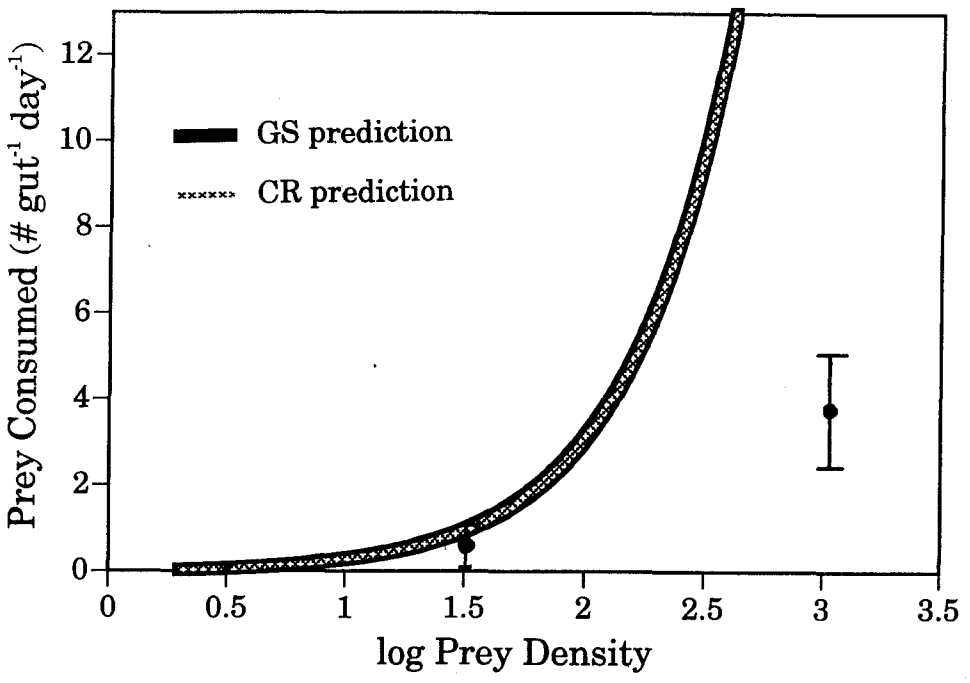

FIGURE 3. The number of prey in *Arctonöe vittata* trochophores vs. log prey density. The black curve is the prediction of the GS model. The thin white curve, directly overlaying the black curve, is the CR model prediction. Black dots indicate the mean # of prey gut^{-1} at each prey density (n=24 trochophores for each prey density). Error bars are 95% Confidence Intervals.

Discussion

The number of veligers consumed by trochophores at the Low and Medium prey densities is consistent with the predictions of the GS model. It appears the model accurately predicts the number of bivalves eaten by *A. vittata* larvae. It should be noted that, although capture success may not always be 100%, it is quite high and predation variance may then obscure potential discord between predation observations and encounter predictions.

Encounter Radius

When the modeled encounter radius was increased, observed encounters no longer fell directly on the curves (Figure 2). Larger-than-actual encounter radiuses fail to predict the number of veligers ingested. The encounter radiuses, used to help create the range of prediction curves, are intended to reflect potential mistakes in the measurements of ambiguous remote encounter radiuses. A radius of 420 μm may seem far off *A . vittata's* actual encounter radius of 210 μm. Indeed, it exceeds the trochophore body radius by 100%. For small predators with ambiguous remote-sensing encounter radiuses, however, a slight anthropogenic mistake in radius determination could easily result in 100% overestimation of actual encounter radiuses. The GS encounter model is sensitive to the encounter radius parameter. Careful observations are needed to reliably determine encounter radiuses for use in encounter rate model estimates.

With High prey density, the actual number of veligers consumed by *A. vittata* larvae is less than predicted by models. This is most likely a result of predator satiation. Indeed, *A. vittata* larvae in the High prey density treatment, with an average of 4 veligers each, appeared to have very full guts. Predators from the High prey density treatment did, however, have a wide range of veliger numbers in their guts (0-10). One might expect less variation in predation if encounters far exceed consumption ability. This variation might be explained, however, by the relationship between number of prey per gut and predator size: larger trochophores ingest more veligers. The trochophores used in this experiment, despite the fact that they were of equal age, varied in size. Predator size significantly correlated

with the number of prey captured ($r = .79$; $df = 1, 22$; $p = 0.000005$). This suggests that predation upon veligers in the High prey density treatment was limited more by predator capacity than prey availability or encounters.

Holling (1959) describes a type II predator functional response curve, where predation rate decreases as predator satiation sets an upper limit to food consumption. The type III curve resembles the type II curve in having an upper limit to consumption, but differs in that low consumption at low prey density results from the lack of a search image or low hunting efficiency. Low consumption described by a type II curve, on the other hand, is simply the result of few encounters. If we assume the models accurately predict encounters, the agreement between model predictions and actual consumption at the Low and Medium prey densities is consistent with a type II curve. This in turn supports the claim that *A. vittata* trochophores forage by cruising randomly and have a high veliger capture success rate.

Comparison of actual predation by *A. vittata* trochophores with model predictions reveals that estimates are sensitive to increased encounter radiuses. Even estimates calculated using an encounter radius 100% too large are inaccurate and, therefore, it is important to reliably and accurately determine encounter radiuses.

Prey Swimming Speed

The main difference between the two encounter models is that the CR model treats prey as passive particles while the GS model does not. When prey swimming speed is low the difference between model outputs small. If

prey speed is very low relative to that of the predator, then prey speed is negligible with regard to estimating encounters (see Figure 4, curves 5 and 6). When predator and prey swimming speeds are more similar than those of *A. vittata* and *C. gigas,* prey speed may affect encounter estimates and should be considered in calculating encounter estimates. To illustrate this, I used more similar predator and prey swimming speeds to estimate encounters and then compared between the GS and CR models. Figure 4 illustrates GS and CR prediction curves for three relative predator and prey

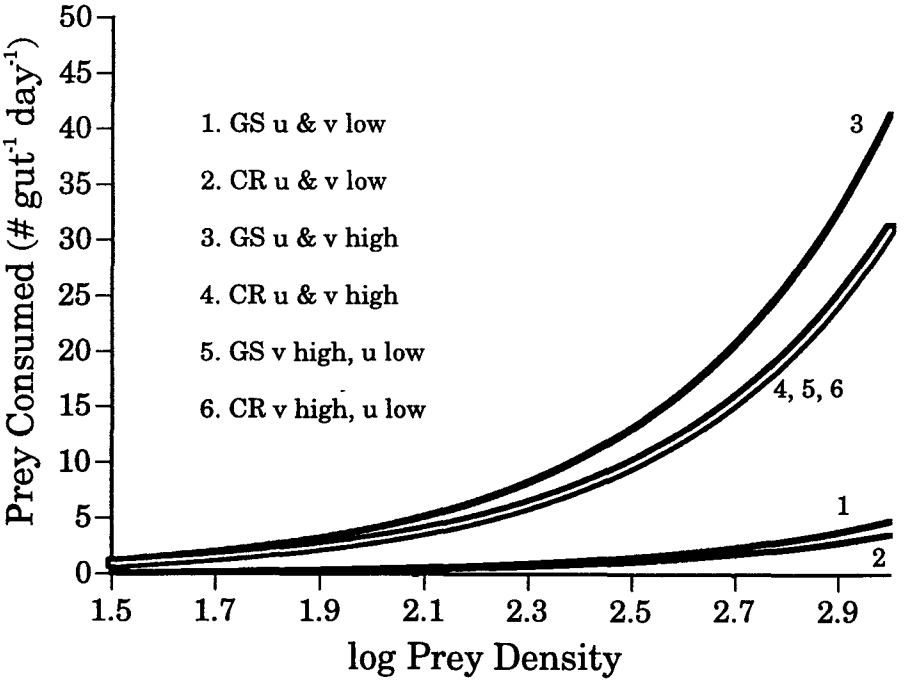

FIGURE 4. Encounter prediction curves for the GS and CR encounter models: curves 1 & 2 (GS and CR, respectively) when predator and prey swimming speeds (v and u) are both low (*C. gigas* veliger swimming speed used for both predator and prey); curves 3 and 4 (GS and CR, respectively) when v and u are both high (*A. vittata* trochophore swimming speed used for both predator and prey); curves 5 and 6 (GS and CR, respectively) with appropriate v and u values for *A. vittata* and *C. gigas* (superimposed curves plotted from Figure 3).

swimming speeds. Model comparisons are made at low similar speeds (curves 1 and 2), high similar speeds (curves 3 and 4), and disparate speeds (curves 5 and 6). For the low swimming speeds, the swimming speed of bivalve veligers (0.03 cm s^{-1}) was always used. For high swimming speeds, the swimming speed of *A. vittata* (0.26 cm s^{-1}) was always used. For example, 0.30 mm s^{-1} was used as the swimming speed for both the predator and prey in calculating prediction curves 1 and 2. For every set of comparisons, one curve is the prediction of the GS model (curves 1, 3, and 5) and the other curve is the prediction of the CR model (curves 2, 4, and 6). Unlike the nearly identical prediction curves resulting from calculations with disparate swimming speeds, The GS and CR prediction curves, overlaying one another when predator and prey swimming speeds are similar, separate as swimming speeds diverge. In other words, when swimming speeds (u and v) become similar, whether low or high, the prey's swimming speed becomes important in calculating encounter predictions. This phenomenon is more pronounced (i.e., the GS and CR curves are farthest apart) when similar swimming speeds are also high (Figure 4, curves 3 and 4). The swimming speed of *A. vittata* trochophores is approximately one order of magnitude greater than the swimming speed of *C. gigas* veligers.

Like the larvae of *A. vittata,* many predators swim faster than their prey. In these cases, both the GS and CR models may be employed with equal utility. One need only account for prey swimming speed, or use the GS model, when predator and prey swimming speeds are relatively

similar. How low relative to predator swimming speed must prey swimming speed be before it can be ignored? In *A. vittata* and *C. gigas*, where prey speed was negligible in estimating encounters, predator swimming speed exceeds that of the prey by approximately an order of magnitude. One order of magnitude or greater relative difference in predator and prey swimming speeds may be an appropriate cut-off for neglecting prey speed in encounter estimates—a cruising predator is primarily responsible for prey encounters when its swimming speed is 10x that of its prey.

Conclusion

Predation rates decrease when invertebrate larvae are presented to predators at near-natural densities which are relatively low. Consequently, predation on planktonic invertebrate larvae has rarely been observed under the most natural laboratory conditions (Johnson and Shanks, 1997; Johnson and Brink, 1998). The results of this study's comparisons between predation and encounter model predictions indicate that low or absent predation may be explained in part by low encounters at near-natural prey densities. Johnson and Brink (1998) examined predation by *Arctonöe vittata* trochophores on *Crassostrea gigas* veligers with the same methods, range of prey densities, and results as the current study. Likewise, Johnson and Shanks (1997) observed low or absent predation for 4 predator-prey combinations when larvae were presented at near-natural prey densities. Predator-prey combinations included *Upogebia pugettensis* zoeae

feeding on urchin blastulae, *U. pugettensis* zoeae feeding on urchin plutei, unidentified hydromedusae feeding on barnacle nauplii, and *Obelia* sp. hydromedusae feeding on urchin blastulae. These predators may not regularly consume these larvae at natural densities, which are low. The natural diet of these planktonic, suspension-feeding predators may be frequently encountered phytoplankton, protists, or abundant metazoans, rather than relatively scarce invertebrate larvae. If this is the case, invertebrate larvae may be rarely consumed because they are rarely contacted.

The Gerritsen and Strickler (1977) planktonic encounter model can accurately predict encounters when details of predator-prey interactions are known. These details include the ratio of the predator's time spent foraging, the predator's average swimming speed when foraging, the relative prey swimming speed in relation to the predator, prey density, and predator encounter radius. The most difficult parameter to measure in remote-sensing predators may be the encounter radius, but the radius must be determined accurately because the GS model is sensitive to radius variation. Prey swimming speed can usually be determined without difficulty, but may be unnecessary to include when prey are slow relative to the predator. In this latter case, the GS and CR models may be employed with equal utility. Encounter estimates enhance investigations of population biology, planktonic mortality, and behavioral ecology. Accurate measurements of encounter radius and knowledge of when to include prey

swimming speed are important for correct estimation of planktonic encounters.

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Bridge

The most valuable data in this doctoral dissertation is that acquired in field observations and experiments in chapter V. Field observations measure predation on a variety of invertebrate larvae by a natural plankton assemblage. Observed predation is compared to estimated encounters of larvae with predators in corrals using the planktonic encounter model examined in chapter IV. Data from field experiments manipulating prey density and background plankton, analogous to laboratory experiments described in chapters II and III, are also given in chapter V. Generally, the results of field experiments corroborate findings in the laboratory—predation is low when larvae are presented at natural densities with background plankton present.

CHAPTER V

PREDATION ON PLANKTONIC MARINE AND ESTUARINE INVERTEBRATE LARVAE

Abstract

Predation on invertebrate larvae is a potentially important source of mortality and may influence the numbers of larvae in the plankton. We conducted *in situ* and laboratory experiments to evaluate predation on larvae by near-natural plankton assemblages. Corrals, or mesocosms, were used to capture a column of whole seawater and its inherent suite of potential predators at natural densities. To these corrals, we added known numbers of larvae marked with calcein. Marked larvae included the plutei of the sand dollar *Dendraster excentricus*, veligers of the oyster *Crassostrea gigas*, and veligers of the snail *Littorina plana*. Most potential predators were captured with the natural plankton assemblage, but some were added to corrals at natural densities to ensure their universal inclusion in experiments. A wide variety of potential predators were captured in or added to corrals. After 24-h corrals were collected and the fate of marked larvae, determined. Predation on unmarked invertebrate larvae, captured at natural densities as background plankton, was also quantified. Recovery of marked larvae was often 100%, enabling a thorough and direct determination of predators and predation rates. Under the most natural

conditions, only 1 of 9 experiments with plutei showed any pluteus predation (a single individual in the gut of the hydromedusa *Proboscidactyla flavicirrata*). Veligers were also often completely untouched, but appear to experience more predation than plutei. The main predators of bivalve veligers were the heterotrophic dinoflagellate *Noctiluca scintillans* and the hydromedusa *Proboscidactyla flavicirrata*. Potential instantaneous mortality due to *N. scintillans* was as high as -.07 day^{-1} and could result in a loss of 87% of a planktonic population in 28 days.

