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## IMPACT OF PLANKTIVOROUS FISHES ON DISPERSAL, HATCHING, AND MORPHOLOGY OF ESTUARINE CRAB LARVAE<sup>1</sup>

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**Abstract.** The effect of planktivory on life history patterns of estuarine crabs was studied by determining preferences of common estuarine fishes for crab larvae in the laboratory and the upper Newport River estuary, North Carolina. Plankton samples (68) and fishes were collected from an upstream and a downstream site, on spring and neap low tides, and during the day and night. Over 99.6% of the plankters collected were decapod larvae, copepods, barnacle nauplii, and cyprids. Predominant fishes in the upper estuary were silversides, *Menidia menidia*, anchovies, *Anchoa mitchelli*, and killifish, *Fundulus heteroclitus*, as is typical for other estuaries on the east coast of the United States. Gut contents of 1861 fishes 15–100 mm long were analyzed. Silversides and anchovies preyed upon crab larvae more often than did killifish, and are most likely to influence the life history patterns of crabs inhabiting upper estuaries.

Fishes that eat crab larvae are more abundant in estuaries than coastal waters during summer. Fishes in the estuary and the laboratory showed strikingly similar preferences for prey. In order of descending preference, natural populations of fishes preferred copepods, crab larvae that are exported from estuaries (*Uca*, *Sesarma cinereum*), and decapod larvae that develop in estuaries (*Sesarma reticulatum*, *Palaemonetes*, *Rhithropanopeus harrisi*). In the laboratory, juvenile and adult silversides and killifish preferred *Artemia* nauplii to crab larvae, they fed randomly on *Uca* larvae, and they avoided *R. harrisi* larvae. These planktivores preferred zoeae that are exported to coastal waters over those that are retained because exported larvae are smaller and have shorter spines. While the large size and spines of retained larvae protect them from their predators in estuaries, vulnerable zoeae may emigrate from estuaries to coastal waters because the rate of encounter with predators offshore is less than in estuaries.

The risk of predation also appears to vary spatially and temporally within the estuary. Predation generally was greatest upstream in shallow, narrow areas of the upper estuary on diurnal neap tides. The spatial gradient in predation apparently was due largely to the great abundance of fishes, and particularly small zooplanktivorous fishes, occurring upstream. In contrast, temporal patterns of planktivory were not due to differences in fish size and abundance, but to diurnal foraging of fishes and changes in the availability of prey. Resident zooplankters generally were preyed upon more during neap tides, perhaps because they remained nearer to the substrate on spring tides to prevent being swept downstream. *Uca* and *S. cinereum* zoeae were eaten in similar numbers during diurnal neap and spring tides because most zoeae had been transported downstream before dawn when fishes resumed feeding.

Estuarine crabs may have responded to predictable trends in planktivory by dispersing newly hatched zoeae downstream on nocturnal ebb tides, regardless of where larvae develop. Small vulnerable zoeae eventually disperse offshore, whereas large well-defended zoeae apparently remain in estuaries. Peak hatching on spring high tides may not have evolved to expedite transport to coastal waters, but instead may facilitate dispersal of larvae of semiterrestrial crabs from the shore where mortality may be high. This study suggests that predation pressure exerted by planktivorous fishes is predictable in time and space, and the timing of larval release, dispersal patterns, and larval morphologies of estuarine crabs have evolved together to reduce the risk of planktivory regardless of whether zoeae develop offshore or in estuaries.

*Key words:* crab larvae; dispersal; hatching rhythms; life histories of estuarine crabs; migration; planktivorous fishes; predation; spines.

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## INTRODUCTION

A large body of literature suggests that the morphologies and behaviors of freshwater plankters are affected by predators (Zaret 1980). The morphological and post-encounter behavioral defenses (Cowden et al. 1984, Pennington and Chia 1984, Morgan 1987a, 1989), vertical and horizontal positions (Christy 1982, Morgan 1987a), and hatching rhythms (Johannes 1978, Christy 1982, 1986, Frank and Leggett 1982) of marine larvae also may be determined by predators. Here I suggest that the morphologies, behaviors, dispersal patterns, and hatching rhythms of estuarine crab larvae are coupled to reduce the risk of fish predation, which is predictable in time and space.

Many fishes enter productive estuaries to feed and spawn during summer when crab larvae hatch and develop, so that fishes generally are more abundant in estuaries than they are offshore (Percy and Richards 1962, Weinstein 1979, Kneib 1984a, Rozas and Hackney 1984, Talbot and Able 1984, see Morgan 1986). The biomass of fishes in tidal pools and shoals of upper estuaries during summer ranges from 54.5 to 152.4 g/m<sup>2</sup> (Nixon and Oviatt 1973, Crabtree and Dean 1982), but is only 1.84–6.33 g/m<sup>2</sup> in lower, deeper portions of estuaries (Oviatt and Nixon 1973, Turner and Johnson 1973), and 0.28–3.10 g/m<sup>2</sup> in the South Atlantic Bight (Wenner et al. 1979, Sedberry and Van Dolah 1984). The gradient in fish abundance may result largely from the distribution of young fishes. Young fishes predominate in low-salinity marshes and tidal creeks, and they progressively move downstream as they develop (Percy and Richards 1962, McErlean et al. 1972, Subrahmanyam and Drake 1975, Weinstein 1979, Crabtree and Dean 1982, Rozas and Hackney 1984, Talbot and Able 1984). Young fishes also tend to be planktivorous regardless of their dietary preferences as adults (Hunter 1980, Turner 1984). Thus, not only are fishes much more abundant in estuaries than coastal waters during summer; they are more likely to be planktivorous and may have a considerable impact on estuarine zooplankters (Thayer et al. 1974, Bengston 1984, Fulton 1985).

If fishes are important predators of crab larvae, then the life histories of crabs may reflect spatial and temporal patterns of planktivory. Estuarine crabs display two broad patterns of larval dispersal: zoeae 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 (Pinschmidt 1963, Sandifer 1975, Christy and Stancyk 1982, Cronin 1982, Truesdale and Andryszak 1983, Epifanio et al. 1984, Hsueh 1988). Because predation is predictably greater in estuaries than offshore, dispersal to the coastal ocean may be characteristic of larvae that are vulnerable to planktivores, whereas retention may be

common among better defended zoeae (Christy 1982, Strathmann 1982). At least some vulnerable zoeae are known to hatch on spring high tides and at night (Forward 1987). Such timing of hatching would lead to rapid seaward transport of zoeae on high-amplitude nocturnal ebb tides (Christy 1982) when few planktivorous fishes feed (Hunter 1980, Lazzaro 1987). Thus, the timing of hatching and the dispersal of vulnerable zoeae may aid their escape from abundant planktivores that feed during the day in upper estuaries.

I demonstrate that juvenile and adult fishes in laboratory feeding trials and natural populations prefer zoeae that are exported from estuaries to those that develop within estuaries. I also show that the risk of planktivory is greatest during diurnal neap tides at the head of an estuary, thus allowing retention in upper estuaries only of well-defended larvae and enforcing selection for flushing of vulnerable newly hatched larvae downstream on nocturnal ebb tides.

