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Morphological and behavioral antipredatory adaptations of decapod zoeae

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Summary. Zoeae of some species of estuarine decapods are retained in the estuary throughout development while others are exported into nearshore coastal waters. The horizontal migrations of decapod zoeae to coastal waters may have evolved to reduce the probability of encountering planktivorous fishes which are most abundant in the estuary. If so, then the morphological vulnerability of zoeae to fish predation should be inversely related to the number of predators occurring where they develop. Six species of estuarine decapod zoeae were offered to *Menidia menidia* and *Fundulus heteroclitus*. The behavioral interactions were observed to determine the prey's vulnerability to predation, and the mode of operation and relative effectiveness of their defenses. Feeding trials and behavioral observations both demonstrated that *M. menidia* 6–16 mm long preferred *Uca minax* and *Callinectes sapidus* zoeae, which are exported from the estuary, to *Rhithropanopeus harrisi*, *Sesarma reticulatum* and *Palaemonetes pugio*, which are retained within estuaries. *Pinnotheres ostreum* zoeae develop in the lower estuary and fish demonstrated an intermediate preference for the zoeae. *Menidia menidia* 20–40 mm long showed similar preferences for *R. harrisi*, *S. reticulatum*, *P. ostreum* and *U. minax* as did small silversides. Large-mouthed demersal fish, *Fundulus heteroclitus* 6–10 mm long, also preferred *U. minax* to *R. harrisi*, but more readily preyed on zoeae than did *M. menidia*. The exported species of zoeae have shorter spines and smaller bodies than do retained zoeae, except *P. ostreum* which is small, spineless and passively sinks when attacked by fish. Other retained species of zoeae also have postcontact behavioral defenses which enhance the effectiveness of their morphological defenses. Zoeae do not evade attacks by fishes, but fishes quickly learned to avoid zoeae, which increases the effectiveness of the zoeae's antipredatory adaptations.

Key words: Adaptations – Zoeae – Planktivory – Spines – Dispersal

Zooplankters have long been known to undergo diurnal vertical migrations, but it is not widely recognized that they also make extensive horizontal migrations. Existing evidence best supports the hypothesis that vertical migrations are undertaken to reduce the probability of encountering zooplanktivorous fishes in illuminated waters (Zaret and

Suffern 1976; Stitch and Lampert 1981; Gliwicz 1986). Horizontal migrations of some decapod zoeae from estuaries along the east coast of the United States to coastal waters may also reduce fish predation, because fishes are most abundant in these estuaries during the summer when decapods hatch (McErlean et al. 1972; Cain and Dean 1976; Subrahmanyam and Drake 1975; Weinstein 1979; Crabtree and Dean 1982). The silverside, *Menidia menidia*, the anchovy, *Anchoa mitchelli*, and the killifish, *Fundulus heteroclitus*, are the predominant fishes in the upper estuary where many decapods reside (Richards and Castagna 1970; Derickson and Price 1973; Targett and McCleave 1974; Cain and Dean 1976). Silversides and anchovies eat plankton as adults (Bengston 1984; Smith et al. 1984), and all fish larvae are planktivorous (Hunter 1980; Turner 1984). Larval and juvenile fishes are particularly abundant in low salinity marshes (Cain and Dean 1976; Weinstein 1979), and the great abundance of young fishes can have a considerable impact on estuarine zooplankton communities (Thayer et al. 1974; Bengston 1984). Thus, predation on larval populations of invertebrates may be great in the upper estuary.