To learn causes of the overall low predation, *in situ* corral experiments were conducted which presented marked prey at near-natural and unnaturally high prey densities and in the presence or absence of natural background plankton (i.e., the natural suite of diverse plankton in whole, unfiltered seawater). All predation observed at high prey densities decreased or disappeared at near-natural prey densities. This suggests that part of the lack of predation in corrals could be the result of few predator-prey encounters. Predation was also decreased by the presence of natural background plankton. Background plankton may occupy the predators time and decrease opportunities for encounters with larvae, obscure larvae from detection or capture, or serve as substitute food. The impact of predation on corral populations was extremely variable, which is probably the case in the field. While *N. scintillans* was a significant predator in 2 of 10 *in situ* experiments, the majority of observations showed that veliger and pluteus larvae suffered little or no predation. Thus, planktonic predation may not always be a major source of larval mortality.

Introduction

The majority of marine and estuarine invertebrates have complex life-histories that include planktonic larvae which reside in the water column for hours to months (Levin and Bridges, 1995). Larvae may develop from free-spawned ova or be released from adults or egg cases after a period of brooding or encapsulation. A single adult invertebrate can produce vast numbers of these planktonic propagules. For example, during a single spawning season one female sand dollar (*Dendraster excentricus*) can spawn 3.8×10^5 eggs (Morris et al., 1980), one female dungeness crab (*Cancer magister*) can release 2.5×10^6 larvae (Morris et al., 1980), a female oyster (*Crassostrea gigas*) can spawn 55.8×10^6 ova (Galtsoff, 1964), and the sunflower star *Pycnopodia helianthoides* may release as many as 160×10^6 eggs (Chia and Walker,1991). These larvae then develop in the plankton until competent for settlement and metamorphosis. The numbers of competent larvae present in local plankton correlates with recruitment to benthic communities (Connell, 1985; Gaines et al., 1985; Roughgarden et al., 1991). These studies of supply-side ecology have investigated the important relationship between planktonic larval supply and benthic community composition. Recruitment to benthic populations can be determined by the supply of larvae available in the plankton (Roughgarden et al., 1984; Connell, 1985; Gaines et al., 1985; Roughgarden et al., 1991).

The number of new recruits to the benthic adult assemblages can be high—the barnacle *Semibalanus balanoides* was observed to settle in

densities reaching 215 individuals cm^{-2} (Connell, 1985). When compared to the area's estimated propagule production, however, these newly metamorphosed juveniles are few. Some studies attempt to estimate mortality rates by contrasting propagule production with benthic recruitment (see Rumrill, 1990 for review). These studies have estimated mortality rates to be from 0.03 day^{-1} in the cone snail *Conus quercinus* (Perron, 1986) to 0.80 day^{-1} in the clam *Mya arenaria* (Ayers, 1956), but cannot distinguish between larval and early juvenile mortality. Many planktonic mortality studies suffer from the drawbacks and potential biases of anecdotal information and indirect evidence (Strathmann, 1985), limiting available reliable knowledge of the sources and importance of mortality. High mortality rates are expected, however, because invertebrate populations are generally stable over time, and mortality must occur between spawning or release and recruitment. Possible sources of planktonic mortality include fertilization failure (Babcock et al., 1992; Brazeau and Lasker, 1992), starvation (Olson and Olson, 1989; Boidron-Métairon, 1995), lethal temperatures (Pechenik, 1987), the absence of the proper settlement substratum (Jackson and Strathmann, 1981), transport away from suitable settlement sites (Farrell et al., 1991; Roughgarden et al., 1991), predation on embryos and larvae (Rumrill, 1990; Morgan, 1995a), and pathogens and genetic abnormalities (Thorson, 1946, 1950, 1966; Rumrill, 1990). Only pathogens and genetic abnormalities have not been investigated.

Planktonic invertebrate larvae can be consumed either by benthic suspension-feeders or planktonic predators. Planktonic embryos and larvae may encounter benthic suspension-feeding predators shortly after release, incidentally during their planktonic life, or as they attempt to settle and test the benthos for a suitable substratum. Benthic predators may form a "wall of mouths" (Emery, 1973) and can make the acquisition of a settlement site a hazardous undertaking. Organisms associated with coral reefs may consume as much as 60% of passing zooplankton, which included the larvae of crustaceans, polychaetes, cnidarians, molluscs, and echinoderms (Glynn, 1973). Suspension-feeding barnacles also inhibited recruitment of colonial ascidians and bryozoans in field experiments conducted by Young and Gotelli (1988). The anthozoans *Alcyonium siderium* and *Metridium senile* captured and consumed planktonic invertebrate larvae (Sebens and Koehl, 1984). Not all suspension-feeders, however, consume invertebrate larvae. For instance, Bingham and Walters (1989) found that settling larvae escaped predation by suspension-feeding ascidians and Rumrill (1987) calculated the risk of predation, by 2 species of benthic suspension-feeders consuming *Asterina miniata* brachiolaria larvae, to be 1.2% per saltation event (i.e., settlement or re-suspension). Additional evidence of low predation by ascidians includes their lack of effect on larval recruitment in a study by Young (1989). Mortality of settling larvae by benthic suspension-feeders is clearly variable, but much more investigation is necessary to determine the overall risk of predation presented by benthic suspension-feeders.

Planktonic predators of invertebrate larvae have been studied in the laboratory, in the field through correlation of high predator abundance and larval decline, and by gut content analysis of field-caught predators. Laboratory experiments have investigated the following factors and their effect on larval predation rates: antipredator defenses (Pennington and Chia, 1984; Morgan 1987, 1989), developmental stage and post-contact behavioral responses (Rumrill et al., 1985; Pennington et al., 1986), larval size (Pennington and Chia, 1984; Rumrill et al., 1985; Rumrill, 1987), container size (Toonen and Chia, 1993), prey density (Rumrill et al., 1985; Pennington et al., 1986; Johnson and Shanks, 1997, Johnson and Brink, 1998), and background plankton presence (Johnson and Shanks, 1997; Johnson and Brink, 1998). In a review on larval mortality, however, Rumrill (1990) points out a caution with regard to laboratory experiments on predation:

> An important limitation is that the majority of laboratory experiments have been conducted in small containers at prey densities that are 2 to 3 orders of magnitude greater than natural densities of larvae in the plankton. Direct extrapolation of mortality rates from laboratory studies is unwarranted because rates of predation in the laboratory are strongly dependent upon the size of the experimental container. (Rumrill, 1990, p. 173)

In order for laboratory experiments to provide information that is directly applicable to estimates of natural mortality, much more information must first be collected about specific natural predator-prey relationships with confirmation that the containers employed do not create artifacts.

Predation on planktonic larvae can be studied in the field by identifying pelagic predators whose abundance is inversely correlated with that of larvae. One example of this is the predatory ctenophore *Mnemiopsis leidyi*, whose abundance has been negatively correlated with larval abundance and recruitment of crustaceans and fish (Nelson, 1925; Burrell and Van Engel, 1976; Cowan et al., 1994). This method requires, however, the fortuitous monitoring of key predators and the need to assume that larval decline in the plankton is due, in whole or part, to predation by these predators.

Another method of monitoring predation on planktonic invertebrate larvae is by gut content analysis of potential predators. Indeed, predators have been identified based upon their gut contents. Examples of invertebrate larval predators identified in this manner include the ctenophore *Mnemiopsis leidyi* (Nelson, 1925; Burrell and Van Engel, 1976), the hydromedusa *Phialidium* sp. (McCormick, 1969), decapod larvae (Lebour, 1922), and salmon fry (Bailey et al., 1975). Unfortunately, some of these predators may have consumed larvae in cod-end plankton buckets and predation may be an artifact of collection. For example, chaetognaths are known to feed unnaturally or at increased rates on plankton in collection reservoirs (Feigenbaum and Maris, 1984).

Because predation in the plankton may be determined by opportunity, or encounters between predators and prey (see laboratory evidence of density-dependent predation— Rumrill et al., 1985; Pennington et al., 1986; Johnson and Shanks, 1997, Johnson and Brink, 1998), many predators may

feed unnaturally when concentrated with potential prey in plankton samples. Even if it is assumed, however, that the presence of larvae in predator guts is not an artifact of collection, predator gut analysis has not been an effective method for evaluating the impact of predation on larval populations. When gut content studies have identified predators, the focus has often been on the composition of the predator's diet. Invertebrate larvae are a minor part of predator diets. However, the relative importance of predation has not yet been determined for an individual larva throughout the duration of larval life. Since data on the concurrent density of planktonic prey is rarely offered, little can be said about the importance of particular predators in the ecology of larval invertebrates. For example, Bailey et al. (1975) observed that salmon fry had preyed upon decapod larvae. Only 9% of salmon fry guts sampled, however, contained decapod larvae. Decapods only represented 1% of the diet by volume. Decapod larvae are not likely to be an important component of young salmon diets and nothing is known of the potential impact on decapod populations by salmon predators. Some hydromedusae of *Phialidium* sp. consume invertebrate larvae, but less than 10% of predators sampled contained larvae and, in those, larvae comprised less than 3% of identified prey (McCormick, 1969). As with decapod larvae and salmon fry, these larvae are not likely to be an important component of *Phialidium* sp. diets and nothing is known of the potential impact on larval populations by this predator. Because this data focuses on predator diets rather than larval risk, important questions still remain. How important is planktonic

predation over a larva's planktonic life? What is the daily risk of predation for an individual larva from *all* potential predators?

It is possible to evaluate predation risk using gut contents in combination with known digestion rates and field densities of predators and prey. This has been done to evaluate predation on adult copepods by larval fish (Purcell, 1990) and on copepods, fish eggs, and fish larvae by coelenterates (Purcell et al., 1994; Chandy and Greene, 1995). These results cannot be extrapolated to predation on invertebrate larvae because these predators may preferentially consume copepods, larval fish, or eggs, and digestion times vary with prey type and size (Purcell, 1982; Chandy and Greene, 1995). According to Purcell (1982), this combination approach to evaluating *in situ* predation requires accuracy in measurements of digestion times for particular prey, identification of digested prey, converting size to dry weight and carbon, and determining predator and prey densities from plankton tows. We would add that predator digestion times for particular food types can vary tremendously depending on the total amount of food in the gut. For instance, trochophore larvae of the scaleworm *Arctonöe vittata* will pass bivalve veligers within 3 to 4 hours when several veligers have been consumed and more are available. A lone veliger in the gut of *A. vittata*, however, may remain in the gut for as long as a day (K. Johnson, pers. obs.). In spite of the potentially inaccurate assumptions, estimates using gut contents, digestion times, and densities may more accurately estimate field mortality than estimates based upon laboratory predation studies (Purcell, 1982). Laboratory studies of predation

are potentially fraught with behavioral artifacts (Reeve 1977, 1980), but it is unknown whether indirect field studies or laboratory experiments provide the best estimate of field mortality.

This study describes experiments conducted both in the field and in the laboratory. All experiments examined predation on larvae under the most natural conditions possible. Most field studies were designed to simply observe predation on invertebrate larvae, expose predator identities, and determine predation rates under near-natural conditions. These observational field studies test the hypothesis that populations of invertebrate larvae suffer significant predation in near-natural plankton assemblages. To examine factors affecting predation rates, field and laboratory studies test the hypotheses that 1) proportion of predation on a larval population changes with prey density and 2) natural background plankton reduces predation rates.

This study uses natural assemblages, including a diverse suite of potential predators, enabling us to directly determine the predation risk for experimental larval populations. Corrals were inoculated with marked and enumerated invertebrate larvae at the start of 24 h experiments. By marking prey, we could know initial prey densities, retrieve larvae after the experiment, determine the number of survivors, and identify the natural predators. Observations of predation are direct and can be related directly to the potential impact of predation on experimental populations of invertebrate larvae. Corral assemblages also included wild (i.e., randomly caught and unmarked) invertebrate larvae at natural densities. We were

able to examine predation risk for captured wild larvae using predator gut content analyses, known wild prey densities, and a planktonic predator-prey encounter model. Finally, corrals were also used to manipulate prey density and "background plankton" presence, examining their effect on predation rates.

These field observations and experiments provide a direct assessment of predation's importance for larvae in an experimental assemblage. The following strengths of experimental design contribute to the data's value for examining predation as an important source of larval invertebrate mortality. Larval species examined as prey include 3 species of marked larvae and several other species of wild larvae representing 4 phyla. The data were collected from interactions with captured natural assemblages, each with a diversity of potential predators representing all defined planktonic feeding strategies (Greene, 1985). Initial densities of marked larvae were known, allowing more powerful analysis of observations. Predators and prey interacted at natural densities, eliminating the possibility of artifactual behavior induced by abnormal densities. Marked larvae were easily visible in the guts of predators. Corral volumes far exceeded the practical capacity of laboratory containers and reduced artifacts resulting from small volumes. Finally, corral samples were collected and fixed immediately at the close of experiments, minimizing the possibility of artifactual predation in the concentrated sample. Studies such as this, investigating *in situ* predation on larvae, can be valuable for determining the potential sources of significant larval

mortality, analyzing factors that shape benthic communities, discussing the life history evolution of benthic marine invertebrates with complex life cycles, and identifying critical areas of future research.