## METHODS AND MATERIALS

*Feeding trials in the laboratory*

Ovigerous fiddler crabs, *Uca minax*, were collected from their burrows immediately prior to spring tides. Ovigerous mud crabs, *Rhithropanopeus harrisi*, were lured by oyster shells into traps constructed of wire mesh. Silversides, *Menidia menidia*, and killifish, *Fundulus heteroclitus*, were seined from marshes and tidal creeks, respectively. All organisms were collected from the Neuse and Newport River estuaries, North Carolina.

Ovigerous crabs were placed in 19-cm culture dishes with filtered water of 25‰ salinity. Crabs were maintained in incubators at 25°C under a 12:12 light:dark photoperiod until larvae hatched.

Fishes 20, 40, 60, and 80 mm standard length (SL) were placed singly in 10-L circular tanks, and allowed to adjust to laboratory conditions for several days prior to experimentation. Three hundred crab larvae of one species were fed to each fish along with enough *Artemia* nauplii to ensure that 10–40% of the nauplii remained after a 6–8 h period, as determined in preliminary feeding trials. This procedure enabled hungry fish to graze indiscriminately initially, while enough prey remained to reflect their preference subsequently. Prey remaining at the conclusion of feeding trials were collected on a sieve (250- $\mu$ m mesh). Then the number of zoeae were counted and the number of *Artemia* nauplii were estimated by subsampling five aliquots of nauplii in a known volume of seawater. On the following day fish were fed 300 larvae of the alternate species together with the same quantity of *Artemia* nauplii. Ten replicates for each size class of fish species were conducted, except only two were performed for 20-mm silversides.

Fishes and plankton were collected in June and July from Newport Narrows at the head of the Newport River estuary and a quarter of the way (3.3 km) down

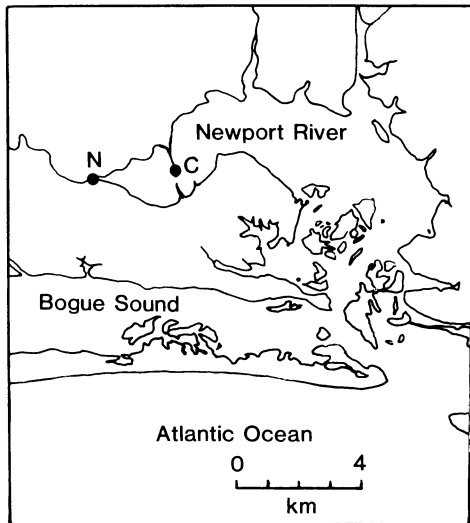


FIG. 1. Sampling sites (N = Newport Narrows, C = Cross Rocks) in the Newport River estuary, North Carolina.

the estuary at Cross Rocks (Fig. 1). Samples were collected on diurnal spring and neap low tides at both sites. Samples were collected at low tides because large numbers of fishes could be seined reliably then. Samples also were collected at night at the downstream location to determine whether or not fishes fed nocturnally. A tidal creek just upstream from the Cross Rocks site also was sampled once on a nocturnal spring high tide. At least five plankton tows and three fish seinings were taken during each sampling period. Fishes were collected with a 16-m seine with 7-mm mesh. Plankton was collected using a plankton net with a 30-cm diameter mouth and 300- $\mu$ m mesh. The length of plankton tows was gauged using a flowmeter attached inside the mouth of the net, so that  $\approx 2$  m<sup>3</sup> of water were sampled. A plastic sieve (7-mm mesh) was attached inside the mouth of the collecting cup to exclude ctenophores. The sieve probably also excluded other large zooplankters, such as fish, mysids, and shrimp, resulting in an underestimate of their numbers. All samples were preserved with formaldehyde.

Plankton samples were split using a Folsom plankton splitter, the most precise device for subsampling invertebrate plankters (Van Guelpen et al. 1982). One-eighth of the sample was counted under a dissecting microscope. Decapod zoeae were identified to species and instar, and other organisms were classified into broad taxa, e.g., copepods.

*Menidia menidia*, *F. heteroclitus*, and the bay anchovy, *Anchoa mitchelli*, were the three most abundant species of fishes at the two sites. Guts of 30 specimens were analyzed, if available, for each of four size classes of these fishes: 15–25, 35–45, 55–65, and >65 mm SL. A total of 1861 guts were examined. After rinsing fishes in freshwater, stomachs were removed, slit longitudinally, and the contents washed into a watch glass marked with a grid. All prey items were enumerated. Decapod

zoeae were identified to species and instar, and other taxa were lumped into broad categories as described above.

The amount of time prey were retained in the guts of silversides was determined. Twenty-four fish 40–60 mm SL were maintained in 10-L containers at 28° and 25‰ seawater, and fed 10 000 *Artemia* nauplii 24 h prior to the beginning of the experiment. Then fish were allowed to feed for 1 h on field-caught plankton, which primarily contained copepods and *Uca* larvae. Approximately 1000 copepods and *Uca* larvae were fed to fish. Guts of three fish were examined immediately after the cessation of the 1-h feeding period, and seven fish each were examined 1, 3.5, and 5 h later.

The preferences of fishes for prey in the field and laboratory were determined using Chesson's (1983) index of electivity. Preferences of fishes for prey in the field were calculated using a form of the index that assumed that the reduction in food density due to consumption was insignificant compared to the amount of food available. Because food was depleted by fishes in laboratory feeding trials, electivities were calculated using a form of the index that did not assume constant food densities. I determined electivities of natural pop-

TABLE 1. Densities of organisms collected in plankton tows from the Newport River estuary, North Carolina.

Taxon	Density (no./m <sup>3</sup> )	
	Mean	SE
<i>Uca</i> zoeae	8195.07	911.53
Copepoda	4541.22	392.66
Barnacle nauplii	1168.05	146.66
Hydromedusae	401.74	87.21
<i>Sesarma reticulatum</i> zoeae I	87.38	11.46
Cyprids	60.09	6.06
<i>Rhithropanopeus harrisi</i> zoeae I	49.40	7.47
<i>Palaemonetes</i> zoeae I–X	37.21	3.00
<i>Sesarma cinereum</i> zoeae I	14.64	3.19
Gastropod veligers and postlarvae	12.77	3.22
<i>R. harrisi</i> zoeae II	9.21	2.14
Ostracoda	7.15	6.65
Polychaete setigers	6.99	1.12
Fish larvae	6.03	1.30
Mysidacea	4.33	0.99
<i>R. harrisi</i> zoeae III	3.66	1.02
Nematoda	3.52	1.17
Juvenile shrimp	2.70	0.67
<i>Mnemiopsis leidyi</i>	2.62	0.82
Foraminifera	2.54	0.71
Amphipoda	2.04	1.17
<i>R. harrisi</i> zoeae IV	1.81	0.53
Polychaeta	1.33	0.33
Isopoda	1.26	0.41
Hymenoptera and Coleoptera	1.23	0.39
Chaetognatha	1.08	0.27
<i>S. reticulatum</i> zoeae II	0.86	0.34
<i>Pinnotheres ostreum</i> zoeae I	0.73	0.27
Brachyuran megalopae	0.50	0.22
Anomuran zoeae	0.43	0.26
<i>Pinnixa</i> zoeae	0.40	0.16
Cumacea	0.28	0.14
<i>Panopeus herbstii</i> zoeae	0.28	0.27
<i>S. reticulatum</i> zoeae III	0.20	0.18
<i>Lucifer faxoni</i>	0.05	0.05

