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Predation by planktonic and benthic invertebrates on larvae of estuarine crabs

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Abstract: The ability of 11 species of planktonic and benthic invertebrates to prey on larvae of two estuarine species of crabs was determined in the laboratory. Ten of 11 of these predators with diverse feeding modes consumed crab larvae. Two of three planktonic invertebrates tested ate more larvae of the fiddler crab, *Uca minax* (LeConte, 1855), than larvae of the mud crab, *Rhithropanopeus harrisii* (Gould, 1841), and 4 of 8 benthic invertebrates consumed more *U. minax* larvae. None of the invertebrates ingested more *R. harrisii* than *U. minax* larvae. The larger size of *R. harrisii* larvae rather than their longer spines likely deterred most invertebrates, although differences in swimming speed, avoidance behavior or penetrability of the exoskeleton also may account for the differential predation on the two species. Available information on the distribution, abundance and feeding habits of potential predators of crab larvae was reviewed and synthesized with results of this study to determine if dispersal patterns of estuarine crabs likely have evolved in response to predictable trends in predation by invertebrates. Preliminary evidence for this hypothesis is equivocal but suggests that particular taxa of hydromedusae are more likely to influence dispersal of estuarine crabs than are other planktonic and benthic invertebrates.

Key words: Crab larva; Dispersal; Estuary; Invertebrate; Planktivory; Predation

INTRODUCTION

Thorson (1950) argued that predation was the major source of mortality for larvae of marine invertebrates. However, few studies have been designed specifically to address this hypothesis, and consequently predation remains as one of the least understood factors that affects the distribution and abundance of larvae (Young & Chia, 1987). Recently, several investigators have conducted simple feeding trials in the laboratory to identify invertebrate predators and possible antipredatory adaptations of larvae of molluscs, echinoderms, polychaetes, ascideans, bryozoans, hydrozoans and barnacles (see Young & Chia, 1987 for review; Steinberg & Kennedy, 1979; Rumrill et al., 1985; Young & Bingham, 1987; Young, 1988, 1989; Young & Cameron, 1989; Pennington, 1990; Purcell et al., 1991). Several investigators also have determined preferences of invertebrates in natural populations for invertebrate larvae (Lebour, 1922, 1923; Sebens & Koehl, 1984; Barange, 1988; Bingham & Walters, 1989).

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Marine invertebrates have a wide variety of feeding modes, and our limited knowledge of their preferences for larvae makes it difficult to assess the impact of predatory invertebrates on the population dynamics and evolution of life histories of marine organisms. Previous studies have suggested that planktivorous fishes may have a profound influence on the life histories of estuarine crabs (Morgan, 1989, 1990; Morgan & Christy, 1992a,b), but whether predatory invertebrates exert such influence is understood poorly. Predatory invertebrates potentially may affect larval morphologies, postcontact antipredatory behaviors of larvae, the timing of larval release, and vertical and horizontal migrations of larvae.

This study was undertaken as a first step towards determining if invertebrates are important predators of crab larvae. I have conducted simple feeding trials in the laboratory and reviewed available literature on the feeding habits and distribution and abundance patterns of potential predators of crab larvae (1) to identify major planktonic and benthic invertebrates that prey on larvae, (2) to determine whether these predators are more abundant in estuaries or coastal waters, (3) to determine the effectiveness of larval defenses against predatory invertebrates, and (4) to discuss the possible influence of predatory invertebrates on larval dispersal by estuarine crabs.

MATERIALS AND METHODS

The relative vulnerability of first instar *Uca minax* (LeConte, 1855) and *Rhithropanopeus harrisii* (Gould, 1841) larvae (Fig. 1) to 11 species of invertebrates with different feeding modes (Table I) was determined. Larvae were maintained in proximity to predators to reveal differences in the susceptibility of larvae that are chronically exposed to predatory invertebrates. The experiment was designed solely to determine

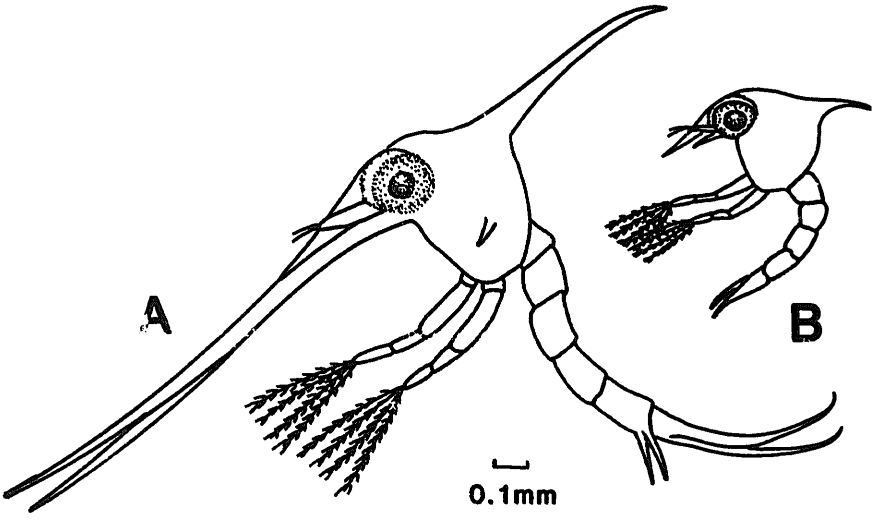

Fig. 1. First instar larvae of (A) *Rhithropanopeus harrisii* and (B) *Uca minax*.