Methods

Marked Larvae

Marked larvae included pluteus larvae of the sand dollar *Dendraster excentricus*, veliger larvae of the snail *Littorina scutulata*, and d-hinge veliger larvae of the oyster *Crassostrea gigas*. Adult breeding stock of *D. excentricus* were collected from the North Spit, Coos Bay, Oregon and from West Sound, Orcas Island, Washington. Adult *L. scutulata* were collected from Sunset Bay, Oregon and Friday Harbor, Washington. Embryos and larvae were obtained using methods described in M. Strathmann (1987). D-hinge larvae of the oyster *C. gigas* were provided by Whiskey Creek Oyster Farms (Tillamook, Oregon).

Larvae were marked with fluorescent Calcein (Sigma Corp.), which is permanently incorporated into skeletons as calcium carbonate is laid down. Larvae were cultured in filtered seawater on diets of *Isochrysis galbana* and *Rhodomonas* sp. in the presence of Calcein at a concentration of 200-500 ppm. Larval behavior and development appears normal in the presence of Calcein (Rowley, 1993; pers. obs.). Calcein is primarily comprised of $CaCO_3$, which should not affect predator preference for larvae. Though there is also a fluorescent molecule in Calcein, it is bound in the

larval skeleton. Even if the fluorescene does taste bitter to the predator, lethal predation would be required for the unpleasant taste to be discovered. For example, the Calcein incorporated into sand dollar skeletons is completely internal and would not be tasted until after the maceration of dermal tissue. Finally, digested skeletons retain their Calcein component and are visible in the guts of predators and in fecal pellets.

Seeded Predators

In some experiments (see Tables 1 and 2) naturally occurring predators were seeded in corrals at natural densities to ensure consistent representation in all treatments and replicates. Seeded predators were collected at high tide by slowly towing a plankton net equipped with a large blind cod-end (after Reeve, 1981). Predators were quickly removed from the plankton sample to isolation in filtered seawater using a large bore pipette or a small cup. Experiments began within 24 hours of predator collection

One predator, the trochophore larva of the scaleworm *Arctonöe vittata*, was cultured for use in corrals. Adult specimens, commensal with the keyhole limpet *Diodora aspera*, were collected with their host from the west shore rocky intertidal of San Juan Island, Washington. Individuals of *A. vittata* were spawned and larvae were cultured using the methods described by Phillips and Pernet (1996) with the addition of *Coscinodiscus radiatus* (CCMP 310) as a food source. Fertilized eggs were cultured in 600-ml beakers at densities of ~500 l^{-1}. Larvae approximately 21 days old were used as predators in experiments.

Corrals, Deployment, and Collection

Experiments were conducted in corrals made of flexible 20-mil clear PVC sheeting. Corrals held 123 liters of seawater when deployed. For corral design and dimensions, see Figure 1D. Corrals were water tight except for cod-end collection buckets. Each bucket had 8 portholes covered with 53-μm Nitex mesh and a total filtering area of 176.4 cm^2. For deployment, corrals were collapsed longitudinally and fastened in the collapsed position with a securing line (Figure 1A). Corrals were submerged and lowered to the appropriate depth (see deployment depth, Figure 1A) with a 3-point bridle, harness and line. After the corral was at depth and the disturbed water column had cleared from directly above the corral, the securing line was released (Figure 1B). The corral was then drawn slowly surfaceward with the bridle line (Figure 1C). The cod-end bucket remained at depth as the mouth of the corral was drawn surfaceward, eventually breaking the surface of the water. The corral was suspended by floats for the 24 h experiment. This resulted in the quiet capture and isolation of a natural assemblage of plankton and potential predators (See corral contents, Table 5), including delicate predators such as chaetognaths and coelenterates, at natural densities.

It should not automatically be assumed that behavior and feeding in corrals reflects that which would occur in a natural environment. The feeding behavior of some predators can be altered by small laboratory containers (e.g., Toonen and Chia, 1993) and natural turbulence,

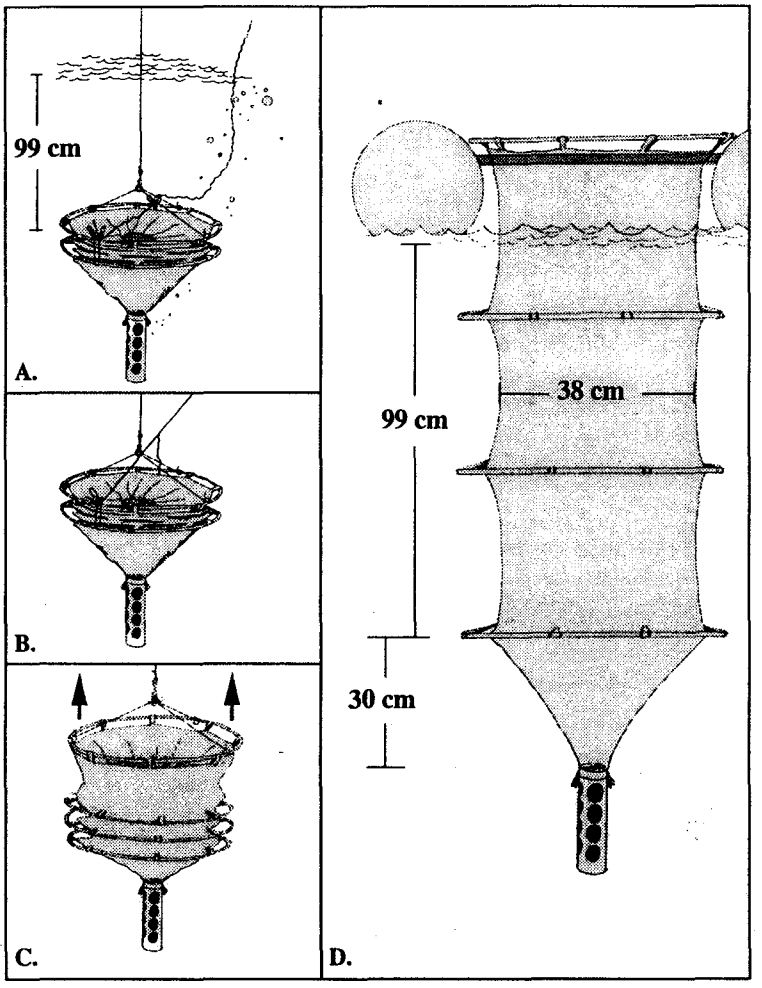
dampened in corrals, enhances encounters between planktonic organisms. The most compelling argument for low container effects in corrals is the fact that large numbers of predators fed on larvae under unnatural laboratory conditions, but did not consume them in corrals. It is most parsimonious to assume that, as conditions were made more natural (i.e., increased container volume and turbulence relative to the laboratory), predation in 123-l corrals more closely reflects nature than predation observed in 3-l laboratory containers.

At the close of experiments, corrals were hauled from the sea and captured water exited through the cod-end bucket. Contents were fixed immediately in 4% buffered formalin. Filter screens were washed repeatedly to free plankton from the mesh and ensure collection of all of the sample. Samples were stored in the dark.

Observation Experiments

One observation experiment consisted of 4 corrals inoculated with known numbers of marked larvae. A total of 10 experiments were conducted, 2 in the boatbasin at Charleston, Oregon (43°21'10" N, 124°19'50" W), and 8 from the dock of Friday Harbor Laboratories, Friday Harbor, Washington (48°32'10"N, 123°00'19" W). In some experiments, rare suspected potential predators were added to corrals. These potential predators were present in surrounding plankton, but were seeded in corrals to ensure their consistent representation in the randomly captured assemblages. Table 1 provides a summary of experiment location,

FIGURE 1. *In situ* corrals: deployment and dimensions. A. Corral with slack line securing the collapsed position is lowered to depth with taught bridle line. B. At depth, slack line unties as it is pulled, freeing the corral for expansion. C. With the bridle line, the corral is pulled surfaceward, quietly capturing a column of seawater and natural plankton assemblage. D. Corral is suspended at the sea surface by floats for the duration of the experiment. Corral volume is approximately 123 liters.


99 cm
A.
B.
C.
D.
38 cm
99 cm
30 cm

numbers of marked larvae added, and the identities and numbers of seeded potential predators. Table 1 also indicates whether experiments were started during the day or night, which should effect which potential predators are randomly captured in corrals. Night experiments were started between 10:00 pm and 1:00 am.

After corrals were deployed, a known number of marked larvae were added to each corral. Marked larva corral densities were intended to reflect the high end of potential natural densities. Our survey of the literature indicates that, for many invertebrate larvae, the experimental densities selected (0.4 to 1.0 liter^{-1}) are reasonable natural densities (Carriker, 1951; Zimmerman, 1972; Cameron and Rumrill, 1982; Rumrill et al., 1985; Emlet, 1986; Miller, 1995). Following inoculation, corral assemblages were mixed with 2 gentle vertical strokes of a perpendicular 400 cm^2 paddle. For the experiments indicated, seeded predators were then added to corrals (Table 1). Experimental assemblages were allowed to interact *in situ* for 24 h. Floats suspending the corrals were tethered to the dock. Currents did not distort corral shape or volume.

Whole fixed samples were sorted at 100x magnification with epifluorescent microscopy and an FITC filter. Marked larvae were tallied, fate noted (i.e., in guts or free-living and apparently alive at the time of fixation), and predator identities recorded. Selected predators were observed under epifluorescence to check for marked prey, then dissected for identification and counting of gut contents.

TABLE 1. Summary of observational experiments. Experiments were conducted at Coos Bay (CB) or Friday Harbor (FH). Seeded potential predators are the hydromedusae a) *Proboscidactyla*, b) *Sarsia*, and c) *Aglantha*, d) the ephyrae of the scyphomedusa *Aurelia*, e) the chaetognath *Sagitta*, f) small postlarval sticklebacks, g) brachyuran zoeae, h) anomuran zoeae, and i) trochophores of the polynoid polychaete *Arctonöe vittata*. Potential predators also include randomly captured animals.

			Marked prey (numbers corral^{-1})			
Exp.	Site	Day/ Night	Sand dollar plutei	Bivalve veligers	Gastro veligers	Seeded potential predators corral^{-1} (# in parentheses)
1	CB	D	100	100	----	----
2	CB	D	100	----	----	----
3	FH	D	100	100	----	----
4	FH	D	----	50	50	a (2), b (1)
5	FH	N	100	20	50	a (2), e (1)
6	FH	N	100	100	----	a (2)
7	FH	N	100	100	----	a (1), c (1), e (4)
8	FH	D	100	100	----	f (2), d (3)
9	FH	D	50	50	----	d (5), g (5), h (1)
10	FH	D	123	123	----	a (2), d (2), g (3), h (1), i (2)

Potential predators and background plankton were counted for each corral. Absolute numbers were determined for relatively large potential predators (> 500 μm). Background plankton, including small potential predators, wild invertebrate larvae, and potential alternative food items for

predators, were counted in 25% sample aliquots. Resulting counts for background plankton are given as estimated # corral^{-1}. Organisms counted in 25% aliquots included large diatoms, dinoflagellates, small copepods, copepod nauplii, barnacle nauplii, wild (unmarked) gastropod and bivalve veligers, and small polychaete larvae.

Manipulation Experiments

Two corral experiments manipulating natural conditions were conducted from the dock at Friday Harbor Laboratories, Friday Harbor, Washington. The first experiment manipulated marked prey density and the presence of background plankton. The four treatments were 1) near-natural prey densities in 53-μm-filtered seawater; 2) near-natural prey densities with background plankton (unfiltered seawater); 3) unnaturally high prey densities in 53-μm-filtered seawater; 4) unnaturally high prey densities with background plankton (unfiltered seawater). Experiments always used pluteus larvae of the sand dollar *Dendraster excentricus* and veliger larvae of the oyster *Crassostrea gigas* as marked prey. The near-natural prey density used was 0.81 larvae liter^{-1} (Zimmerman, 1972; Miller, 1995). Unnaturally high prey densities were 100 larvae liter^{-1}. Corrals in treatments with 53-μm-filtered seawater were deployed by lowering them into the water cod-end-first. Seawater was then screened as it passed through the cod-end and into the corral, allowing plankton < 53-μm to enter the corral and excluding larger plankton. After the corral was submerged to deployment depth, it was suspended from surface floats. Selected

predators were then added to all treatments to determine the effects of prey density and background plankton on predation rates. Each treatment was replicated 3 times. All replicates could not be run simultaneously, so one complete set of the four treatments was run daily for three consecutive days. All other aspects of this experiment (deployment, collection, and sorting) were identical to methods described for the observation experiments.

In the second manipulation experiment, prey densities were held constant, but the presence of background plankton was manipulated. The treatments were 1) near-natural prey densities in filtered seawater and 2) near-natural prey densities with background plankton present (unfiltered seawater). Near-natural densities were 1 larva liter^{-1}. As with the first manipulation experiment, corrals in the treatment with 53-μm-filtered seawater were deployed by submerging them cod-end-first. Each treatment consisted of 3 replicates and the entire experiment took place simultaneously. All other aspects of this experiment (deployment, collection, and sorting) were identical to methods described for the observation experiments. Table 2 provides a summary of predators seeded in both manipulation experiments.

Laboratory Experiments

Laboratory roller table experiments were conducted with the hydromedusa *Proboscidactyla flavicirrata*, a predator present in several

TABLE 2. Summary of seeded predators in manipulation experiments.