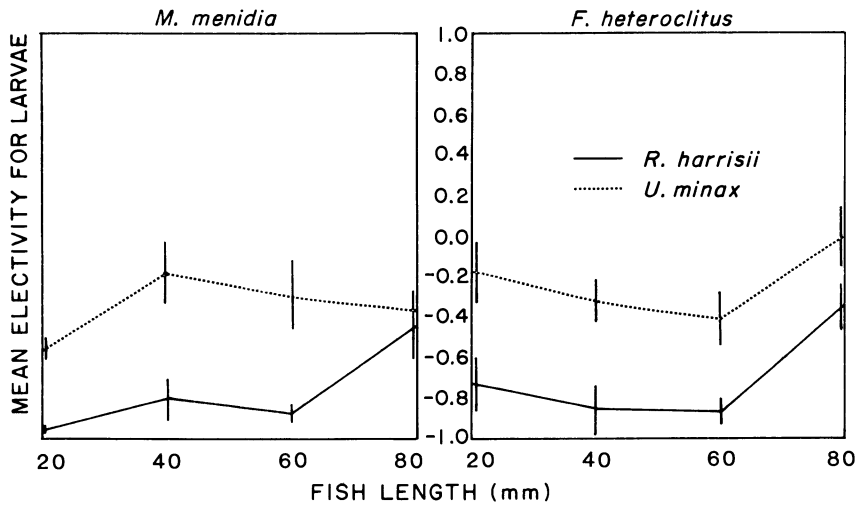


FIG. 2. Mean electivities of *Menidia menidia* and *Fundulus heteroclitus* 20–80 mm long for *Rhithropanopeus harrisii* zoeae, *Uca minax* zoeae, and *Artemia* nauplii in the laboratory.

ulations of fishes for the nine most abundant plankters (exclusive of gelatinous zooplankters, which were not eaten), which accounted for 99.6% of all zooplankters collected (Table 1). The remaining plankters were summed and grouped into a 10th category composed primarily of demersal and benthic prey, which probably were underrepresented in the plankton samples. Such prey were included in analyses because large fishes consumed many demersal prey and their exclusion appeared to bias electivities more than their inclusion.

The *G* test was used to analyze differences in lengths of fishes collected at upstream vs. downstream sites, but all other data were analyzed using the analysis of variance. Data were log-transformed prior to analysis when necessary to meet the assumptions of the analysis of variance.

## RESULTS

### *Vulnerability of crab larvae to planktivorous fishes*

In laboratory feeding trials, all size classes of silversides and killifish fed preferentially on *Artemia* nauplii, and avoided both species of crab larvae (as indicated by the negative values shown in Fig. 2). Of those crab larvae eaten, all size classes of both fishes (except perhaps 80-mm silversides) preferred *U. minax* larvae that are exported from estuaries to *R. harrisii* larvae that are retained (Fig. 2, Table 2).

Mean numbers of plankters per cubic metre collected from the upper Newport River estuary are listed in Table 1. Only first-instar larvae of the crabs *Uca* spp. and *Sesarma cinereum* were present in the upper estuary, indicating that larvae of these species dispersed downstream. However, all larval instars of the crabs *R. harrisii* and *Sesarma reticulatum* and the grass shrimp *Palaemonetes* spp. were present in the upper estuary.

*Menidia menidia*, *Fundulus heteroclitus*, and *Anchoa mitchelli* accounted for nearly all fish collected, but small numbers of other species also were collected (Table 3). The preferences of all size classes of fishes combined for the 10 prey categories were ranked and are presented in Table 4. Overall, the three most abundant species of fishes preferred larvae that are exported from estuaries and non-decapod plankters to larvae that are retained in estuaries throughout development.

Small fishes generally were more likely to eat crab larvae than were large fishes. Fishes <45 mm consumed and preferred more small prey including copepods, first-instar *Uca* larvae, barnacle nauplii, cyprids, and first-instar *S. reticulatum* larvae, and fishes >55 mm preferred large prey ("others"), including fishes, shrimps, and insects (Fig. 3, Table 5). Small silversides preferred barnacle nauplii and cyprids, and large silversides preferred first-instar *S. cinereum*, *Palaemonetes*, and "others." Large silversides preferred these prey not only because they are capable of capturing larger prey, but because they primarily occur

TABLE 2. Analyses of variance of electivities of *Menidia menidia* and *Fundulus heteroclitus* for *Rhithropanopeus harrisii* vs. *Uca minax* zoeae, in the laboratory in the presence of *Artemia* nauplii. Significance levels: \*  $P = .05$ , \*\*  $P = .01$ , \*\*\*  $P = .001$ .

Source	df	MS	F
<i>M. menidia</i>			
Zoeae	1	0.4259	27.1274***
Fish length	3	0.0515	3.2803*
Z × F	3	0.0738	4.7006**
Error	56	0.0157	
<i>F. heteroclitus</i>			
Zoeae	1	1.0720	75.2178***
Fish length	3	0.2294	16.0984***
Z × F	3	0.0178	1.24989
Error	77	0.0143	

TABLE 3. List of fishes collected at the Newport Narrows (upstream) and Cross Rocks (downstream) sites, Newport River estuary, North Carolina.

Species	Newport Narrows	Cross Rocks
<i>Menidia menidia</i>	X	X
<i>Anchoa mitchelli</i>	X	X
<i>Fundulus heteroclitus</i>	X	X
<i>Fundulus majalis</i>		X
<i>Mugil cephalus</i>	X	X
<i>Leiostomus xanthurus</i>	X	X
<i>Micropogonius undulatus</i>	X	X
<i>Cynoscion</i> spp.	X	X
<i>Bairdiella chrysura</i>	X	X
<i>Lagodon rhomboides</i>	X	X
<i>Paralichthys</i> spp.	X	X
<i>Trinectes maculatus</i>	X	X
<i>Symphurus plagiatus</i>	X	X
<i>Strongylura marina</i>	X	X
<i>Pomatomus saltatrix</i>	X	X
<i>Opsanus tau</i>		X
<i>Anguilla rostrata</i>		X
<i>Syngnathus</i> spp.		X
<i>Synodus foetens</i>		X
<i>Selene vomer</i>		X
<i>Caranx hippos</i>		X
<i>Monocanthus hispidus</i>		X
Gobiidae		X

downstream with these prey. Small anchovies preferred copepods, first-instar *Uca* larvae, and barnacle nauplii, and large anchovies preferred first-instar larvae of *R. harrisi* and "others."