TABLE I

Mean size and minimum and maximum size of 11 planktonic and benthic invertebrate predators, diameter of containers used for feeding trials, number of crab larvae fed of each species, and number of replicates. Measurements (M.): L, length; W, width; H, height; OW, operculum width; BW, base width; TW, distance for tip of tentacle to opposing tentacle tip.

Predator	Taxon or common name	Predator size (mm)			Dish (cm)	No. larvae	No. trials
		M.	Mean	Min–max			
Planktonic							
Sagitta hispida	Chaetognath	L:	7.5	7–8	11.5	20	19
Eutima mira	Hydromedusa	W:	5.2	5–8	11.5	20	15
Mnemiopsis leidyi	Ctenophore	L:	20	4–30	20.5,63	40,100	20
Benthic							
Styela plicata	Ascidean	H:	39	28–82	20.5	100	19
		W:	24	13–42			
Aiptasia pallida	Anemone	BW:	10	2–17	11.5	40	15
		TW	26	11–50			
Balanus amphitrite	Barnacle	OW:	8	6–10	11.5	20	19
		BW:	10	7–14			
		H:	9	7–14			
Caprella penantis	Amphipod	L:	5	3–8	11.5	10	18
Palaemonetes pugio	Shrimp	L:	27	22–30	11.5	40	20
Rhithropanopeus harrisii	Crab	W:	10	9–11	11.5	40	20
Geukensia demissa	Mussel	L:	56	48–75	11.5	40	10
Crassostrea virginica	Oyster	L:	64	56–82	11.5	40	10

the relative vulnerability of larvae to invertebrates and was not intended to simulate natural conditions. Reliable information on the relative effectiveness of morphological defenses of crab larvae was obtained from this experiment, but the forced proximity of predators and prey may have overestimated predation rates if larvae rely primarily on detection and avoidance of certain types of predators (see Forward, 1986). The small containers used as arenas also may have affected feeding rates of predators (de Lafontaine & Leggett, 1987), and investigators should not consider these data to be accurate estimates of absolute feeding rates on crab larvae.

These two species of crabs were chosen because of the different morphologies of their larvae. Larvae of *R. harrisii* are large and have long spines that apparently defend them against planktivorous fishes better than the short spines of small *U. minax* (Fig. 1; Morgan, 1987a, 1989, 1990). These species also were selected because adults inhabit the same area of the estuary and newly hatched larvae are exposed to the same suite of predators. The preferences of predators for only first instar larvae were determined because the two species have different dispersal patterns (Sandifer, 1975; Christy & Stancyk, 1982) that later may expose them to different assemblages of predators.

Ovigerous crabs and invertebrate predators were collected from the Newport and Neuse River estuaries, North Carolina. They were maintained individually in 20.5-cm culture dishes at 25 °C and 25‰ seawater and under a photoperiod of 12 h light:12 h dark. The size of containers and the number of larvae used in feeding trials depended on predator size (Table I). The volume of water held by 11.5, 20.5 and 63 cm containers was approximately 300 ml, 1.5 l and 19 l, respectively. Larvae also were fed to grass shrimp, *Palaemonetes pugio*, that were isolated in three 76 l (20 gal) aquariums. Predators were starved at least 1 day before experimentation. Newly hatched *U. minax* or *R. harrisii* larvae from single females were offered to predators that were isolated in containers. Half of the predators were fed larvae of one species and the others were fed larvae of the other species. On the following day, these predators were fed the same number of the opposite species of larvae. The same protocol was followed to determine if the long spines of *R. harrisii* larvae deter predation by 10 of these 11 species of invertebrates. In this experiment, the dorsal, rostral and antennal spines of *R. harrisii* larvae were amputated or left intact before larvae were fed to predators (see Morgan, 1989, for further details). In both sets of feeding trials, the number of prey remaining after 24 h was counted daily and compared by analysis of variance. Larvae of the two species were offered separately to predators to comply with statistical requirements for independence of prey selection (see Peterson & Renaud, 1989). To ensure that larvae were healthy during feeding trials, sibling larvae were held in three containers without predators for 24 h. Feeding trials were repeated if an average of more than one of 20 or two of 40 or more larvae died in these controls.

RESULTS

FEEDING TRIALS

A variety of invertebrates are capable of preying on crab larvae. Of the 11 species of invertebrates, only mussels did not consume crab larvae. Thus, all 3 planktonic invertebrates and 7 of 8 benthic invertebrates tested ate crab larvae.

Of the 10 species that consumed larvae, 6 ate more larvae of *U. minax* and none ate more *R. harrisii* larvae (Fig. 2, Table II). Two of the 3 planktonic invertebrates species (hydromedusa, chaetognath) ate more *U. minax* than *R. harrisii* larvae, but ctenophores readily consumed both species of larvae. Four of the seven benthic invertebrates also ate more *U. minax* than *R. harrisii* larvae (ascidean, anemone, barnacle, oyster), and the remainder preyed on each species in similar amounts (caprellid amphipod, grass shrimp, mud crab). Many larvae were not eaten by ascideans, oysters and mussels but were entangled in mucus, rejected as pseudofeces, and later died.