Exp.	Seeded potential predators corral^{-1} (# in parentheses)
1	*Proboscidactyla* (2), *Aurelia* ephyrae (2), *Muggiaea* colony (1), brachyuran zoeae (3), anomuran zoea (1), *Arctonöe* trochophores (6)
2	*Proboscidactyla* (2), *Aurelia* ephyrae (2), small stickleback (1), brachyuran zoeae (2), anomuran zoea (1), *Arctonöe* trochophores (2)

corral experiments. *P. flavicirrata* was selected for laboratory investigation because of the consistent occurrence of large mollusc larvae in the guts of corral specimens. Experiments were conducted on a roller table (Omori & Ikeda 1984, Larson & Shanks 1996), which rolled 3-liter cylindrical tanks at 0.75 rpm and prevented plankton from settling. Every 2 hours, tanks were gently tumbled once and then replaced on the roller table facing the opposite direction. A single predator was housed in each tank. Though enclosed, plankton do not suffer oxygen depletion during the experimental time frame (Larson & Shanks 1996). The roller table was maintained at 12 °C in a constant temperature room with a 14:10 Light:Dark cycle for 24 hours. Observations of predators and prey in roller tanks revealed that they were evenly distributed, remained suspended in the water, and exhibited apparently normal behavior

Hydromedusae were collected in Coos Bay, Oregon at high tide or in Friday Harbor, Washington and shipped to Oregon for use in roller table

experiments. Individual medusae were dipped from the plankton. Medusae were maintained in filtered seawater and used in experiments within 2 to 10 days of capture or shipment and exhibited no apparent behavioral or physiological damage. Veligers (both 90-μm and 280-μm in length) of the oyster *Crassostrea gigas* were used as prey. Oyster larvae were obtained from Whiskey Creek Oyster Farms, Tillamook, Oregon, and maintained on a diet of *Isochrysis galbana* and *Rhodomonas* sp.. At the end of each experiment, predators and remaining prey were collected and fixed with 4% buffered formaldehyde. Counts of prey consumed were made using a compound microscope with cross-polarized light.

The first *P. flavicirrata* roller table experiment examined predation on veligers of the oyster *Crassostrea gigas* at either of two prey sizes and each at either of two prey densities. Also, all treatments were conducted in either filtered seawater or in the presence of whole seawater (with background plankton). The resulting 8 treatments were each replicated 3 times for a single day's experiment. The entire experiment was repeated on 2 consecutive days for a total of 6 replicates for each treatment. The near-natural prey density was 50 l^{-1} and based upon the highest bivalve veliger densities in the literature (Carriker, 1951). The second prey density was unnaturally high (1000 l^{-1}) and intended to increase encounters and predation for comparison with predation in the near-natural prey density.

The second *P. flavicirrata* roller table experiment examined predation in 3 treatments, all at the near-natural prey density of 50 l^{-1}. Each treatment was replicated 6 times. The 3 treatments were 1) d-hinge

veligers (90-μm in length) as prey, 2) large veligers (280-μm in length) as prey, and 3) both d-hinge and large veligers as prey. Treatment 3 used each of the two veliger size classes at the full density of 50 l^{-1}.

Results

Marked larvae fluoresced brightly when excited by UV light and viewed through an FITC filter. Glowing skeletons were visible against the background plankton from corrals (Figure 2, A and B) and in the guts of predators (Figure 2, C-F).

Observation Experiments

The high recovery of marked larvae (Table 3) allows reliable estimates of mortality in the corral. For the 3 marked larval types used in 10 different observational experiments, mean recovery was 99-100% in 15 of 20 cases (1 case = 1 larval type in one experiment). Recovery was 100% in all replicates in 5 cases. The lowest mean recovery was 96.50% for marked bivalve veligers in experiment 7. The fate of unrecovered larvae cannot be determined. All evidence indicates, however, that marked animals are visible in any condition (i.e., free-living, in predator guts, or in fecal pellets). Therefore, it is assumed that unrecovered larvae were not more likely to have been victims of predation than recovered larvae from the same corrals.

Observations of predation on marked bivalve veligers are summarized in Table 4. In 4 of 9 experiments using marked bivalve larvae,

FIGURE 2. A. Field of view from sample sorting with myriad phytoplankton and background plankton, viewed under white light. B. Same view as 'A', observed under epifluorescence (FITC filter) to reveal the location of a marked pluteus. C. The heterotrophic dinoflagellate *Noctiluca scintillans* observed under white light. D. Same view as 'C', observed with epifluorescence to reveal a phagocytized marked veliger. E. Majid zoea flattened with slide coverslip and observed under white light. F. Same view as 'E', observed under epifluorescence. Fluorescent bolus of a crushed marked pluteus skeleton visible in the zoea's intestine.

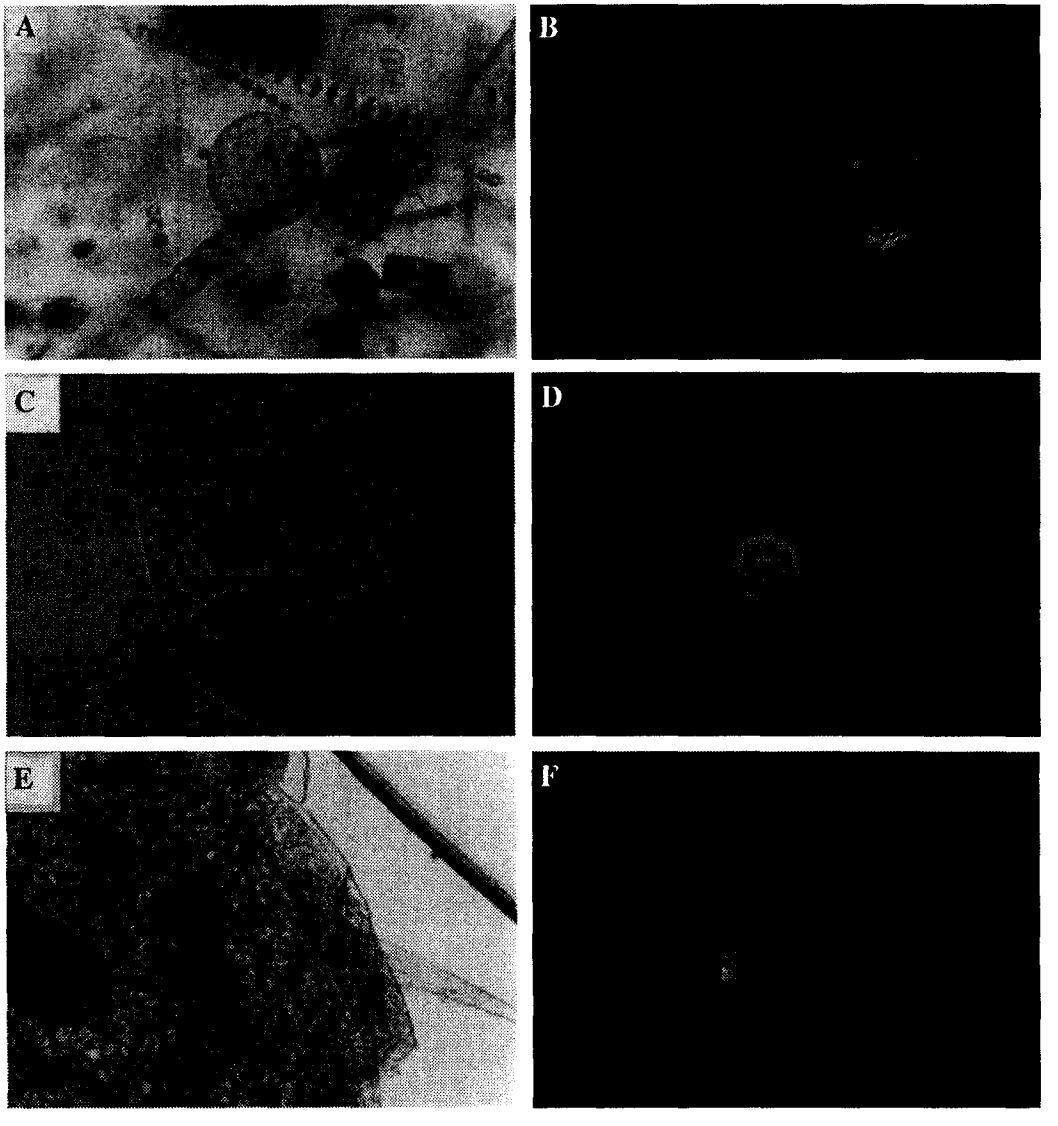

A
B
C
D
E
F

TABLE 3. Mean recovery of marked larvae in observational experiments (n = 4 in all cases).

	Mean % recovery (SD)		
Exp.	Plutei	Bivalve vel	Gastropod vel
1	100.0 (0.0)	100.0 (0.0)	——
2	99.5 (0.6)	——	——
3	99.5 (1.0)	99.0 (1.4)	——
4	——	100.0 (0.0)	98.3 (1.5)
5	98.0 (0.8)	100.0 (0.0)	99.3 (1.2)
6	96.5 (3.4)	97.5 (2.4)	——
7	99.3 (1.0)	96.5 (4.5)	——
8	99.7 (0.6)	99.7 (0.6)	——
9	99.5 (1.0)	100.0 (0.0)	——
10	99.7 (0.5)	98.9 (1.2)	——

absolutely no predation on bivalves was observed. This in spite of the fact that 100% of the larvae were usually recovered. In 9 experiments using marked pluteus larvae, only a single consumed pluteus larva was observed, preyed upon by *P. flavicirrata* in experiment 10. No predation on gastropod veligers was observed.

Table 4 also shows calculations of mortality (day^{-1}) for consistent observed predators. Instantaneous mortality, M, can be calculated as follows (Rumrill, 1990):

$$M = \ln (N_o/N_t)/ t$$

N_o is the initial number of prey in a specified water mass. N_t is the final prey abundance in that same water mass after time t.

Table 4. Predation on marked bivalve veliger larvae from observational experiments. Instantaneous mortality (M) represents the mean loss to corral populations in 24 h. In three cases below (4, 6b, and 8) indicated predators consumed only a single marked bivalve veliger.

Exp.	M (day^{-1})	Estimated loss after 28 days	Predator responsible (total number of veligers consumed in all replicates)
1	0.000	0%	No predator (0)
3	-0.070	87%	*Noctiluca scintillans* (28)
4	-0.005	13%	*Proboscidactyla flavicirrata* (1)
5	0.000	0%	No predator (0)
6a	-0.035	63%	*Noctiluca scintillans* (14)
6b	-0.003	7%	Spionid metatrochophore (1)
7	0.000	0%	No predator (0)
8	-0.003	7%	*Gasterosteus aculeatus* (1)
9	0.000	0%	No predator (0)
10	-.004	11%	*Proboscidactyla flavicirrata* (2)

Predators responsible for observed predation on marked bivalves are indicated in Table 4. In observational experiments 4 and 8, only a single marked veliger was consumed (i.e., no predation on marked bivalves was observed in 3 of the 4 replicates). Likewise, in addition to predation by *N. scintillans* in experiment 6, a single spionid metatrochophore larva consumed a marked veliger. Two marked bivalve veligers were observed in the guts of the hydromedusa *Proboscidactyla flavicirrata* in experiment 10. The identity and numbers of background plankton are given in Table 5. In all, experimental corrals captured dozens of potential predator types representing a wide variety of planktonic feeding strategies (Greene, 1985).

The following predators were selected for determination of their non-marked gut contents: all cnidarians, all ctenophores, chaetognaths, fish, and *Arctonöe* trochophore larvae. These predators were selected because they are considered by many to be important predators, their typical prey sizes encompass the sizes of larvae in corrals, and guts contents could be viewed or dissected with relative ease. The most common prey items found in predator guts were copepods and other crustaceans, including the larvae of copepods and barnacles, and phytoplankton. Predators of copepod and barnacle nauplii include *Sagitta* sp., *Gasterosteus aculeatus*, *Pleurobrachia bachei*, and the hydromedusae *Proboscidactyla flavicirrata*, *Sarsia* sp., and *Phialidium* sp.. These same coelenterates were also observed to contain wild, unmarked bivalve or gastropod veligers. Polychaete larvae were observed in the guts of *P. bachei*, *P. flavicirrata*, and

Sarsia sp.. Polychaete numbers were estimated from clusters of undigested setae.

Manipulation Experiments

Results for the corral experiment which simultaneously manipulated prey densities and the presence of background plankton are given for marked plutei (Figure 3A) and marked veligers (Figure 3B). For both larval types, predation in filtered seawater at high prey densities was almost completely eliminated at lower, near-natural prey densities. At the high prey densities, the inclusion of natural background plankton reduced predation on plutei by an average of 37% and on bivalves by an average of 23%. When prey were presented at near-natural prey densities and in the presence of natural background plankton, no predation was observed on marked larvae. Predators responsible for the predation graphed in Figure 3 included two hydromedusae, a scyphozoan developmental stage, decapod zoeae, and a polychaete trochophore. These predators are summarized in Table 6 by prey type and treatment.

Results of the second manipulation experiment were consistent with the findings of the first manipulation experiment. Predation was generally low, with the only observed predation on a single marked bivalve veliger in filtered seawater. When prey (veligers and plutei) were presented under the most natural conditions (at near-natural prey densities and in the presence of natural background plankton) no predation was observed on marked larvae.

TABLE 5. Background plankton in observational experiments, including potential predators randomly captured when corrals were loaded (mean numbers corral-1). Additional potential predators not shown here include those seeded in corrals (see experimental setup, Table 1).