Like silversides and anchovies, small killifish preferred smaller prey such as copepods and barnacle nauplii, and large killifish preferred "others" (Fig. 3, Table 5). However, killifish were smaller than the other fishes when they switched to larger prey. Killifish did not consume *R. harrisi*, *S. reticulatum*, or *S. cinereum* larvae, and *Uca* and *Palaemonetes* larvae were rarely eaten. Thus, killifish are much less likely to eat larvae than are silversides and anchovies.

Fishes also frequently consumed large amounts of detritus. Detritus was present in 85% of killifish guts and 32% of silverside guts at the upstream site, and 6 and 1% of their guts, respectively, at the downstream

location. Only 1 of 501 anchovies examined from both sites contained detritus. The guts of most of the killifish were packed with detritus, and frequently contained very few prey. Silversides did not fill their guts with detritus as often as did killifish, so that prey were usually more abundant.

#### *Spatial and temporal risk of planktivory in estuaries*

More species of fishes were collected downstream than upstream, but fishes appeared to be much more abundant upstream. The abundance of fishes was not quantified due to inherent difficulties of comparing collections taken by seining.

Fishes were smaller at the upstream site ( $G = 231.02$ , 3 df,  $P < .001$ ). The numbers of 20, 40, 60, and >65 mm fishes available for gut content analysis at the upstream site were 470, 281, 23, and 4, and the numbers at the downstream site were 346, 488, 207 and 42 fishes. Thus, more 20-mm fishes were collected upstream and more 60- and 80-mm fishes were found downstream.

The number of a prey type consumed by fishes usually depended upon its abundance. Higher densities of copepods, barnacle nauplii, cyprids, *Uca* spp., first-instar *R. harrisi* larvae, and first-instar *S. reticulatum* larvae occurred upstream than downstream, but more first-instar *S. cinereum* larvae and "others" were collected downstream (Fig. 4, Table 6). Consequently, more barnacle nauplii, cyprids, and first-instar *Uca*, *R. harrisi*, and *S. reticulatum* larvae were consumed at the upstream site, and more copepods, first-instar *S. cinereum* larvae (which do not occur upstream), and "others" were eaten at the downstream site (Fig. 5, Table 6). Smaller prey also may have been eaten at the upstream site due to the large abundance of small fishes. If so, then fishes at the upstream site should have preferred smaller prey. Indeed, fishes preferred copepods, first-instar *Uca* larvae, barnacle nauplii, cyprids, *R. harrisi* larvae, and first-instar *S. reticulatum* larvae at the upstream site, but preferred first-instar *S. cinereum* and "others" at the downstream site (Fig. 6, Table 6).

TABLE 4. Ranked electivities (Elect.) of *Menidia menidia*, *Anchoa mitchelli*, *Fundulus heteroclitus* by species and collectively (Total) for prey, including zoeae that were exported from (E) or retained in (R) upper estuaries, in the Newport River estuary, North Carolina.

Prey	Dispersal pattern	Total		<i>M. menidia</i>		<i>A. mitchelli</i>		<i>F. heteroclitus</i>	
		Elect.	Rank	Elect.	Rank	Elect.	Rank	Elect.	Rank
Copepods		.66	1	.67	1	.69	1	.61	2
Others		.59	2	.29	2	.36	3	.88	1
<i>Uca</i> I	E	.06	3	.07	5	.38	2	-.90	5
Cyprids		-.06	4	.19	3	.03	4	-.86	4
Barnacle nauplii		-.24	5	.08	4	-.64	8	-.56	3
<i>S. cinereum</i> I	E	-.59	6	-.55	6	-.38	6	...	...
<i>S. reticulatum</i> I	R	-.75	7	-.53	7	-.52	5	...	...
<i>Palaemonetes</i> I-X	R	-.81	8	-.62	8	-.62	7	-.96	6
<i>R. harrisi</i> I	R	-.90	9	-.82	9	-.92	9	...	...
<i>R. harrisi</i> II-IV	R	-.98	10	-.97	10	-.99	10	...	...

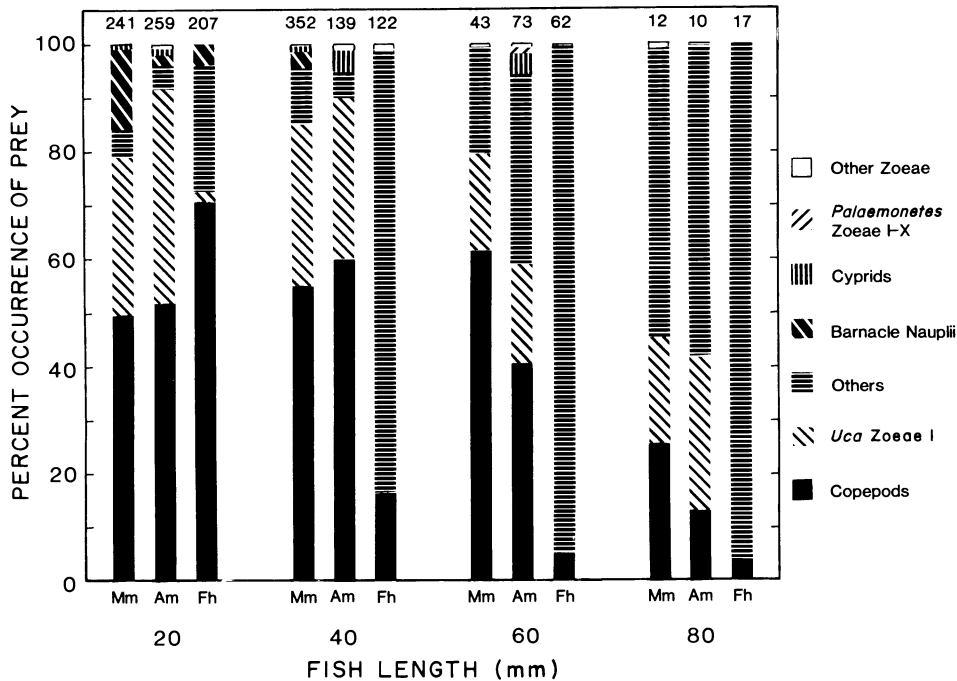


FIG. 3. Percent occurrence of prey types in the guts of *Menidia menidia* (Mm), *Anchoa mitchelli* (Am), and *Fundulus heteroclitus* (Fh) 20–80 mm long collected from the Newport River estuary, North Carolina. The number above each bar indicates the number of guts examined.

Plankters that are retained in estuaries were apparently more likely to remain near the substrate on spring than neap ebb tides, and therefore fewer were available to fishes. Copepods, barnacle nauplii, first-instar *S. reticulatum* larvae and *P. pugio* larvae were more abun-

dant on diurnal neap than spring low tides; otherwise similar numbers of plankters were collected during these tides (Fig. 4, Table 6). More copepods, barnacle nauplii, and cyprids were consumed on neap than spring tides (Fig. 5, Table 6). Fishes preferred first-instar *Pa-*

TABLE 5. Analyses of variance of electivities of small fishes (standard length [SL] < 45 mm) vs. large fishes (SL > 55 mm) of three species for various zooplankters.