Although fewer *R. harrisii* larvae were eaten by predators, the elongate spines of these larvae were not effective in deterring most of the predators tested. Only hydrozoan medusae ate significantly fewer spined than despined larvae (Fig. 2, see Morgan, 1989, for ANOVA table).

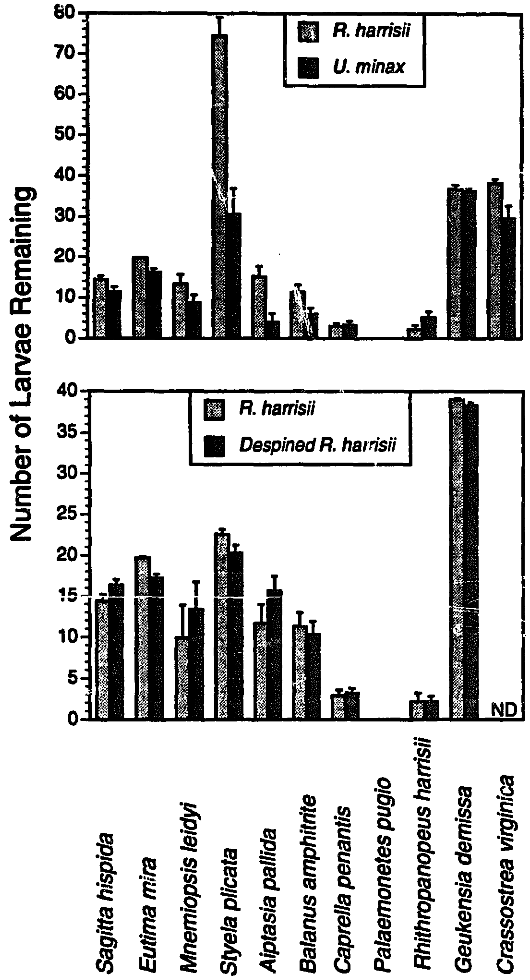

Fig. 2. Mean number of surviving *Rhithropanopeus harrisii* and *Uca minax* larvae fed to 11 planktonic and benthic invertebrates (top), and despined and spined *R. harrisii* larvae fed to 10 of the 11 species of invertebrates (bottom). ND, no data.

TABLE II

Analysis of variance of the number of *U. minax* and *R. harrisii* larvae eaten by invertebrates.

Predator	df	MS	*F*	*p*
Sagitta hispida	1,18	79.61	4.31	0.045
Eutima mira	1,14	90.13	17.54	0.0003
Mnemiopsis leidyi	1,19	207.59	2.34	0.14
Styela plicata	1,18	18348.03	31.51	0.0001
Aiptasia pallida	1,14	886.60	10.89	0.003
Balanus amphitrite	1,18	208.45	5.88	0.02
Caprella penantis	1,17	1.00	0.10	0.76
Rhithropanopeus harrisii	1,19	87.03	3.33	0.08
Geukensia demissa	1,9	1.13	0.19	0.67
Crassostrea virginica	1,9	378.45	7.17	0.02

TABLE III

Occurrence of predation on crab larvae or megalopae by planktonic and benthic predators in the plankton (Field) or laboratory. The occurrence of predation is expressed as [a] the percentage of larvae in gut contents or [b] the number of larvae per predator. When quantitative values were not available, qualitative estimates of the frequency of occurrence of larvae in guts are presented. 'Present' indicates that larvae were eaten, but the frequency of occurrence of larvae in guts was not estimated. Whether laboratory feeding trials (Lab) or gut content analysis of predators that were collected from the field (Field) were conducted also is indicated.

Predator	Occurrence	Study	Ref.
Pelagic predators			
Cnidaria			
Hydromedusae			
Aequorea victoria	1.4%[a]	Field	Purcell & Mills, 1988
	0.1–0.6[b]	Field	Purcell, 1989
Bougainvillia principes	0.6%[a]	Field	Purcell & Mills, 1988
Cosmetira pilosella	occasional	Field	Lebour, 1922, 1923
Eutonina indicans	0.5%[a]	Field	Purcell & Mills, 1988
Obelia geniculata	occasional	Field	Lebour, 1922, 1923
Phialidium gregarium	0.5%[a]	Field	McCormick, 1969
Phialidium hemisphericum	occasional	Field	Lebour, 1922, 1923
Phialidium sp.	1.8%[a]	Field	Purcell & Mills, 1988
Proboscidactyla flavicirrata	14.3%[a]	Field	McCormick, 1969
	present	Lab	Spencer, 1975
Polyorchis penicillatus	7.3%[a]	Field	Arkett, 1984
	1.7%[a]	Field	McCormick, 1969
Rathkea octopunctata	occasional	Field	Lebour, 1922, 1923
Staurophora mertensi	occasional	Field	Fraser, 1969
Turris pileata	common	Field	Lebour, 1922, 1923
Velella velella	1.5%[a]	Field	Bieri, 1961
Siphonophora			
Agalmea elegans	present	Field	Biggs, 1977
Agalmea okeni	present	Lab	Biggs, 1976
Rosacea cymbiformis	present	Lab & Field	Biggs, 1976, 1977
Scyphomedusae			
Aurelia aurita ephyrae	occasional	Lab	Lebour, 1922
	1.1[b]	Field	Lebour, 1923
Cyanea capillata	present	Lab	Fraser, 1969
	present	Lab	Fancett & Jenkins, 1988
Chrysaora isosceles	occasional	Lab & Field	Lebour, 1923
Stomolophus meleagris	common	Field	Phillips et al., 1969
Cubomedusae			
Carybdea alata	present	?	Larson, 1976
Carybdea marsupialis	present	?	Larson, 1976
Chiropsalmus quadrimanus	common	Field	Phillips et al., 1969
Ctenophora			
Pleurobrachia pileus	occasional	Field	Lebour, 1922, 1923
Crustacea			
Copepoda			
Unidentified	present	Lab	Knudsen, 1960
Stomatopoda			
Squilla empusa larvae & postlarvae	present	Lab	pers. obs.