	Experiment #									
Species	1	2	3	4	5	6	7	8	9	10
Protoperdinium	0	0	365	0	0	0	32423	7740	3150	25364
Noctiluca	1531	413	540	489	404	375	0	0	0	0
Coscinodiscus	0	0	0	0	0	0	12938	6420	9923	10025
Tintinnids	193	376	164	0	0	0	0	0	14	0
Copepods (Cal)	653	565	922	737	817	1838	2543	840	1215	1520
Copepods (Harp)	0	101	101	225	72	55	113	16	26	21
Copepod nauplii	1806	545	1849	1787	1812	23464	9428	8640	4275	3755
Barnacle nauplii	1439	440	1068	334	268	949	270	43	42	35
Barnacle cyprid	0	13	0	0	0	27	0	8	4	12
Amphipods (G)	0	0	0	0	0	0	0	3	0	0
Amphipods (H)	0	0	0	1	28	2	9	11	3	5
Cryptoniscid	0	0	0	0	0	0	0	5	1	0
Anomuran zoea	0	0	0	0	2	0	2	0	4	1
Brachyuran zoea	0	0	0	0	0	2	1	0	5	3
Megalopa	0	0	0	0	0	0	0	0	0	0
Cladoceran	0	0	11	8	1	0	0	0	0	0

TABLE 5. Continued.

Species	Experiment #									
	1	2	3	4	5	6	7	8	9	10
Ostracoda	0	0	0	0	0	0	1	3	0	0
Cumacea	0	0	0	0	0	0	5	0	0	0
Euphausid zoea	0	1	0	0	1	1	0	0	0	0
Salt water mite	0	0	2	0	0	0	0	0	0	0
Obelia	21	0	22	35	3	0	2	0	3	1
Phialidium	0	1	0	1	0	1	3	0	1	0
Aglantha	0	0	0	0	0	0		0	1	0
Leptomedusa	0	42	0	8	1	0	2	0	19	0
Rathkea	0	1	0	0	0	0	0	0	0	0
Pleurobrachia	1	2	1	0	0	0	0	0	1	1
Cydippid larvae	45	0	0	0	0	0	0	0	0	0
Autolytus	0	0	0	0	8	4	5	3	4	1
Spionids	0	0	0	0	0	0	228	35	26	11
Metatrochophore	792	259	415	240	167	662	70	13	7	3
Nectochaeta	0	0	0	0	0	0	7	0	0	0
Mitraria	8	0	0	0	0	0	0	0	0	0
Magelona	42	50	16	0	0	0	0	0	0	0

TABLE 5. Continued.

Species	Experiment #									
	1	2	3	4	5	6	7	8	9	10
Trochophores	34	42	8	12	24	27	0	0	0	0
Cyphonautes	0	3	6	22	15	17	5	8	4	0
Pilidia	16	0	0	0	0	0	0	0	0	0
Doliolaria	0	3	0	0	0	0	0	0	0	0
Ophioplutei	0	0	14	0	0	0	0	0	0	0
Echinoplutei	241	48	5	0	23	0	0	0	0	0
Little urchins	7	0	0	0	0	0	0	0	0	0
Veligers (Biv)	404	83	112	0	0	192	96	115	126	48
Veligers (Gast)	13	26	9	50	22	30	9	19	8	15
Egg cases	0	0	0	0	4	3	0	0	0	0
Embryos	216	148	53	0	0	95	0	0	0	0
Eggs	92	331	0	0	48	4	0	0	0	0
Chaetognaths	20	26	22	9	67	71	62	32	15	13
Larvaceans	234	9	89	114	102	55	16	8	31	20
Larval fish	0	0	0	0	0	0	1	0	0	0

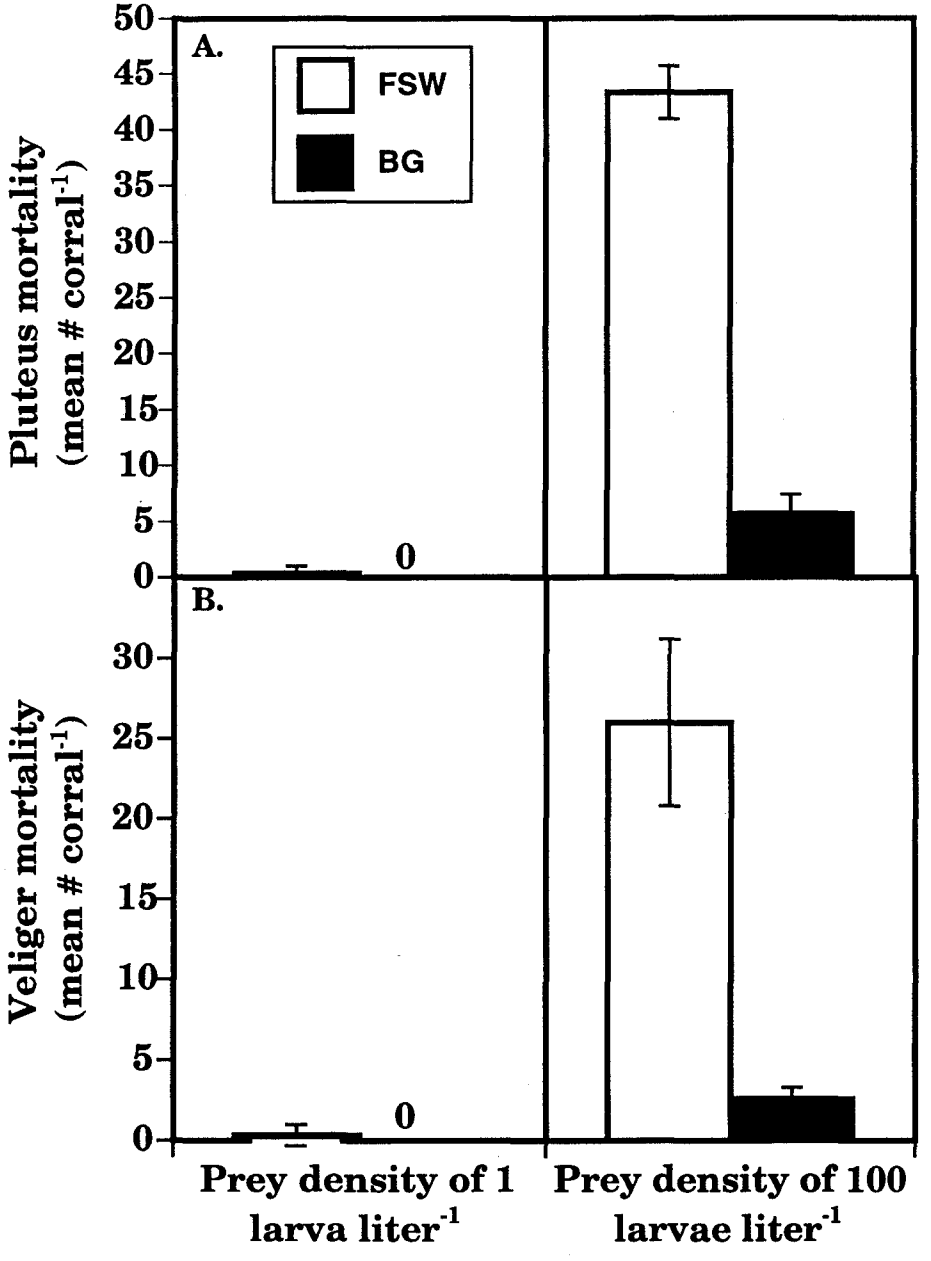


FIGURE 3. The effects of prey density and background plankton on larval mortality for A. marked plutei and B. marked veligers. Clear bars are 53-μm-filtered seawater treatments (FSW). Black bars are background plankton treatments (BG). Cases of zero mean and variance in mortality are indicated by a '0'. Error bars are 95% Confidence Intervals.

TABLE 6. Manipulation experiment: predators on marked pluteus (P) and marked veliger (V) larvae by treatment. Experiments were conducted at each prey density either in 53-μm-filtered seawater (fsw) or with background plankton present (BG). (Total number of prey consumed in all 3 replicates given in parentheses).

	Low prey density		High prey density	
	fsw	BG	fsw	BG
Proboscidactyla	V(1)	0	P(83)/V(57)	P(13)/V(4)
Phialidium	0	0	0	V(4)
Aurelia ephyra	0	0	P(4)/V(1)	P(1)
Brachyuran zoea	P(1)	0	P(17)	P(1)
Anomuran zoea	0	0	P(2)	P(1)
Arctonoe	0	0	V(16)	0

Laboratory Experiments

The hydromedusa *Proboscidactyla flavicirrata* consumed small and large bivalve veligers under all conditions (Figure 4). Small (d-hinge) veligers were consumed most frequently when presented at unnaturally high prey densities in filtered seawater (mean = 60.5 larvae gut^{-1}). Large veligers, however, were not consumed significantly more when presented at high prey densities and in filtered seawater than in other treatments. Presenting prey in the presence of background plankton at the high prey density dramatically reduced predation on d-hinge veligers from 60.5 gut^{-1} to 15.5 gut^{-1}. When offered a choice of d-hinge and large veligers, each at the same prey densities, *P. flavicirrata* reduced predation on d-hinge veligers from 10.0 gut^{-1} to 1.5 gut^{-1} in favor of persistent predation on large bivalve larvae (Figure 5).

Discussion

Predation on marked plutei and veligers in these experimental assemblages was low in most cases. This may be due to the exclusion of important natural predators, though dozens of potential predators representing diverse foraging strategies (Greene, 1985) were captured or seeded in corrals. Thus, we seek alternative explanations to account for the lack of predation. Infrequent encounters at near-natural prey densities may reduce predation by predators which might otherwise consume larvae. Also, naturally occurring background plankton may somehow interfere

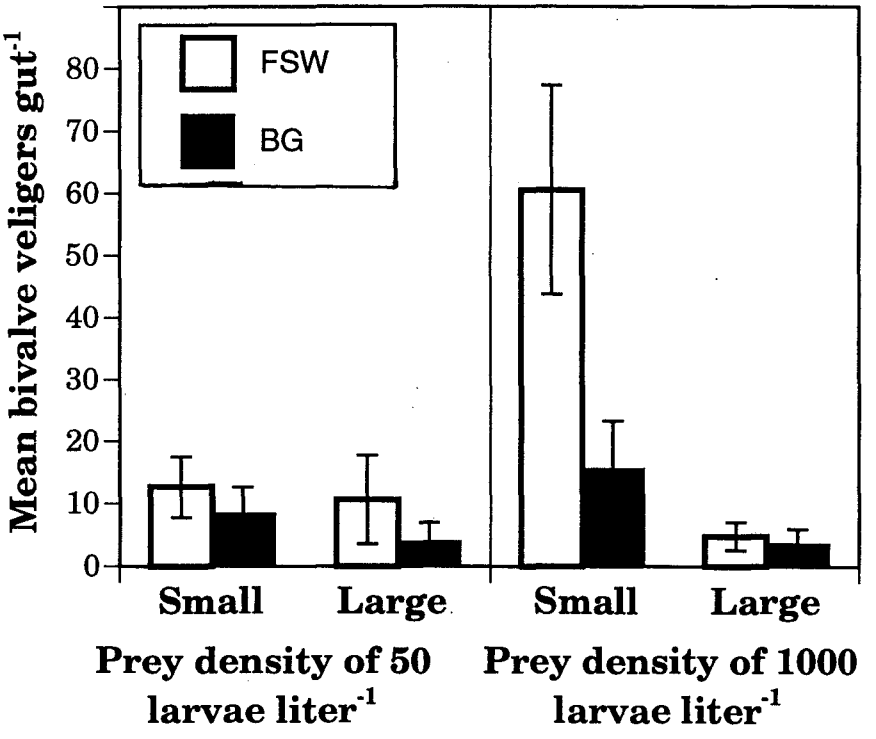


FIGURE 4. Mean number of bivalve veligers consumed by the hydromedusa *Proboscidactyla flavicirrata* in laboratory experiments. The treatments are: 53-µm-filtered seawater (FSW) with *small* bivalve veligers as prey; natural background plankton (BG) with *small* bivalve veligers as prey; 53-µm-filtered seawater (FSW) with *large* bivalve veligers as prey; natural background plankton (BG) with *large* bivalve veligers as prey. Error bars are 95% Confidence Intervals.

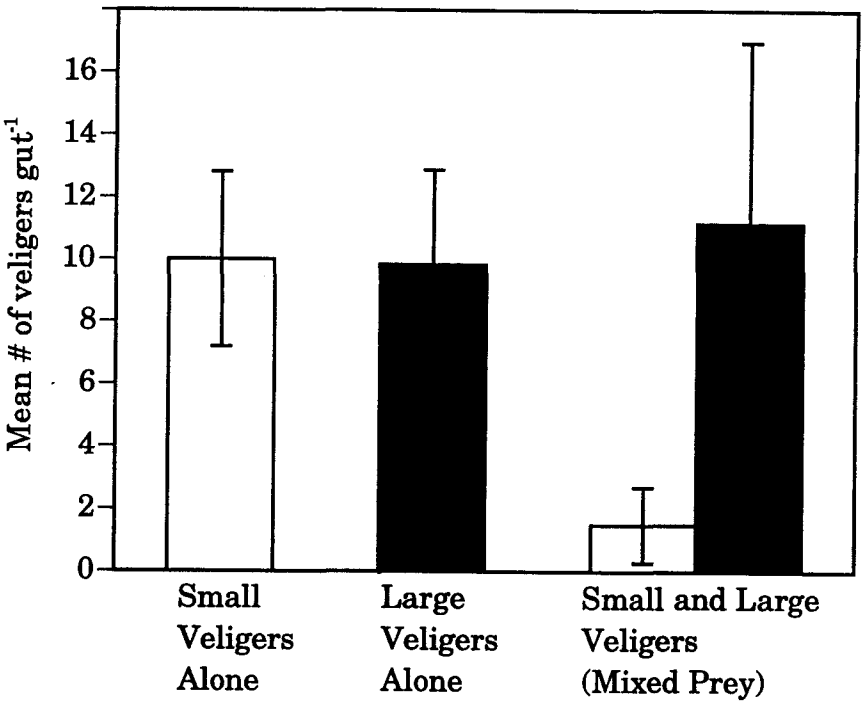


FIGURE 5. Laboratory predation by *Proboscidactyla flavicirrata* on small, large, and mixed (large and small) bivalve veligers. Each prey size was always presented at the near-natural high density of 50 larvae liter^{-1}. Error bars are 95% Confidence Intervals.

with predation in the following ways: predators may spend time handling or consuming background plankton, reducing encounters with larvae; predators may become satiated after consuming background plankton; background plankton may obscure larvae from detection or capture. Whatever the explanation, potentially low planktonic predation rates challenge what has become a paradigm in marine invertebrate life history theory—that predation on meroplanktonic invertebrate larvae is high.