Prey	Source of variation	<i>Menidia menidia</i>		<i>Anchoa mitchelli</i>		<i>Fundulus heteroclitus</i>		Total for the three species	
		df	F	df	F	df	F	df	F
Copepods	Fish size	1	<0.01	1	17.69***	1	73.88***	1	64.26***
	Error	662		477		441		1584	
<i>Uca</i> I	Fish size	1	2.50	1	9.57**	1	1.13	1	16.64***
	Error	662		477		441		1584	
Barnacle nauplii	Fish size	1	15.70***	1	5.38*	1	6.44*	1	38.50***
	Error	662		477		441		1584	
Cyprids	Fish size	1	16.63***	1	1.99	1	1.88	1	24.34***
	Error	662		477		441		1584	
<i>R. harrisi</i> I	Fish size	1	1.34	1	7.58**	1	0	1	0.09
	Error	662		477		441		1584	
<i>R. harrisi</i> II–IV	Fish size	1	2.45	1	0.29	1	0	1	0.52
	Error	662		477		441		1584	
<i>S. reticulatum</i> I	Fish size	1	0.71	1	3.79	1	0	1	7.08**
	Error	662		477		441		1584	
<i>S. cinereum</i> I	Fish size	1	11.98***	1	0.89	1	0	1	0.40
	Error	662		477		441		1584	
<i>Palaemonetes</i> I–X	Fish size	1	10.71**	1	0.07	1	0.29	1	0.95
	Error	662		477		441		1584	
Others	Fish size	1	16.88***	1	206.80***	1	80.06***	1	246.12***
	Error	662		477		441		1584	

\*  $P \leq .05$ , \*\*  $P \leq .01$ , \*\*\*  $P \leq .001$ .



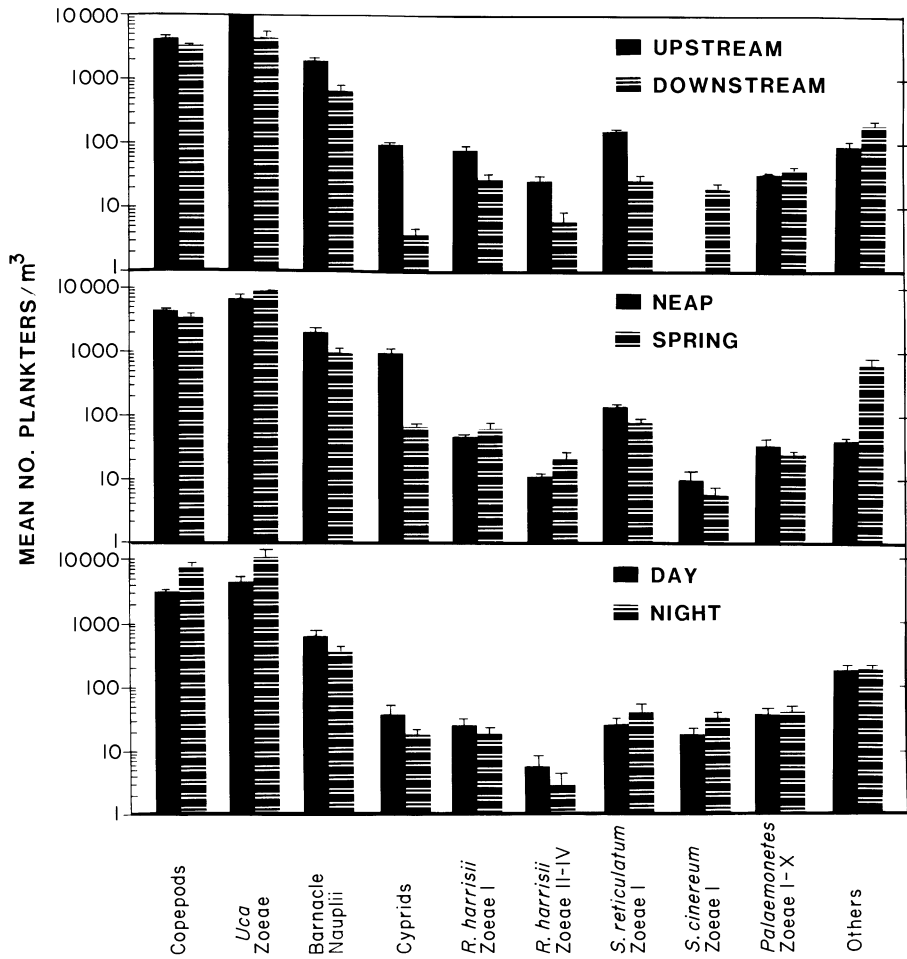


FIG. 4. Mean number of 10 most abundant plankters collected per cubic metre in the Newport River estuary, North Carolina, by site, tide, and time of day. Samples were collected at night only at the downstream site.

*laemonetes* larvae when feeding on neap rather than spring tides, whereas they preferred *Uca* larvae on spring tides (Fig. 6, Table 6).

Fishes did not appear to feed at night. Guts of fishes contained more zooplankton during the day (Fig. 5, Table 6), and only partially digested prey at night. Digested prey often were present in fish midguts collected at night, because collections were usually taken within several hours after nightfall. However, fishes collected late at night had empty stomachs. Gut evacuation rates of silversides obtained in the laboratory compare with those obtained in the field, assuming that fish cease feeding at night. The guts of silversides were packed with undigested prey immediately after fishes ceased feeding. After 1 h, the guts of four fish were filled with zooplankton and three had stomachs that were slightly less full. After 3.5 h, three fish had remains in their stomachs and four fish only had prey in their mid- and hindguts. After 5 h, all seven fish had empty stomachs and midguts. Similar evacuation rates for silversides were obtained by Peters et al. (1974).

## DISCUSSION

### *Vulnerability of larvae to planktivorous fishes*

The upper estuary was dominated by silversides, killifish, and anchovies, as is typical for other estuaries on the east coast of the United States (Richards and Castagna 1970, McErlean et al. 1972, Derickson and Price 1973, Subrahmanyam and Drake 1975, Hillman et al. 1977, Hoff and Ibara 1977, Crabtree and Dean 1982, see Morgan 1986). Anchovies and silversides frequently preyed on crab larvae as they do in other estuaries (Springer and Woodburn 1960, Mulkana 1966, Carr and Adams 1973, Spight 1981, Lucas 1982, Smith et al. 1984, Cadigan and Fell 1985). Killifish preyed on larvae infrequently in the Newport River estuary as they did elsewhere (Kneib 1986), perhaps because they do not encounter them often. Silversides and anchovies often forage in shoals and channels of estuaries (Butner and Brattstrom 1960, Crabtree and Dean 1982), whereas killifish primarily feed on marsh surfaces and