TABLE III

(Continued)

Predator	Occurrence	Study	Ref.
Decapoda			
Rhithropanopeus harrisii			
larvae & megalopae	present	Lab	pers. obs.
Callinectes sapidus megalopae	present	Lab	pers. obs.
Benthic predators			
Cnidaria			
Tubularia sp.	present	Lab	Mackie, 1966

PREDATION ON CRAB LARVAE BY PLANKTONIC INVERTEBRATES

Much of our knowledge of the feeding habits of planktonic invertebrates has come from feeding trials using copepods or fish larvae. However, crab larvae have been offered to planktonic invertebrates in the laboratory, and gut content analyses of predators that have been taken from natural populations reveal their dietary preferences in the field (Table III). These studies permit tentative inferences about the potential impact of planktonic invertebrates on crab larvae.

Most reports of predation on crab larvae have been obtained by examining the gut contents of planktonic predators during the summer when crab larvae are abundant in estuaries and nearshore coastal waters (Woodmansee, 1958; Christy & Stancyk, 1982; Williams & Collins, 1986; Morgan, 1990). These studies show that crab larvae are preyed on by 14 species of hydromedusae, 4 scyphomedusae, 3 cubomedusae, 3 siphonophores, 1 ctenophore, 1 copepod and larvae of 1 species of stomatopod and 2 species of crabs (Table III). Several of the major groups of planktonic predators have not been shown to feed on crab larvae, including chaetognaths, hyperiid amphipods, euphausiids, and decapod shrimps. However, 13 other planktonic invertebrate specimens have been reported to feed on unidentified decapod zoeae, which may include crab larvae. These include 5 species of hydromedusae (Lebour, 1922; McCormick, 1969; Phillips et al., 1969; Larson, 1987), 1 scyphomedusa (Thiel, 1964), 1 ctenophore (Lebour, 1922, 1923), 1 chaetognath (Reeve, 1966), 1 hyperiid amphipod (Sheader & Evans, 1975), 1 euphausiid (Holt & Tattersal, 1905), and 3 decapod shrimps (Aizawa, 1974; Omori, 1974).

Gelatinous zooplankters comprise 86% of planktonic invertebrates that have been reported to feed on crab larvae and 76% of those reported to feed on crab larvae or unspecified decapod larvae. Although these predators may have received the most attention by investigators, abundant gelatinous zooplankters may indeed be most likely to affect larval populations in estuaries. Miller & Williams (1972) found that the total volume of ctenophores (*Mnemiopsis leidyi*, *Beroe ovata*), hydromedusae (*Nemopsis bachei*) and scyphomedusae (*Chrysaora quinquecirrha*, *Cyanea capitella*, *Aurelia aurita*) in the Patuxent River estuary was 23–39 $\mathrm{l \cdot m^{-3}}$ during summer when crab larvae are produced, and concluded that the standing crop of zooplankton was insufficient to sustain the number of ctenophores and jellyfishes.

Ctenophores

Decimation of estuarine zooplankton populations, including various invertebrate larvae, has been correlated with blooms of *Mnemiopsis leidyi* and *M. mccradyi* (Herman et al., 1968; Miller, 1974; Miller & Williams, 1972; Burrell & Van Engel, 1976; Reeve & Walter, 1978; Kremer, 1979; Deason & Smayda, 1982; Feigenbaum & Kelly, 1984). Along the east coast of North America, these blooms consistently occur during summer when crabs release larvae. Although *M. leidyi* occurs in coastal waters (Bishop, 1972), they are most abundant in upper estuaries (2–23‰) (Schwartz & Chestnut, 1974) where they sometimes fill plankton nets (pers. obs.). The devastating impact of *M. leidyi* on zooplankton populations not only results from their high abundance, but their high clearance rates, which are proportional to the abundance of prey (Kremer, 1979; Monteleone & Dugay, 1988). Populations of the coastal ctenophore, *Pleurobrachia pileus*, are less dense than estuarine populations of ctenophores, but they also can severely reduce standing crops of zooplankton (Reeve & Walter, 1978; Frank, 1986). However, *P. pileus* and other gelatinous predators do not appear to control the summer decline in copepod abundance in Dutch coastal waters (Miller & Daan, 1989).