We recognize that our experiments were only for 24 h, while many invertebrate larvae are in the plankton for weeks to months. Several experiments showed no predation in any replicate in 24 h. If we assume that, given another 24 h, a single predation event would have occurred, then instantaneous mortality would be -0.00125 day^{-1}. After 28 days in the plankton, this maximum estimate of mortality in these corrals results in a population loss of only 3.4%. Thus, of a single female's 1.0×10^5 fertilized offspring, 9.7×10^4 would survive predation and be available for recruitment.

The manipulation experiments provide clues to why predation was infrequent in the observational experiments. Many captured and seeded predators did prey on marked veligers and plutei when prey were presented at unnaturally high densities or in the absence of natural background plankton. Natural treatments mimicking the observational experiments, however, produced results consistent with observational experiments and reduced or eliminated predation. Johnson and Shanks (1997) and Johnson and Brink (1998) made similar observations in laboratory studies of

planktonic predation on echinoid embryos, plutei, barnacle nauplii, and bivalve veligers. Predation on echinoid and barnacle larvae by leptomedusae and anomuran zoeae, prevalent when prey were presented at unnaturally high densities or in filtered seawater, was reduced or eliminated under the most natural conditions (Johnson and Shanks, 1997). Likewise, the most natural laboratory conditions reduced or eliminated predation by 4 types of larval polychaetes on bivalve veligers (Johnson and Brink, 1998). An analogous study investigated the effects of nongrazeable particles, similes for natural background plankton, on prey capture by a tintinnid, a rotifer, a gastropod veliger, and young copepods and found that background could affect feeding rates (Hansen et al., 1991).

The simplest explanation for reduced predation at near-natural prey densities is that the predators and prey do not encounter one another at such low densities. Alternatives to low encounters include background plankton interference and changes in predator behavior at near-natural larval dentsities. We used the Gerritsen and Strickler (1977) model to estimate predator-prey encounters in corral experiments. This encounter model uses predator encounter radius R, prey density N_h, and predator and prey swimming speeds, v and u, respectively, to determine the number of encounters Z_p of a single predator with its prey for $v \geq u$:

$$Z_p = \frac{\pi R^2 N_h}{3} \left(\frac{u^2 + 3v^2}{v}\right)$$

This formula was used to estimate for each experiment the mean total encounters of marked larvae with potential predators in a corral. Potential predators are those which were seeded in corrals plus those background predators which might prey on larvae (e.g., relatively large animals). Potential predators along with estimates of their body radiuses and swimming speeds are presented in Table 7. For all predators, body radius was used as a minimum encounter radius. Some predators may sense prey at a distance using remote visual, chemical, or vibratory sensory mechanisms (Horridge and Boulton, 1967; Giguere and Northcote, 1987; Giske et al., 1994). Determination of remote encounter radiuses is complicated (Gerritsen and Strickler, 1977) and for simplicity in these estimates we used the minimum estimate of encounter radius—the radius of the predator's body. Estimated encounters are given for marked plutei (Table 8) and marked bivalve and gastropod veligers (Table 9) for each experiment. Encounter estimates given are the mean number of larvae expected to be consumed (if successful capture rate is 100%) corral^{-1} for each of the potential predators.

Corral totals are tallied for all potential predators. Because little is known about natural predator-prey relationships in the plankton, some predators may not have the ability to prey on these larval types. Unfortunately, not enough information is available to confidently exclude many questionable potential predators. We therefore offer two sets of estimates to evaluate potential predation by all possible predators as well as by a subset of more likely predators. Our subset of predators, used to

TABLE 7. Predator encounter radiuses (R) and predator and prey swimming speeds (v and u, respectively) used in calculating encounter estimates for Tables 9 and 10. 'R' is a minimum estimate of encounter radius—predator body radius.

Predators	R (cm)	v (cm/s)	Source for 'v'
Calanoid copepods	0.02	1.2	Strickler, pers. comm.
Harpacticoid copepods	0.02	0.6	personal obs.
Gammarid amphipods	0.04	1.0	personal obs.
Hyperiid amphipods	0.04	1.5	personal obs.
Cryptoniscid	0.01	0.6	personal obs.
Anomuran zoeae	0.03	0.9	Knudsen, 1960; Latz and Forward, 1977; Cronin and Forward, 1980; Forward and Cronin, 1980; Sulkin, 1973; Sulkin, 1975
Brachyuran zoea	0.03	0.9	Knudsen, 1960; Latz and Forward, 1977; Cronin and Forward, 1980; Forward and Cronin, 1980; Sulkin, 1973; Sulkin, 1975
Cumacea	0.06	2.0	personal obs.
Euphausid zoea	0.04	1.5	personal obs.
Obelia	0.02	0.5	approx. sinking rate
Phialidium	0.3	0.5	approx. sinking rate
Aglantha	0.2	2.0	personal obs.
Leptomedusa	0.03	0.5	approx. sinking rate

TABLE 7. Continued.

Predators	R (cm)	v (cm/s)	Source for 'v'
Rathkea	0.03	0.5	approx. sinking rate
Pleurobrachia	0.4	0.5	approx. sinking rate
Cydippid larvae	0.01	0.6	personal obs.
Proboscidactyla	0.3	0.5	approx. sinking rate
Sarsia	0.1	0.5	approx. sinking rate
Aurelia ephyra	0.06	0.2	personal obs.
Autolytus	0.02	1.9	personal obs.
Spionid metatrochophores	0.02	0.1	Konstantinova, 1969
Misc. metatrochophores	0.04	0.1	Konstantinova, 1969
Nectochaeta	0.03	0.1	Konstantinova, 1969
Magelona	0.02	0.3	personal obs.
Misc. trochophores	0.04	0.2	Konstantinova, 1969
Arctonöe trochophore	0.02	0.3	Pernet, pers. comm.
Chaetognaths	0.1	0.3	personal obs.
Larval fish	0.2	1.2	personal obs.

Prey		u	Source for 'u'
Pluteus larvae	N/A	0.015	personal obs.
Bivalve veliger larvae	N/A	0.03	Hidu & Haskin, 1978
Gastropod veliger larvae	N/A	0.09	Konstantinova, 1966

estimate conservative encounters, included only predators observed in the laboratory to consume the larvae.

Two observed predators, the heterotrophic dinoflagellate *N. scintillans* (experiments 3 and 6) and juveniles of the threespine stickleback *Gasterosteus aculeatus* (experiment 8), were potentially of great importance to their prey populations. These predators each have a life history unique from that of our other potential predators. In the case of *N. scintillans*, predation on veligers is yet another example of how protists can upset the paradigms of traditional food webs (Capriulo et al., 1991; Jeong, 1994; Glasgow et al., 1995). The threespine stickleback *G. aculeatus* is an effective predator on nauplii, but, even with 1 animal, was probably over-represented in corrals. *Noctiluca scintillans* predation in experiments 3 and 6 and *G. aculeatus* predation in experiment 8 are not addressed in Tables 9 and 10, but are examined in depth later in the discussion.

Mean estimated encounters for the observational experiments, where prey densities were intended to reflect natural densities, ranged from near 0 to as high as 269 (encounters of prey with large calanoid copepods in experiment 7) for only one predator type. The highest overall encounter rate was in experiment 7 where the calculations suggested 354 encounters. The fewest overall estimated encounters was 24.5 in experiment 5. Actual predation due to these predators was, however, completely absent in experiments 1, 2, 5, 7, and 9, and nearly absent in experiments 3, 4, 6, 8, and 10. The sum of observed predation on plutei for all experiments was 0.3 corral^{-1}. The sum of conservative estimates (i.e., estimates of encounters

TABLE 8. Estimates of marked pluteus encounters with predators in observational experiments. These numbers are corral^{-1} estimates (the mean of estimates from all replicates for a single experiment). Seeded predator names are underlined. Underlined *numbers* are the estimates of predators confirmed to prey on plutei under some conditions (e.g., in the laboratory, in filtered seawater, or with unnaturally high prey densities). Underlined numbers are used to calculate more conservative corral^{-1} encounter estimates based on the predators confirmed ability to prey on plutei. Known encounters of predators with marked plutei in corrals (i.e., observed predation) is given for comparison with mathematical estimates.

Estimated pluteus encounters with potential predators (corral^{-1})

	Experiment #								
Potential Predator	1	2	3	5	6	7	8	9	10
Copepods (Cal)	69	60	98	87	195	269	89	64	198
Copepods (Harp)	0	1	1	1	1	2	0	0	0
Amphipods (G)	0	0	0	0	0	0	0	0	0
Amphipods (H)	0	0	0	4	0	1	1	0	1
Anomuran zoeae	0	0	0	0	0	0	0	0	0
Brachyuran zoeae	0	0	0	0	0	0	0	1	1
Euphausiid zoeae	0	1	0	1	0	0	0	0	0
Obelia	1	0	1	0	0	0	0	0	0
Phialidium	0	10	0	0	12	30	0	4	0
Aglantha	0	0	0	0	0	20	0	10	0
Leptomedusa	0	12	0	0	0	1	0	3	0
Rathkea	0	0	0	0	0	0	0	0	0

TABLE 8. Continued.

Estimated pluteus encounters with potential predators (corral^{-1})									
	Experiment #								
Potential Predator	1	2	3	5	6	7	8	9	10
Proboscidactyla	0	0	0	20	20	10	0	0	24
Sarsia	0	0	0	0	0	0	0	0	0
Aurelia ephyrae	0	0	0	0	0	0	1	0	0
Pleurobrachia	18	9	13	0	0	0	0	7	22
Cydippid larvae	1	0	0	0	0	0	0	0	0
Autolytus	0	0	0	1	1	1	1	0	0
Spionids	0	0	0	0	0	2	0	0	0
Misc. metatrochs	31	10	16	7	26	3	1	0	0
Nectochaeta larvae	0	0	0	0	0	0	0	0	0
Magelona	1	1	0	0	0	0	0	0	0
Misc. trochophores	2	3	1	2	2	0	0	0	0
Arctonöe	0	0	0	0	0	0	0	0	0
Chaetognaths	0	0	0	0	1	0	0	0	0
Larval fish	0	0	0	0	0	5	0	0	0
Total estimated	122	107	130	122	257	354	93	90	247
Observed predation	0	0	0	0	0	0	0	0	0

Table 9. Estimates of marked veliger encounters with predators in observational experiments. These numbers are corral^{-1} estimates (the mean of estimates from all replicates for a single experiment). Seeded predator names are underlined. Underlined *numbers* are the estimates of predators confirmed to prey on the veligers under some conditions (e.g., in the laboratory, in filtered seawater, or with unnaturally high prey densities). Underlined numbers are used to calculate a more conservative corral^{-1} estimate of contact with potential predators. Known encounters of marked veligers with potential predators (i.e., observed predation) are given for easy comparison with mathematical estimates. Predation on bivalve veligers by *N. scintillans* in experiments 3 and 6 is later in the discussion.

Estimated encounters corral^{-1} of veliger larvae with potential predators

	Bivalve Veligers									Gastropod Veligers	
	Experiment #										
Potential predator	1	3	4	5	6	7	8	9	10	4	5
Copepods (Cal)	69	98	39	17	195	269	89	64	198	39	43
Copepods (Harp)	0	1	2	0	1	2	0	0	0	2	1
Amphipods (G)	0	0	0	0	0	0	0	0	0	0	0
Amphipods (H)	0	0	0	0	0	1	1	0	1	0	2
Anomuran zoeae	0	0	0	0	0	0	0	0	0	0	0
Brachyuran zoeae	0	0	0	0	0	0	0	1	1	0	0
Cumaceans	0	0	0	0	0	10	0	0	0	0	0
Euphausiid zoeae	0	0	0	0	0	0	0	0	0	0	0
Obelia	1	1	1	0	0	0	0	0	0	1	0
Phialidium	0	0	5	0	12	30	0	4	0	5	0

TABLE 9. Continued.

Estimated encounters corral^{-1} of veliger larvae with potential predators											
	Bivalve Veligers									Gastropod Veligers	
	Experiment #										
Potential predator	1	3	4	5	6	7	8	9	10	4	5
Aglantha	0	0	0	0	0	20	0	10	0	0	0
Leptomedusa	0	0	1	0	0	0	0	3	0	1	0
Rathkea	0	0	0	0	0	0	0	0	0	0	0
Proboscidactyla	0	0	10	4	20	10	0	0	24	10	10
Sarsia	0	0	1	0	0	0	0	0	0	1	0
Aurelia ephyrae	0	0	0	0	0	0	1	0	0	0	0
Pleurobrachia	18	13	0	0	0	0	0	7	22	0	0
Cydippid larvae	1	0	0	0	0	0	0	0	0	0	0
Autolytus	0	0	0	0	1	1	0	0	0	0	1
Spionids	0	0	0	0	0	2	0	0	0	0	0
Misc. metatrochs	32	17	5	1	26	3	1	0	0	6	4
Nectochaets	0	0	0	0	0	0	0	0	0	0	0
Magelona	1	0	0	0	0	0	0	0	0	0	0
Misc. trochs	2	1	0	0	2	0	0	0	0	0	1
Arctonöe	0	0	0	0	0	0	0	0	0	0	0

TABLE 9. Continued.