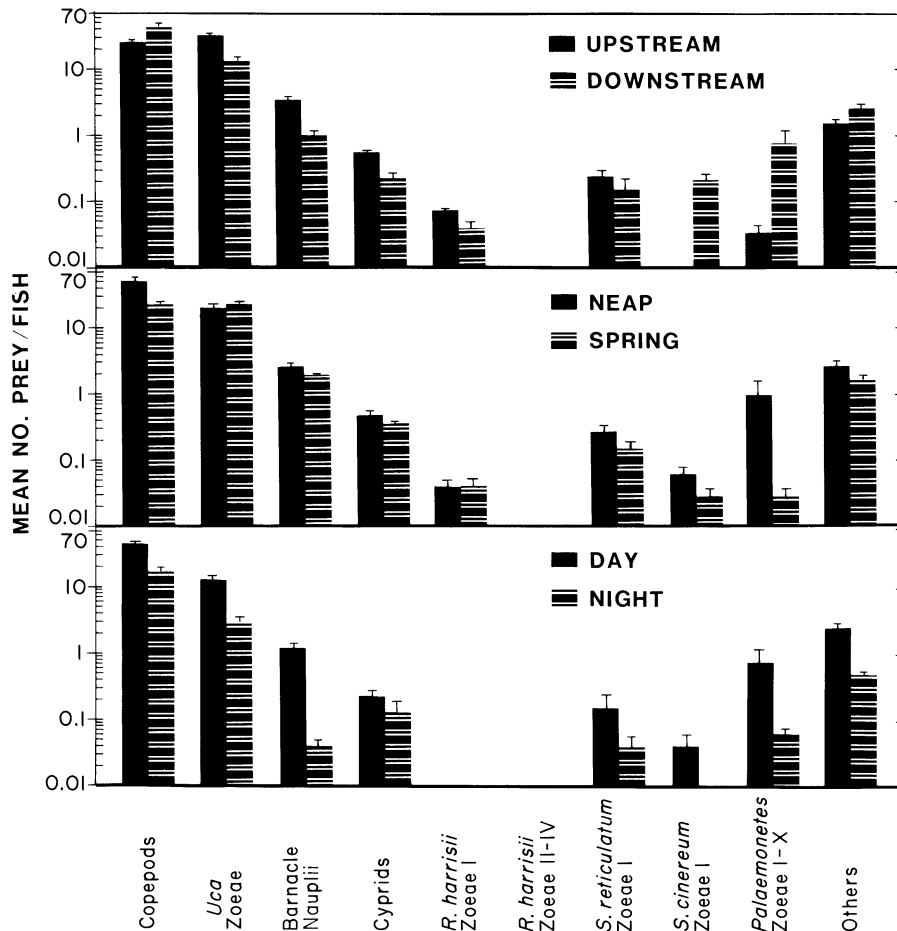


FIG. 5. Mean number of top 10 prey types in the guts of *Menidia menidia*, *Fundulus heteroclitus*, and *Anchoa mitchelli* collected in the Newport River estuary, North Carolina, by site, tide, and time of day. Samples were collected at night only at the downstream site.

in tidal creeks (Kneib 1984a). Thus, silversides and anchovies are the most likely fishes to affect the dispersal and morphology of larvae of crabs inhabiting estuaries of the east coast of the United States.

Zoeae that are retained in the estuary apparently have particularly effective morphological and behavioral antipredatory adaptations that permit them to coexist with large numbers of estuarine fishes, whereas vulnerable larvae may migrate to coastal waters where the risk of encountering planktivorous fishes is reduced. Natural populations of silversides, anchovies, and killifish preferred zoeae that are exported from the estuary (*Uca*, *Sesarma cinereum*) to those that develop within the estuary (*Sesarma reticulatum*, *Palaemonetes*, *Rhithropanopeus harrisi*). Indeed, retained zoeae were the least preferred zooplankters in the upper estuary.

Fishes in the field and laboratory showed strikingly similar preferences for zoeae. In previous laboratory feeding trials (Morgan 1987a), larval and juvenile silversides and killifish ate more zoeae that are exported from the estuary (*Callinectes sapidus*, *Uca minax*, *S.*

*cinereum*) than those that are retained (*Pinnotheres ostreum*, *Palaemonetes pugio*, *R. harrisi*). In the current study, juvenile and adult fishes preferred abundant alternative prey (*Artemia* nauplii in the laboratory or copepods in the field) to crab zoeae, fiddler crab zoeae that develop offshore were taken randomly, and mud crab zoeae that develop in the estuary were strongly avoided.

The vulnerability of zoeae to fishes depends upon their morphological and behavioral defenses and size; zoeae that are exported from estuaries generally may be small and short spined. Spines and postcontact antipredatory behaviors of zoeae appear to have evolved specifically to deter small planktivorous fishes (Morgan 1989), and they deter even large fishes when spineless prey are available. Dorsal and rostral spines increase the size of zoeae dorso-ventrally. Upon attack, zoeae flare their antennal spines at right angles to the dorsal and rostral spines and arch their spinous abdomen over the carapace. Thus, spines enlarge and protect crab larvae in three dimensions, so that it is difficult for fishes to manipulate zoeae for ingestion. Consequently,