Although *M. leidyi* can decimate standing crops of zooplankton in the upper estuary, they rarely consume crab larvae (Cronin et al., 1962; Burrell & van Engel, 1976), including *R. harrisii* and *U. minax* larvae, which occur abundantly there (Morgan, 1990). Both *R. harrisii* and *U. minax* larvae have a shadow response that enables them to avoid contact with ctenophores (Herrnkind, 1968; Forward, 1986), which readily ingest them during feeding trials in the laboratory. Some larvae are eaten or become inescapably trapped in mucus, while others escape by crawling from the stomodeum and swimming away (Madin, 1988). *R. harrisii*, and many other crab larvae, flare their antennal spines upon contact with predators (Morgan, 1987b, 1989). The antennal spines of *R. harrisii* larvae were flared inside the guts of ctenophores (pers. obs.), but whether this enhances escape by reducing contact with colloblast cells before ingestion is unclear.

The other abundant estuarine ctenophore, *Beroe ovata*, feeds primarily on ctenophores (Swanberg, 1974). Its congener, *B. cucumis*, also rarely eats decapod larvae and primarily preys on copepods (Lebour, 1922, 1923). *P. pileus* chiefly preys on copepods and fish larvae in coastal waters and occasionally feeds on crab larvae (Table III).

Hydromedusae

Hydrozoan medusae are very abundant in estuaries (Cronin et al., 1962; Phillips et al., 1969; Morgan, 1990), and may decimate standing stocks of zooplankton (Zelickman et al., 1969; Fulton & Wear, 1985). Of the hydromedusae, Limnomedusae, Trachymedusae and most Anthomedusae primarily prey on crustaceans and other hard-bodied prey (Purcell & Mills, 1988). Other investigators also have found that hydromedusae commonly prey on crustacean larvae from natural populations (Cronin et al., 1962; Phillips et al., 1969). Indeed, 14 species of hydromedusae feed on crab larvae (Table III). Crab larvae comprised the major portion of the diet of *Turris pileata* in 2 consecutive years, and *Proboscidactyla flavicirrata* and *Polyorchis penicillatus* commonly feed on crab larvae (Table III). Five additional species have been reported to eat decapod larvae of which *Sarsia princeps* and *N. bachei* appear to do so frequently (Lebour, 1922; McCormick, 1969; Phillips et al., 1969; Larson, 1987). Some hydromedusae may have a considerable impact on crab larvae because they attain high densities and consume as many as 50 *Artemia* nauplii per hour (Phillips et al., 1969).

Scyphomedusae

Sea nettles, *C. quinquecirrha*, and winter jellyfish, *Cyanea capitella*, are abundant in upper estuaries where *R. harrisii*, *U. minax* and other estuarine crabs reproduce (Cargo & Schultz, 1967; Herman et al., 1968; Miller & Williams, 1972; Miller, 1974). Although they primarily eat *M. leidyi* and fish larvae (Cargo & Schultz, 1967; Phillips et al., 1969; Turner, 1982), *C. capitella* sometimes feeds on crab larvae and *C. quinquecirrha* preys on crustacean zooplankton when ctenophores are absent (Kelly, 1983). The moon jellyfish, *Aurelia aurita*, is common during the summer in lower estuaries and coastal waters, where it primarily feeds on copepods and fish larvae, but it also occasionally eats decapod larvae (Fraser, 1969; Feigenbaum & Kelly, 1984; Moller, 1984; Van der Veer & Oorthuysen, 1985). Lebour (1922) observed that *A. aurita* would eat crab larvae only in the absence of its preferred prey, which are gelatinous zooplankters, chaetognaths and fish larvae. This may explain why Lebour (1923) found that crab larvae were the commonest prey of these medusae during 1 of 2 years when 63% of medusae contained crab larvae. Even then, only about one crab larva was found in each medusa (Table III). Cabbageheads, *Stomolophus meleagris*, produce copious strands of nematocyst-laden mucus instead of tentacles to capture prey, and it feeds almost exclusively on crab larvae, copepods and other small crustaceans in coastal waters (Phillips et al., 1969). Another rhyzostomid medusa, *Rhizostoma octopus*, reportedly has preyed on decapod larvae (Thiel, 1964).

Cubomedusae and siphonophores

Sea wasps and siphonophores occur more abundantly in coastal waters than estuaries (Phillips et al., 1969; Biggs, 1977). Calycophore and physonect siphonophores are predisposed by their array of nematocysts to prey on crustaceans (Purcell & Mills, 1988), and 3 species of siphonophores are known to prey on crab larvae (Table III). Three species of sea wasps also eat crab larvae or megalopae, including *Chiropsalmus quadrimanus*, which does so commonly (Table III).

Chaetognaths

Chaetognaths are transported from the continental shelf into the estuary, and therefore are comparatively rare in upper estuaries (Cronin et al., 1962; Grant, 1977; Morgan, 1990). However, even in the lower estuary where chaetognaths feed overwhelmingly on copepods (Sullivan, 1980; Edmunds et al., 1983; Fulton, 1984), they may be of minor trophic significance (Canino & Grant, 1985). *Sagitta hispida* feed on decapod larvae in the laboratory (Reeve, 1966), but chaetognaths have not been observed to prey on crab larvae in situ.