Estimated encounters corral^{-1} of veliger larvae with potential predators

	Bivalve Veligers									Gastropod Veligers	
	Experiment #										
Potential predator	1	3	4	5	6	7	8	9	10	4	5
Chaetognaths	0	0	0	0	1	0	0	0	0	0	0
Larval fish	0	0	0	0	0	5	0	0	0	0	0
Total estimated	123	131	63	25	258	354	93	90	247	64	62
Observed predation	0	0	0	0	0	0	0	0	1	0	0

with confirmed laboratory predators) of pluteus-predator encounters was 146 encounters corral^{-1}. Assuming estimates are correct, this indicates an average capture success rate of 0.21%. Similar comparisons for encounter estimates with bivalve veligers show that, for all predators excepting *N. scintillans*, average capture success rate is 0.54%.

Assuming swimming speeds and encounter radiuses used in calculations are accurate, then low predation may be due to low capture success rates, predator preferences, predator inability to consume larvae, or the effects of background plankton. For example, the hydromedusa *Proboscidactyla flavicirrata* is known, based upon gut content data, to be a predator of wild bivalve veligers (C. Mills, pers. communication). Estimates suggest that this medusa had many opportunities to consume (i.e., encounters with) marked veligers in corrals. In spite of the estimates, however, only 3 marked bivalve veligers were consumed (1 in experiment #4 and 2 in experiment #10). *P. flavicirrata*'s capture success rate is unknown. Consequently, it is possible that all estimated contacts were made and the predator failed to retain the prey. An alternative explanation is that *P. flavicirrata* prefers and somehow selects other prey. Wild bivalve veligers consumed by *P. flavicirrata* in corrals were much larger (250-350-μm) than the marked d-hinge oyster veligers (90-μm) added to corrals. Our laboratory experiments showed, *P. flavicirrata* feeds selectively on 280-μm veligers over 90-μm d-hinge veligers, supporting the idea that prey selection may be partially responsible for low predation on the added small marked veligers.

Some animals we have labeled as "potential predators" may actually lack the ability to consume the larvae in question. For example, it is unknown whether the abundant large calanoid copepods in corrals are omnivorous or strictly herbivorous. It is therefore possible that these potential predators, often responsible for over half of estimated encounters, would not prey on larvae under any circumstances.

Finally, It has been hypothesized that background plankton can reduce encounters between predators and larvae, obscure larvae from detection or capture, or serve as substitute food, occupying or satiating the predator (Johnson and Shanks, 1997). Indeed, the lack of predation in background plankton treatments (manipulation experiments) may reflect background plankton's influence. If so, planktonic encounter models should incorporate the potential effects of background plankton on encounters. Assuming that high encounter estimates are accurate, that all potential predators consume larvae given the opportunity, and that prey capture success is high, background plankton plays a significant role in reducing predation on invertebrate larvae.

Some predators did, however, consume wild unmarked larvae. Moderate predation was observed on bivalve veligers and more substantial predation was observed on the nauplius larvae of barnacles and copepods. Encounter estimates, analogous to those calculated for marked larvae, predict that predators had ample opportunity to consume wild larvae. Numbers of wild nauplii far exceeded the number of marked larvae in corrals. For example, the corral average of 23,464 copepod nauplii

(experiment 6) is more than 2 orders of magnitude greater than the marked pluteus and veliger densities (100 corral^{-1}). This probably reflects a natural disparity in the larval abundance; pluteus and veliger densities were never observed to be as high as the natural crustacean larva densities captured in the corrals. Consequently, simple encounters, but with a low capture success rate, could explain the higher predation on nauplius larvae by many predators. For example, a failed capture attempt on a pluteus larva may be that predator's only pluteus encounter. On the other hand, a failed attempt to capture a nauplius is sure to be only one of many opportunities.

In the experiment with the high nauplius densities quoted above, an average of 4 copepod nauplii corral^{-1} were consumed by *Phialidium* medusae. This apparently high predation, however, represents an instantaneous mortality of only -0.00017 day^{-1} because of the enormous population size. If this mortality were constant for 90 days in the plankton, only 1.5% of the nauplius larva population would be lost.

Extremely high prey abundance may influence predator behavior and the evolution of foraging, providing alternative explanations for the disparity between predation on plutei and veligers vs. copepod and barnacle nauplii. Predators may seek out prey and become adept at prey capture when prey are abundant (Mȯ́ok et al., 1960; Tinbergen, 1960; Gibb, 1962; Murton, 1971). Predators may evolve effective foraging and capture strategies specifically targeted towards prey which are abundant and consistently available in evolutionary time. Nauplii and other planktonic crustaceans can reach densities of 100,000's or more m^{-3} (e.g., Zimmerman,

1972). In addition to high abundance relative to echinoid and mollusc larvae, nauplii and other crustaceans swim with jerky movements, attracting the attention of visual and vibration-sensing predators (Horridge and Boulton, 1967; Feigenbaum and Reeve, 1977; Bailey and Yen, 1983; Yen, 1987; Yen and Nicoll, 1990; De Mott and Watson, 1991). Nauplii may have more predators and stronger predator-prey relationships than the other larval types investigated.

To help explore predation on wild larvae in corrals, we estimate encounters of several wild larval types and their predators (Table 10). Observed predation is also presented in Table 10 for comparison with encounter estimates. Once again, estimates of encounters are far higher than observations of predation. The same explanations offered for this observation with marked larvae also apply here. Support for an encounter-based explanation includes the relative increase in predation on nauplii when compared to the far less abundant veligers and plutei.

The stickleback *Gasterosteus aculeatus*, starved for 3 days and seeded as a predator in observational experiment 8, had a diet comprised almost entirely of crustacean larvae. Following the corral experiment, the guts of *G. aculeatus* contained an average of 58 copepod nauplii (sd=19.8) and 22 barnacle nauplii (sd≅6.3) each. Total nauplius abundance in the corrals was an average of 8640 and 43 for copepod and barnacle nauplii, respectively. Observed predation by *G. aculeatus* produced instantaneous mortality of -.0067 day^{-1} for copepod nauplii and -0.51 day^{-1} for barnacle nauplii. Therefore, mortality due to three-spined sticklebacks would result

Table 10. Encounter estimates of specified predators with wild invertebrate larvae in corral assemblages over 24 h. Predators, prey, and experiments scrutinized are based upon observations of predators consistently consuming one or more of these larval types. Observed predation is presented immediately below encounter estimates for comparison. 'X' indicates the predator was not present in that experiment (or, in some cases, that the predator was only present in one or two replicates).

		Experiment number					
Predators on copepod nauplii		3	4	5	6	7	10
Pleurobrachia	Estimates	285	X	X	X	X	771
	Mean observed	0	X	X	X	X	4
	Capture rate (%)	0	X	X	X	X	0
Proboscidactyla	Estimates	X	413	418	5419	1089	867
	Mean observed	X	0	0	2	1	0
	Capture rate (%)	X	0	0	0	0	0
Phialidium	Estimates	X	206	X	3387	3266	X
	Mean observed	X	1	X	4	1	X
	Capture rate (%)	X	1	X	0	0	X
Predators on barnacle nauplii							
Pleurobrachia	Estimates	164	X	X	X	X	7
	Mean observed	2	X	X	X	X	0
	Capture rate (%)	1	X	X	X	X	0

TABLE 10. Continued

		Experiment number					
Predators on barnacle nauplii		3	4	5	6	7	10
	Estimates	X	77	62	219	31	8
Proboscidactyla	Mean observed	X	0	0	0	0	0
	Capture rate (%)	X	0	0	0	0	0
	Estimates	X	39	X	137	94	X
Phialidium	Mean observed	X	0	X	0	0	X
	Capture rate (%)	X	0	X	0	0	X
Predators on gastropod veligers							
	Estimates	1	X	X	X	X	3
Pleurobrachia	Mean observed	0	X	X	X	X	0
	Capture rate (%)	0	X	X	X	X	0
	Estimates	X	10	4	6	1	3
Proboscidactyla	Mean observed	X	0	0	0	0	0
	Capture rate (%)	X	1	0	2	0	3
	Estimates	X	5	X	4	3	X
Phialidium	Mean observed	X	0	X	0	0	X
	Capture rate (%)	X	4	X	0	0	X

TABLE 10. Continued

Predators on bivalve veligers		Experiment number 3	4	5	6	7	10
Pleurobrachia	Estimates	15	X	X	X	X	9
	Mean observed	0	X	X	X	X	0
	Capture rate (%)	0	X	X	X	X	0
Proboscidactyla	Estimates	X	0	0	38	10	10
	Mean observed	X	1	1	1	0	1
	Capture rate (%)	X	—	—	2	1	8
Phialidium	Estimates	X	0	X	24	29	X
	Mean observed	X	1	X	0	1	X
	Capture rate (%)	X	—	X	0	4	X

in a 17% loss of copepod nauplii in the corral after 28 days. This is substantial predation, but does not compare to the impact of *G. aculeatus* on the corrals' barnacle nauplius populations—100% consumed in 8 to 9 days! Barnacle nauplii were strongly preferred over copepod nauplii based upon a comparison of gut and corral nauplius ratios (chi-square goodness-of-fit test, $\alpha = 0.0001$). Of course, major predators like *G. aculeatus* are not abundant compared to smaller potential predators we have examined. Also, though these *G. aculeatus* were small, they still swim quickly. Outside of an enclosure one might not expect fish such a *G. aculeatus* to be a threat due to short residence times.

Other predators have developed search strategies that favor crustacean prey. Chaetognaths and some copepods hunt by sensing vibrations in their prey (Horridge and Boulton, 1967; Feigenbaum and Reeve, 1977; Bailey and Yen, 1983; Yen, 1987; Yen and Nicoll, 1990; De Mott and Watson, 1991). Animals hunting in this manner may detect nauplius prey at relatively great distances, and yet ignore near-by ciliated swimmers such as veliger and pluteus larvae. Predation on large wild veligers and nauplii supports the idea that predation can be specific to larval type and vary with larval stage (Rumrill et al., 1985; Pennington et al., 1986).

Marine invertebrate life history evolution is influenced by planktonic mortality rates. Evidence of high planktonic survivorship weakens arguments which explain phylogenetic patterns of larval feeding in terms of high planktonic mortality. If it can be shown that circumstances commonly exist where planktonic larvae suffer little or no predation, then

other sources of mortality may be necessary to continue supporting evolutionary arguments for short planktonic period driven by high mortality. Alternative explanations for patterns of evolution in feeding mode are bolstered by observations of low predation. Low mortality in the plankton lends support to alternative explanations, such as the "use-it-or-lose-it" hypothesis.

Other discussions of life history theory are indirectly affected by the possibility that the plankton can be a low risk environment. One unresolved argument explaining the unique evolution of long planktonic larval periods is the possibility that dispersal reduces the risk of extinction (Strathmann, 1974; Strathmann, 1990). Long-lived planktonic larvae can be carried 10's or 100's of kilometers by ocean currents. In general, long-lived planktonic larvae undoubtedly experience greater dispersal than short-lived species because long-lived larvae are carried greater distances by ocean currents. Possible benefits of wider dispersal include more genetic variation within populations, less inbreeding, less need for simultaneous hermaphroditism, wider geographic range, and fewer extinctions (Strathmann, 1990). These potential long-term population benefits arising from long-distance dispersal might be overwhelmed and lost if predation rates in the plankton are high. If mortality in the plankton is low, however, then populations may be free to experience unfettered selection even for subtle benefits of remaining in the plankton for dispersal.