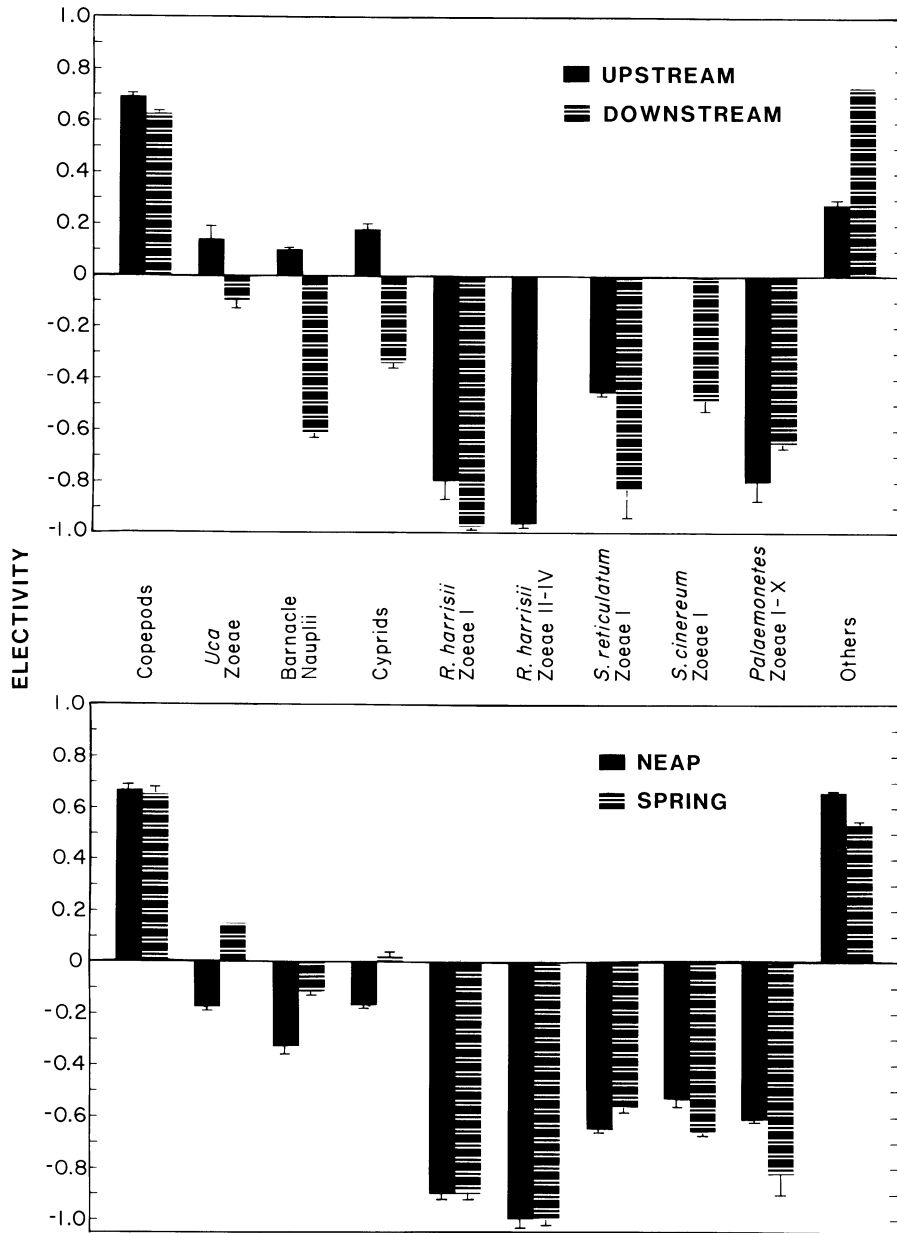


FIG. 6. Mean electivities of *Menidia menidia*, *Anchoa mitchelli*, and *Fundulus heteroclitus* for top 10 prey types collected in the Newport River estuary, North Carolina, by site and tide.

small crab larvae are easier to ingest than large ones (Morgan 1987a, 1989). In this study, fishes preferred the smallest species of crab larvae, and their preferences for the remaining species declined as the total size (body plus spines) of zoeae increased (Fig. 7). That fishes prefer small zoeae is demonstrated more directly by the stronger avoidance of large late-instar than small first-instar *R. harrisi* zoeae.

Evasion apparently is less effective than spination at deterring fish predation. Grass shrimp (*Palaemonetes*) zoeae bear only a short rostral spine (Fig. 7C), and rely primarily upon escape to survive attacks by planktiv-

orous fishes (Morgan 1987a). Despite the superior evasive capabilities, rostral spine, and large size of grass shrimp zoeae, they were preferred over spinous *R. harrisi* zoeae. Furthermore, unarmored evasive copepods were much preferred to the comparably sized and most vulnerable crab zoeae (*Uca*), even though these zoeae were nearly twice as abundant.

*Impact of spatial and temporal risk of planktivory on crab life histories*

The risk of predation appears to be greatest upstream in shallow, narrow areas of the upper estuary on diurnal

TABLE 6. Analyses of variance of densities of zooplankters, numbers of prey in fish guts, and electivities of fishes at upstream and downstream sites, on spring and neap tides, and during night and day at the downstream site for *Menidia menidia*, *Anchoa mitchelli*, and *Fundulus heteroclitus* collectively. *F* ratios and significance levels (\* $P \leq .05$ , \*\* $P \leq .01$ , \*\*\* $P \leq .001$ ) are reported.

Source of variation	df	Copepods	<i>Uca</i> Zoeae I	Barnacle nauplii	Cyprids	<i>R. harrisii</i> Zoeae I	<i>R. harrisii</i> Zoeae II-IV
Plankter densities							
Site	1	5.64*	17.39***	26.39***	20.04***	5.66*	3.28
Tide	1	4.17*	0.40	17.28***	2.60	0.07	0.34
S × T	1	<0.01	2.48	1.43	0.09	2.07	3.81
Error	46						
Plankter densities							
Diel	1	70.49***	3.41	7.78**	7.67**	0.14	0.43
Tide	1	70.32***	8.96**	16.01***	0.07	8.50**	10.50**
D × T	1	44.09***	3.99	21.33***	4.09	<0.01	0.43
Error	32						
Prey numbers							
Site	1	18.32***	31.66***	52.74***	29.34***	13.66***	4.45*
Tide	1	33.77***	0.30	14.70***	9.62**	0.24	0.07
S × T	1	29.80***	0.50	2.00	0.01	0.05	0.07
Error	1543						
Prey numbers							
Diel	1	20.65***	9.30**	7.15**	0.92	0.04	0
Tide	1	45.00***	0.47	7.20**	4.18*	0.04	0
D × T	1	1.70	0.71	6.19*	0.19	2.62	0
Error	1078						
Electivity							
Site	1	9.82**	9.33**	89.14***	49.83***	18.42***	6.53*
Tide	1	0.31	10.98***	0.21	1.01	0.79	1.95
S × T	1	6.16*	32.24***	6.09*	0.43	0.06	1.95
Error	1340						

neap tides. The spatial gradient in predation apparently is due largely to the great abundance of fishes, and particularly small zooplanktivorous fishes, that occurs upstream. More zooplankters were eaten upstream not only because they were more abundant there, but because small fishes abound there and prefer small planktonic prey. The high densities of most plankters at the upstream site may have been due to high productivity or the small cross-sectional area of the estuary (Fig. 1).

In contrast, temporal patterns of planktivory were not due to differences in fish size and abundance, but to diurnal foraging of fishes and changes in the availability of prey. Only 40% of fishes were collected on neap tides when predation was greatest on resident plankters. These zooplankton remain near the substrate during spring ebb tides to prevent being swept downstream (Sandifer 1975, Cronin 1982), and therefore may have been more available to fishes on neap tides. On the other hand, zoeae that are exported from the estuary (*Uca*, *S. cinereum*) were just as abundant on diurnal neap as spring tides, and therefore fishes ate similar numbers of zoeae at these times. Peak hatching by these species occurs during nocturnal spring high tides (Christy and Stancyk 1982, DeCoursey 1983, Salmon et al. 1986), indicating that zoeae were swept downstream on ebb tides before the following day when fishes resumed feeding. The electivities of fishes gen-

erally were not different between neap and spring tides because the size composition of the fish assemblage probably did not change from one lunar phase to the next (Roessler 1970).