Crustaceans

A variety of crustaceans may prey on crab larvae although there is little evidence that they do so. Copepods are the most abundant zooplankters in the sea and potentially may affect densities of crab larvae. Although many copepods are primarily herbivores, some switch to carnivory when algal abundances are low and densities of prey are high (Landry, 1981; Kleppel et al., 1988). However, these copepods prey on microzooplankton, including copepod nauplii and ciliates (Paffenhofer & Knowles, 1980; Gifford & Dagg, 1988), and may not be important predators of larger crab larvae. There also are several groups of predacious copepods that eat fish larvae in the laboratory (Landry, 1978; Bailey, 1984), but only 1 unidentified species has been reported to consume crab larvae during feeding trials (Knudsen, 1960).

Hyperiid amphipods are voracious predators that are common in coastal waters. They mainly prey on copepods, chaetognaths, fish larvae and appendicularians (Sheader & Evans, 1975; Westernhagen et al., 1979; Yamashita et al., 1985). Decapod larvae occasionally have been found in the gut contents of hyperiid amphipods, but they were not consumed abundantly (Sheader & Evans, 1975).

Dense swarms of omnivorous euphausiids and decapod shrimps occur in coastal and oceanic waters (Omori, 1974; Simmard et al., 1986; Stuart, 1986). Euphausiids and sergestids both readily eat fish larvae in the laboratory (Bailey, 1984; Stuart, 1986), but so far, copepods, euphausiids and amphipods are the primary prey in natural populations (Holt & Tattersall, 1905; Aizawa, 1974; Omori, 1974). Euphausiids and shrimps occasionally eat unidentified decapod larvae in the plankton (Aizawa, 1974; Omori, 1974) and might prey abundantly on crab larvae when encountered.

Mysids exert considerable influence on estuarine and freshwater zooplankton communities (Fulton, 1982; Nero & Sprules, 1986). However, mysids may be unlikely predators of crab larvae because they did not prey on them when encountered in the plankton (Fulton, 1982).

Finally, approximately 70% of benthic invertebrates have planktotrophic larvae (Thorson, 1950) and many are carnivorous. However, only crustacean larvae are noted predators of crab larvae. Large crab larvae eat smaller ones and stomatopod larvae and crab megalopae also were observed to consume crab larvae in the laboratory (pers. obs.). Lebour (1923) also noted that megalopae feed on decapod larvae. Crab larvae and megalopae are especially abundant in estuaries but also are prevalent in coastal waters (Christy & Stancyk, 1982, Truesdale & Andryszak, 1983; Roff et al., 1986; Lindley, 1987). Large swarms of stomatopod larvae occur in coastal waters where they voraciously feed on decapod larvae (Lebour, 1924; Komai, 1932; Morgan, 1977) and probably prey abundantly on crab larvae.

PREDATION ON CRAB LARVAE BY BENTHIC INVERTEBRATES

Most benthic invertebrates are filter-feeders that select particles of a particular size. Dense aggregations of benthic invertebrates, such as barnacles, mussels, oysters, polychaetes, sand dollars, ascideans, anemones and corals, may filter many of the larvae that pass over them (e.g., Glynn, 1973). Larvae that are filtered from the water may either be ingested or rejected as pseudofeces, but in either case larvae usually die (Mileikovsky, 1974; pers. obs. for *Styela plicata*, *Crassostrea virginica*). Larval predation by benthic invertebrates, including oysters, mussels and other bivalves, brachiopods, barnacles, hydroids, sponges, polychaetes, and amphipods, is sometimes great (see Mileikovsky, 1974 for review of early references; Timko, 1979; Commito, 1982; Oliver et al., 1982; Ambrose, 1984; Barange, 1988). These invertebrates in nature have been reported to prey on larvae of molluscs, barnacles, annelids, shrimps, echinoderms, bryozoans and ascideans, but not on crab larvae. Anthozoans also did not consume crab larvae that were present in the plankton (Sebens & Koehl, 1984). Only one benthic predator, a hydrozoan, has been reported to prey on crab larvae (Table III), although scyphistomae of *Aurelia aurita* sometimes eat unidentified decapod larvae (Lebour, 1923).

DISCUSSION

DIFFERENTIAL VULNERABILITY OF LARVAE

Larvae of *U. minax* were more vulnerable than *R. harrisii* to most of the 11 predators tested. Differences in spine length between larvae of the two species generally do not appear to explain the differential predation rates, because the elongate spines of *R. harrisii* larvae only deterred one of 10 of these species of predatory invertebrates. Spines effectively increase the size of larvae; however, *R. harrisii* larvae may be too large for most of these predators to handle even without their spines. *Uca* larvae simply may be easier for small predators, such as hydromedusae, chaetognaths and barnacles, and those with narrow siphons, such as ascideans and oysters, to capture and ingest. The overall size of larvae appears to be especially important to tiny hydrozoan medusae, *Eutima mira*, which ate more despined than spined *R. harrisii* larvae.