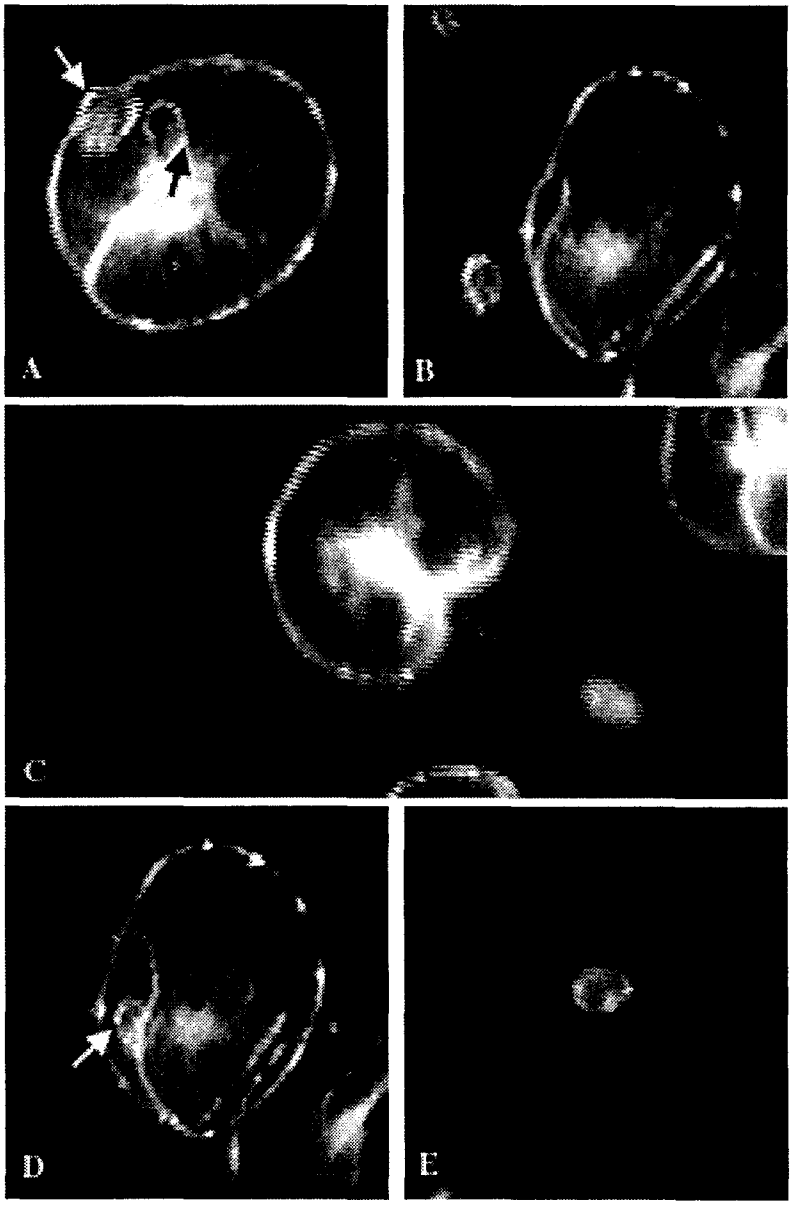
In this discussion of our results, we have until now discussed the majority of experiments which consistently yielded low or nonexistent

predation. Two experiments, however, revealed substantial predation on marked bivalve veligers by the heterotrophic dinoflagellate *Noctiluca scintillans*. This predation represented a substantial threat to the veliger population. *N. scintillans* is notorious for consuming a diverse range of prey (Enomoto, 1956; Prasad, 1958; Hattori, 1962; Kimor, 1979; Kirchner et al., 1996), including metazoans with longer body lengths than the predatory cell's diameter (Prasad, 1958). It is still some surprise, however, that this slow-moving protist can capture and engulf oyster larvae. Mean instantaneous mortality due to *N. scintillans* was -0.07 and -0.04 day^{-1} for experiments 3 and 6, respectively. These instantaneous mortality rates extrapolated over a 28 day planktonic period, a reasonable developmental time for many bivalves, would produce total population losses of 87% and 68%, respectively. We estimate encounters between *N. scintillans* and marked bivalve veligers using another Gerritsen and Strickler equation (Gerritsen and Strickler, 1977) prepared specifically for cases where predator swimming speed is less than that of its prey. For the swimming speed 'v' of *N. scintillans*, we use its ascension rate. Kiørboe and Titelman (1998) contend that ascension (~1 m h^{-1} or 0.028 cm s^{-1}) is the mechanism of active foraging for *N. scintillans*. They also state that *N. scintillans'* collects prey with a large mass of sticky mucus attached to the tentacle. Though *N. scintillans* feeds primarily on immobile prey such as diatoms (Enomoto, 1956; Prasad, 1958; Kiørboe and Titelman, 1998), there are also observations of predation by this dinoflagellate on metazoans (Enomoto, 1956; Prasad, 1958; Hattori, 1962; Kimor, 1979). We observed (Figure 6) *N.*

scintillans capturing bivalve veligers by 'raptorial' feeding with its modified tentacle (Omori and Hamner, 1982). The mucus at the tip of the tentacle (Kiørboe and Titelman, 1998) not only assists in capture, but may increase the encounter radius. The combined length of the tentacle and mucus string from the cell in Figure 6 is 170-μm. As cells ascend and forage, their orientation appears to be random when a long mucus strand is not present (Kiørboe and Titelman, 1998). We, therefore, consider the ascending cell to be oriented for capturing encountered prey only 50% of the time and divide estimated encounters in half to compensate. Prey density was the known density of marked veligers, 0.81 l^{-1}. The predatory dinoflagellate was at relatively low densities in these experiments, 4.5 and 3.1 cells $liter^{-1}$ for experiments 3 and 6, respectively. The resulting encounter estimates between *N. scintillans* and marked bivalve veligers were 0.69 and 0.47 $corral^{-1}$ for experiments 3 and 6, respectively. Assuming 100% capture success, extremely unlikely for this predator-prey combination, an encounter radius of 0.039 cm is required to accurately predict predation. Mucus strands several mm long and ~100-μm wide have been observed, but result in a downward orientation (i.e., the tentacle points downward) of ascending cells (Kiørboe and Titelman, 1998). This fishing strategy, analogous to the dragging of tentacles by many coelenterates, may require a different model for estimating encounters.

Another possibility to consider is that *N. scintillans* and bivalve veligers are concentrated together somewhere within the corral. It is possible that *N. scintillans* aggregates at the surface of the water column

FIGURE 6. Capture of a bivalve veliger by the heterotrophic dinoflagellate *Noctiluca scintillans*. A. The waving tentacle of *N. scintillans* first strikes the body of a newly encountered bivalve veliger. The veliger is indicated by a white arrow and the black arrow points to the base of the tentacle. B. After first contact the bivalve veliger changes direction and swims to escape a possible predator. C. Attached to the tentacle by an invisible strand of mucus, the swimming veliger actually drags the large cell through the water. D. Eventually the prey is reeled in and the tentacle can then manipulate the bivalve. The tentacle repeatedly strokes, drawing the veliger through a food groove, where it will eventually become wedged near the cytostome. E. The veligers is phagocytized at the cytostome. Cross-polarized light causes the calcium carbonate skeleton of the ingested veliger to stand out against the faded cell.


A
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due to the positive buoyancy of cells in seawater (Kesseler, 1966) and the dampened turbulence within corrals. Bivalve veligers concentrate at the surface in stagnant laboratory culture containers (personal observation). Sampling of different depths within the corrals to locate marked larvae indicated that oyster veligers do not aggregate at, and in fact may avoid, the surface. Whatever the mechanism of encounter, *N. scintillans* can consume bivalve larvae (Figure 6).

Large wild bivalve veligers (250 to 350-μm) were also present in experiments 3 and 6 at an average of 112 and 192 corral^{-1}, respectively, and slightly exceeded the numbers of marked oyster veligers. These bivalve larvae, however, were never observed inside of *N. scintillans* in spite of a deliberate examination of *N. scintillans* cell contents. It was not practical, however, to examine every *N. scintillans* cell. Therefore, predation rates rivaling those on marked bivalve veligers might apply to the wild veligers in corrals. *N. scintillans* only preying on small veligers, if true, might be explained by attributes unique to wild veligers. Bivalve larvae 250-μm or larger may be too large for ingestion by *N. scintillans*, though the cells in corrals ranged in size from 500 to 1000-μm. Another attribute related to increased size is greater swimming speed, which may give veligers the ability to pull free from the dinoflagellate's entrapping mucus.

A predator which may also be responsible for natural mortality of bivalve veligers is the hydromedusa *Proboscidactyla flavicirrata*, a consistent corral predator on marked veligers, which was second only to *N. scintillans* in its potential impact on veliger populations. This agrees with

unpublished data on the gut contents of 10 species of wild-caught hydromedusae in Friday Harbor, Washington, collected by Claudia Mills. *P. flavicirrata* was the only species that consumed mollusc larvae. Bivalve and gastropod veligers made up 65-80% of *P. flavicirrata* gut contents by number in the late Spring and 65% in the Autumn (C. Mills, unpubl. data). *P. flavicirrata* does not feed exclusively on larvae, however, and the presence of natural background plankton can significantly reduce predation compared to that observed in filtered seawater (Figure 4). Instantaneous mortality of marked bivalve larvae by *P. flavicirrata* was -.0025 day^{-1}, which could potentially result in a 7% reduction of a veliger population over a 28 day planktonic period. While this is not as dramatic as the potential predation by *N. scintillans*, it is substantial mortality with the potential to influence the numbers of larvae available for recruitment.

Other studies showing differential mortality with development revealed higher vulnerability in earlier stages, as opposed to the vulnerability in later stages observed in our experiments. Early vulnerability in early stage echinoids was attributed to a lack of the larval structures and behavior present in later stages (Rumrill et al., 1985; Pennington et al., 1986). Possible explanations for the reverse pattern observed with *P. flavicirrata* and bivalve veligers may be mechanics- or behavior-based. As a result of increased swimming speed or increased body diameter, larger bivalve veligers may contact tentacles more frequently. Another possible explanation of this predation includes a

behavioral or mechanical response of the medusa to the presence of larger veligers which precludes the capture of d-hinge veligers.

Predation in the corrals was variable. While many experiments showed little or no predation on benthic invertebrate larvae, the presence of *N. scintillans* and *P. flavicirrata* in corrals resulted in limited to high predation. Corral and laboratory experiments show that mortality can vary depending on the interactions between particular species. Larval mortality may also depend on developmental stage or size. The diversity of conditions and species that can influence mortality and cause variation in risk support the idea that the timing of larval release is an important part of invertebrate reproductive ecology and life history evolution (Giese and Kanatani, 1987; Morgan, 1995b). There are likely complex interactions between benthic adults, their planktonic larvae, other components of the plankton, and physical parameters. Loss of propagules may result from some combination of fertilization failure, low food availability, an adverse physical environment, predation, and unfavorable transport. These same factors may also indirectly affect larvae by affecting predators, competitors, and food sources. Deciphering the subtleties of these interactions promises to yield new and exciting discoveries and avenues of research.

Planktonic predation may not always explain the substantial loss which occurs between spawning and benthic recruitment. The fact remains, however, that benthic invertebrates spawn vast numbers of larvae, only a few of which recruit to the adult population. If we accede that there are cases where planktonic predation is not responsible, what is then

the source of great loss? Fertilization failure potentially results in huge losses of spawned eggs. Given the vast number of eggs typically spawned, however, even low fertilization rates produce many planktonic offspring. Some larvae may starve in the plankton, though investigations with soft-bodied larvae suggest that the ability to uptake DOM can prevent starvation (Olson and Olson, 1989). Lethal temperature extremes or fluctuations may directly or indirectly contribute to the mortality of larvae (Pechenik, 1987; Morgan, 1995b). Lack of a suitable settlement site can potentially prevent entire populations from recruiting (Jackson and Strathmann, 1981). For example, if the larvae of an intertidal species are transported permanently away from shore, then none of the population will find a proper place to settle. Finally, substantial post-settlement mortality may occur on the benthos before juveniles are large enough to be scored as recruits to the benthic population.

It is unlikely that any one phenomenon is always or solely responsible for larval mortality. Given the complexities of interaction between the benthos, other planktonic species, and ocean physics, investigators must conceive holistic approaches for measuring mortality. We determined survivorship in near-natural plankton assemblages using *in situ* corrals and methods which allowed us to identify predators. In our investigation, while *N. scintillans* was a significant predator in 2 of 10 experiments, the majority of observations showed that veliger and pluteus larvae suffered little or no predation. Thus, planktonic predation may not always be a major source of larval mortality.

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CHAPTER VI

CONCLUDING SUMMARY

This doctoral dissertation research investigated predation on planktonic invertebrate larvae under the most natural conditions possible in the laboratory and in the field. Laboratory experiments manipulated prey density and the presence of background plankton to determine their effect on predation rates. Results indicate that most predators examined do not prey on selected larvae when conditions are closest to natural (i.e., natural prey densities with background plankton present). Comparisons with unnaturally high prey density and filtered seawater treatments suggest that prey density and background plankton can strongly influence the outcome of predator-prey experiments. Therefore, laboratory experiments are more applicable to nature when natural prey densities and background plankton are used.

In situ experiments with near-natural plankton assemblages usually yielded low predation on marked echinoid, bivalve, and gastropod larvae. One predator of bivalve veligers, shown in two experiments to consume significant numbers of larvae, was the heterotrophic dinoflagellate *Noctiluca scintillans*. Other potential predators, none of which heavily impacted marked larval populations, included a variety of large crustaceans (e.g., copepods, amphipods, and zoeae), various

polychaetes, chaetognaths, fish, ctenophores, and hydromedusae. Recovery of marked larvae, whether unconsumed or in predator guts, was usually 100%. Predator gut contents indicate that crustaceans, including crustacean larvae, are the most common prey of many predators. Juveniles of the threespine stickleback *Gasterosteus aculeatus* consumed many crustaceans and seem to selectively feed on the nauplii of barnacles. While their impact on the wild nauplius populations captured in corrals was heavy, short residence times of *G. aculeatus* should greatly reduce the observed impact in nature.

Field observations and experiments provide a direct assessment of predation's importance for larvae in an experimental assemblage. The following strengths of experimental design contribute to the field data's value for examining predation as an important source of larval invertebrate mortality. Larval species examined as prey include 3 species of marked larvae and several other species of wild larvae representing 4 phyla. The data were collected from interactions with captured natural assemblages, each with a diversity of potential predators. Initial densities of marked larvae were known, allowing more powerful analysis of observations. Predators and prey interacted at natural densities, eliminating the possibility of artifactual behavior induced by abnormal densities. Marked larvae were easily visible in the guts of predators. Corral volumes far exceeded the practical capacity of laboratory containers and reduced artifacts resulting from small volumes. Finally, corral samples were collected and fixed immediately at the close of experiments, minimizing the

possibility of predation artifacts in the concentrated sample. These *in situ* studies are valuable for examining predation and mortality on planktonic invertebrate larvae.

Low predation rates observed in near-natural plankton assemblages may result from low predator-prey encounters. However, model estimates of encounter rates within the corrals indicate that numerous predator-prey encounters should have occurred. One explanation for low predation in spite of encounter estimates is the potential influence of background plankton on predation. Background plankton may serve as substitute food or reduce encounters. Corral manipulations of prey density and background plankton support laboratory findings that natural prey densities and background plankton can reduce or eliminate predation. While *N. scintillans* was a significant predator in 2 of 10 field experiments, the majority of observations from both the field and the laboratory showed that veliger and pluteus larvae suffered little or no predation under near-natural conditions. Thus, planktonic predation may not always be a major source of larval mortality.

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