Although most *Uca* and *S. cinereum* zoeae apparently eluded the many fishes that occur in the upper estuary by hatching on nocturnal spring high tides, it is likely that this hatching rhythm is primarily a consequence of the vertical zonation of adults. Nearly all crabs that have semilunar hatching rhythms are semiterrestrial (Forward 1987; S. G. Morgan, *personal observation*), regardless of whether they export zoeae from the estuary (*Uca*, *S. cinereum*) or retain zoeae in the estuary (*S. reticulatum*). Semiterrestrial crabs may release zoeae when the water level is highest to enhance dispersal of zoeae from the shore and particularly from tidal creeks. Semiterrestrial crabs congregate around tidal creeks (Whiting and Moroshi 1974) and frequently release zoeae there. Nearly three times as many *Uca* zoeae (48 925 vs. 17 281 larvae/m<sup>3</sup>) were collected from a tidal creek on a full moon than downstream in the upper Newport River estuary, and they can attain densities as great as 100 000 larvae/m<sup>3</sup> in tidal creeks (DeCoursey 1983). By hatching on spring high tides, zoeae are less likely to be stranded in shoals and tidal pools (Saigusa 1981; S. G. Morgan, *personal observation*) where physiological stress (Dollard 1980, Morgan

TABLE 6. Continued.

<i>S. reticulatum</i> Zoeae I	<i>S. cinereum</i> Zoeae I	<i>Palaemonetes</i> Zoeae I-X	Others
55.67***	17.00***	0.02	6.00*
13.26***	0.02	19.54***	0.32
10.28**	0.02	2.96	1.33
0.88	1.19	0.04	0.09
2.72	3.13	1.81	11.54**
6.03*	3.64	5.38*	0.07
1.72	21.40***	2.10	5.75*
3.10	1.76	2.23	0.76
0.35	1.76	2.03	18.53***
1.92	6.03*	0.89	12.44***
0.84	1.94	1.13	6.91**
0.84	0.13	0.79	3.14
15.45***	46.99***	2.18	91.84***
0.01	<.01	6.18*	0.23
0.04	<.01	0.01	6.98**

1987b) and potential predators are greatest. Fishes and macroinvertebrates are more abundant in shoal and tidal creeks than in river channels during summer (Springer and Woodburn 1960, Percy and Richards 1962, McErlean et al. 1972, Subrahmanyam and Drake 1975, Markle 1976, Crabtree and Dean 1982, see Morgan 1986). Fishes and shrimps may number more than 5000 individuals/m<sup>2</sup> on low tides in tidal creeks (Kneib 1984b), and may decimate stranded zoeae.

Unlike semiterrestrial crabs, most subtidal crabs hatch on nocturnal high tides of any amplitude (Salmon et al. 1986, Forward 1987). Subtidal crabs may not hatch synchronously about spring high tides, because they release zoeae directly into the main river channel and are unlikely to become stranded with fishes in tidal pools. However, the hatching patterns of subtidal crabs also may have evolved to reduce planktivory. Like semiterrestrial crabs, subtidal crabs also hatch on peak high tides, indicating that zoeae initially disperse downstream regardless of whether zoeae are exported into coastal waters (*Callinectes sapidus*) or are retained in estuaries (*R. harrisii*). *Rhithropanopeus harrisii* larvae frequently hatch on high tides soon after sunset, but if high tides occur too near dawn crabs will release larvae at dusk instead, perhaps to maximize the time for dispersal and development prior to the onset of feeding by diurnal fishes (Forward et al. 1986). Blue

crabs are highly mobile and migrate to the mouth of the estuary to release vulnerable zoeae directly into coastal waters (Millikin and Williams 1984) where they are less likely to encounter planktivorous fishes.

Alternative hypotheses

The high productivity of estuaries also may support more planktivorous invertebrates than coastal waters and intensify selection for these alternative patterns of larval dispersal. However, evidence that the dispersal patterns of estuarine crabs have evolved in response to planktivory by planktonic and benthic invertebrates is equivocal (Morgan 1990). A review of available literature on the abundance, distribution, and food habits of estuarine and coastal invertebrates indicated that estuaries generally support more potential invertebrate predators of crab larvae than do coastal waters, although a higher diversity of predatory invertebrates may occur offshore. The hypothesis also was supported by simple laboratory feeding trials. Two of 3 planktonic invertebrates preferred *U. minax* larvae that are exported to *R. harrisii* larvae that are retained, 4 of 8 benthic invertebrates also preferred *U. minax*, and none of the 11 invertebrates preferred *R. harrisii*. However, published accounts indicated that many estuarine invertebrates do not appear to prey on zoeae in the field, and spines and complementary postcontact behaviors, the main defenses of crab larvae, apparently do not deter many invertebrates. Only 1 of 10 planktonic and benthic invertebrates was deterred by the elongate spines of *R. harrisii* zoeae (Morgan 1989).

Divergent dispersal patterns also could occur if some larvae are more susceptible to physiological stress than others. Because temperature and salinity fluctuations generally are greater in estuaries, species that are susceptible to physiological stress may be exported to

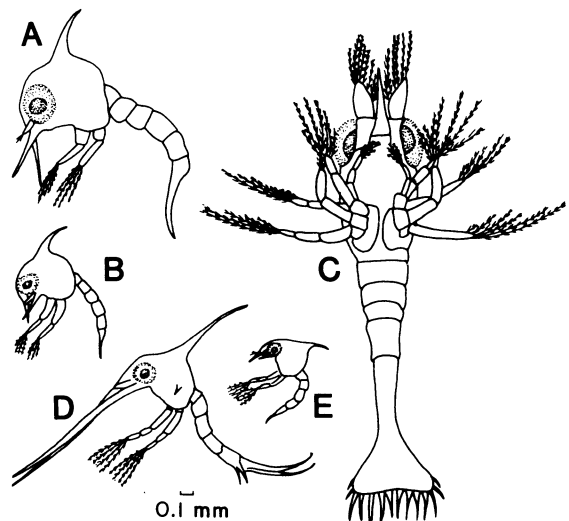


FIG. 7. First instar zoeae of (A) *Sesarma reticulatum*, (B) *Sesarma cinereum*, (C) *Palaemonetes pugio*, (D) *Rhithropanopeus harrisii*, and (E) *Uca minax*.

coastal waters, whereas species with resistant larvae may remain in the estuary. However, existing evidence contradicts this hypothesis. Of two species of crabs that only inhabit upper estuaries where temperature and salinity fluctuations are greatest, larvae of *U. minax*, which are flushed from estuaries, survived extreme temperature and salinity fluctuations better than larvae of *R. harrisii*, which develop within estuaries (Morgan 1987b).

#### CONCLUSIONS

This study suggests that predation pressure exerted by planktivorous fishes is predictable in time and space, and the timing of larval release, dispersal patterns, and larval morphologies of estuarine crabs have evolved in concert to reduce the risk of planktivory regardless of whether zoeae develop offshore or in estuaries. Planktivory by fishes was greatest during the day on neap tides in shallow, narrow, marshy areas of the upper Newport River estuary, North Carolina, where productivity is high and the abundance of young fishes is great. Small, vulnerable crab zoeae apparently are transported downstream where the risk of predation is reduced, whereas well-defended zoeae remain in the estuary. Regardless of whether zoeae are flushed into coastal waters or are retained in estuaries, estuarine crabs apparently hatch on nocturnal high tides to disperse zoeae downstream before dawn when fishes begin feeding. Peak hatching on spring high tides may not have evolved to expedite transport to coastal waters, but instead may facilitate dispersal of larvae of semi-terrestrial crabs from the shore where mortality can be high.

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