Differences in swimming speed, avoidance behavior, or penetrability of the exoskeleton also may account for the differential predation on these larvae. *Uca* larvae are smaller and swim twice as fast as *R. harrisii* larvae (Herrnkind, 1968; Latz & Forward,

1977) and may encounter predators more often (Gerritsen & Strickler, 1977). However, the proximity of predators and larvae during feeding trials minimized these differences. *Rhithropanopeus harrisii* larvae also could have a stronger escape response that might enable them to break free of hydromedusae and anemones (Fulton & Wear, 1985) or the feeding currents of filter feeding benthic invertebrates; however, differences in predator avoidance behavior between larvae of the two species were not observed. Finally, if long spines and thicker exoskeletons are correlated in larvae, as in freshwater rotifers and cladocerans (Williamson, 1983; Dodson, 1984), then nematocysts of the anemone and hydromedusa may have been less able to penetrate the armor of *R. harrisii* than *U. minax* larvae (Fulton & Wear, 1985; Schwartz & Hebert, 1989). However, it is more likely that the longer spines of *R. harrisii* are better at preventing nematocysts from contacting the body (Arkett, 1984).

The chitinous mouthparts and chelae of grass shrimp, mud crabs and amphipods, could easily handle the larval armor of both species. Grass shrimp swam off the bottom to pursue larvae and collected all 40 of them with their chelate maxillipeds and mouthparts within several minutes regardless of whether they were held in shallow culture dishes or deeper aquariums. Mud crabs appeared to rely only on their mouthparts for capturing larvae. Mud crabs and many other species of crabs use their mouthparts to capture their newly-hatched larvae in the laboratory (pers. obs.). Hermit crabs and lobsters also use mouthparts to filter plankters from surrounding waters (Jatzke, 1970; Gerlach et al., 1976). Even though grass shrimps, crabs and lobsters opportunistically prey on benthic organisms and scavenge (Williams, 1984; Posey & Hines, 1991), they may supplement their diets with larvae and other zooplankters that might easily be overlooked during examinations of gut contents.

Similar numbers of *U. minax* and *R. harrisii* larvae survived encounters with ctenophores and mussels during feeding trials. Larvae of both species readily adhered to the colloblast cells of ctenophores and were carried to the distensible coelenteron. Mussels prey on small, weak-swimming invertebrate larvae (Mileikovsky, 1974; Cowden et al., 1984) but did not feed readily on either species of larvae.

POTENTIAL IMPACT OF PREDATORY INVERTEBRATES ON LARVAL MORPHOLOGY AND DISPERSAL

Estuarine crabs and other invertebrates show two broad patterns of dispersal: larvae are either retained in estuaries throughout development by vertically migrating between inflowing and outflowing currents, or they ascend into outflowing surface currents and are exported to coastal waters where they develop before reinvading estuaries as postlarvae (Bousfield, 1955; Wood & Hargis, 1971; Sandifer, 1975; Christy & Stancyk, 1982). Whether or not larvae develop entirely within estuaries may depend upon their relative vulnerabilities to predation, starvation and physiological stress (Strathmann, 1982). Strathmann (1982) and Morgan (1987b) have argued against starvation and physiological stress as selective forces that maintain these disparate dispersal patterns, but predation may influence dispersal if the following criteria are met. Major predators of crab larvae must (1) be more abundant in estuaries than offshore when larvae develop and (2) prefer larvae of species that are exported to coastal waters to those that develop entirely in estuaries (Strathmann, 1982). Previous evidence suggests that differential vulnerability of crab larvae to planktivorous fishes may determine the dispersal patterns and timing of larval release of estuarine crabs (Morgan, 1987a,b, 1990; Morgan & Christy, 1992a,b). Spine length, body size and visibility determine the susceptibility of crab larvae to planktivorous fishes (Morgan 1987a, 1989, 1990; Morgan & Christy, 1992a), which generally appear to be more abundant in estuaries than coastal waters (see Morgan, 1990).

Predatory invertebrates either may intensify or counter selection for these dispersal patterns, depending on their preferences for larvae, distributions and abundances. Because most invertebrates do not rely on vision to capture prey, larval morphologies primarily will determine predation rates on larvae of various species. However, the elongate, numerous spines of crab larvae were ineffective against most invertebrate predators and were very effective against larval and adult fishes (Morgan, 1987a, 1989). This suggests that the primary morphological defenses of crab larvae may have evolved specifically to deter planktivorous fishes rather than predatory invertebrates (Morgan, 1989). Therefore, the question arises whether invertebrates are as influential as planktivorous fishes in shaping other aspects of the life histories of estuarine crabs.

The impact of predatory invertebrates on larvae of estuarine crabs cannot be evaluated fully until their preferences for larvae, feeding rates and population densities are known for estuaries and coastal waters. Unfortunately, even the identity of major predators of crab larvae remains uncertain. Thus far, most invertebrate predators of crab larvae appear to be gelatinous zooplankters. Nearly all of previously reported instances of predation on crab larvae have been by gelatinous zooplankters, and ctenophores and hydromedusae both preyed on larvae during the present study. Most of these gelatinous zooplankters bloom during summer in temperate zone estuaries and may devastate zooplankton populations including crab larvae. However, predation rates may be reduced on especially vulnerable larvae that migrate from estuaries to coastal waters to develop.

Most groups of gelatinous zooplankters presently fail to satisfy all the criteria established by Strathmann (1982). First, most gelatinous zooplankters, including ctenophores, scyphomedusae, cubomedusae and siphonophores, may feed on crab larvae only incidentally. A shadow response apparently enables crab larvae to avoid fatal contacts with ctenophores (Forward, 1986). Presumably, other gelatinous zooplankters also induce a shadow response, which partially may explain why crab larvae have not been reported to occur abundantly in the guts of these predators. Second, when the effectiveness of the shadow response was diminished by maintaining larvae in proximity to predators during feeding trials, ctenophores fed nonselectively on larvae. It is not known if most other types of gelatinous zooplankters would discriminate among crab larvae of various species, but presently it would seem unlikely. Third, several of the groups that commonly prey on crab larvae, including siphonophores, cubomedusae and rhizostomae scyphomedusae (cabbageheads), are more abundant in coastal waters than estuaries.

Only hydromedusae currently appear to be a major selective force in the evolution of larval dispersal patterns of estuarine crabs. First, hydromedusae occur in very high densities in estuaries and bays during summer when crab larvae develop (Cronin et al., 1962; Phillips et al., 1969; Miller & Williams, 1972; Morgan, 1990). Second, hydromedusae comprised nearly all the invertebrates that previously were reported to prey on crab larvae. Several groups of hydromedusae primarily feed on crustaceans (Purcell & Mills, 1988), and three member species commonly ate crab larvae. Indeed, *T. pileata* preferred crab larvae during summer months of a 2-yr study. It is unclear why hydromedusae consume more crab larvae in the plankton than other gelatinous zooplankters; however, many hydromedusae simply may be too small to reduce light intensities sufficiently to initiate a shadow response by larvae. Third, hydromedusae ate more *U. minax* larvae, which are exported to coastal waters, than *R. harrisii* larvae, which develop entirely in estuaries. Larvae of species that are retained in estuaries typically have longer spines and larger bodies than larvae that are flushed from estuaries (Morgan, 1987a, 1990), and the small size of many hydromedusae generally may make it more difficult for them to prey on crab larvae that develop entirely in estuaries.

The two types of dispersal patterns probably cannot be attributed to differential predation pressure exerted on larvae of estuarine crabs by chaetognaths and crustacean zooplankters. Although *S. hispida* ate more *U. minax* than *R. harrisii* larvae in the laboratory, chaetognaths do not appear to be important predators of larvae in the plankton (Lebour, 1922, 1923; Reeve, 1966; Sullivan, 1980; Edmunds et al., 1983; Fulton, 1984); nor are they more abundant in estuaries than offshore. Decapod larvae have been eaten incidentally by crustacean zooplankters, including copepods, hyperiid amphipods, euphausiids, decapod shrimps and stomatopod larvae, but these predators also are generally at least as abundant offshore as in estuaries.

Benthic invertebrates may intensify selection for export or retention of larvae by estuarine crabs, although little supporting evidence exists for this hypothesis. Strathmann (1982) determined that the benthos is as hazardous as the water column for zooplankters and that estuarine waters are more hazardous than coastal waters by comparing instantaneous mortality rates of copepods from each environment. Vulnerable larvae may reduce contact with benthic invertebrates by remaining in seaward flowing surface waters as they migrate from shallow upper estuaries to the continental shelves, where the density of macroinvertebrates at least in some places may be less (Wenner et al., 1983; Dauer et al., 1984; Gaston, 1987). Once in deeper coastal waters, larvae that progressively descend as they develop may be less likely to encounter benthic predators. Alternatively, larvae, and especially later larval instars, frequent bottom currents to be retained in estuaries and often may encounter predatory benthic invertebrates. Results of feeding trials indicated that a variety of benthic invertebrates are capable of feeding on larvae; 7 of 8 species of invertebrates tested ate crab larvae.

Furthermore, four of these species preyed on more *U. minax* than *R. harrisii* larvae, so that larvae of at least one estuarine species that develops in coastal waters are more susceptible to benthic predators than larvae that are retained in estuaries. Nevertheless, crab larvae rarely have been found in the guts of benthic invertebrates in natural populations. This includes anemones and ascideans that readily filtered crab larvae from the water in the laboratory but avoided decapod larvae in the field (Sebens & Koehl, 1984; Bingham & Walters, 1989). Only 1 species of cnidarian has been reported to have preyed on crab larvae in the field. Thus, the behavior of crab larvae and the distribution patterns and feeding trials of benthic invertebrates indicate that benthic invertebrates may intensify selection for export and retention of larvae if they prey on them in the field.

In summary, initial evidence that dispersal patterns of estuarine crabs has evolved in response to predictable trends in the distribution and abundance of planktivorous invertebrates and vulnerability of larvae to predation is equivocal. Although differential preferences of predatory invertebrates for larvae of one pair of representative species of estuarine crabs were demonstrated, the hypothesis that larval export to coastal waters reduces invertebrate predation on vulnerable larvae cannot be substantiated without also showing that natural populations of major invertebrate predators of crab larvae (1) prefer larvae of exported species, and (2) are more abundant in estuaries than coastal waters.

The wide diversity of feeding modes possessed by the many potential predators of larvae makes it difficult to evaluate this complex hypothesis. Although considerable work remains to be done, determining preferences of naturally-occurring invertebrates for estuarine crab larvae would provide a major step toward resolving this issue. Estuarine populations of planktivorous invertebrates should prey abundantly on larvae and prefer first instar crab larvae that are flushed from estuaries to enforce selection for these dispersal patterns.

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