Therefore larvae that are hatched and retained in the upper estuary should encounter the greatest risk of fish predation, and should have evolved very effective morphological or behavioral antipredatory adaptations. The mud crab, *Rhithropanopeus harrisi*, the marsh crab, *Sesarma reticulatum*, and the grass shrimp, *Palaemonetes pugio*, hatch and develop in the upper estuary (Pinschmidt 1963; Sandifer 1973; Cronin 1982), and should have the best defenses against fish predation. The fiddler crab, *Uca minax*, also hatches in the upper estuary, but its zoeae are quickly transported from the estuary. Blue crabs migrate to the lower estuary to release their zoeae which are carried 80 km offshore (Smyth 1980; Provenzano et al. 1983; Truesdale and Andryszak 1983; Millikin and Williams 1984). These zoeae may be exported from the estuary into safer coastal waters because they are morphologically susceptible to fish predation. The pea crab, *Pinnotheres ostreum*, hatches primarily in the middle or lower estuary (Flower and McDermott 1952), and zoeae develop near the mouth of the estuary (Sandifer 1973; Goy 1976). Thus, pea crab zoeae may have better defenses against fish predation than would be expected for fiddler or blue crab zoeae, but less effective antipredatory adaptations than mud crab, marsh crab or grass shrimp zoeae.

The most prominent trait of decapod zoeae that could serve as a defense against predators is their spines. Morgan

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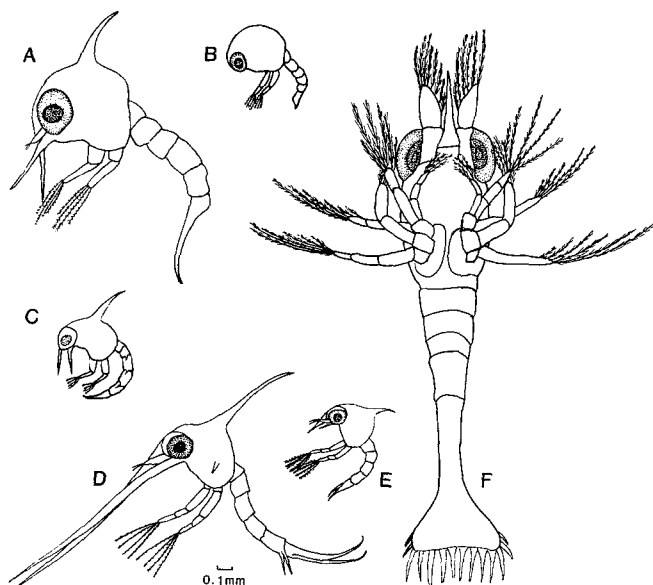


Fig. 1A–F. First instar zoeae of A *Sesarma reticulatum*, B *Pinnotheres ostreum*, C *Callinectes sapidus*, D *Rhithropanopeus harrisii*, E *Uca minax* and F *Palaemonetes pugio* drawn to comparable scale

unpublished work demonstrated that spines increase the size of mud crab zoeae, and thereby reduce predation by small fishes. Consequently, the largest zoeae, including body size and spine length, should be least vulnerable to predation by small fishes. Grass shrimp zoeae are the largest of the six species of zoeae (Fig. 1), but bear only one short rostral spine. Among the crab zoeae, mud crabs have the greatest total size, followed by the marsh crab. Blue crab, fiddler crab and pea crab zoeae are small and should be most preferred by fishes. Pea crab zoeae are spineless, and should be preyed upon most frequently, provided that they rely solely on morphological traits to deter fish predation. However, behavioral antipredatory adaptations may also influence the preferences of fishes for the various zoeae.

Thus, I have subjected the six species of estuarine decapod zoeae to predation by two species of fishes with different feeding modes to determine their vulnerability to predation, and the mode of operation and relative effectiveness of their defenses. If predation enforces selection for defense mechanisms, the vulnerability of zoeae should be inversely related to the number of predators occurring where they develop. Zoeae with the best defenses should be those retained in the upper estuary where planktivorous fishes abound. Zoeae which quickly disperse to coastal waters where fishes are less abundant should be most vulnerable to predation.

Methods and materials

Selection of experimental organisms

Six common species of decapod zoeae were fed to predators: *R. harrisii*, *P. ostreum*, *U. minax*, *C. sapidus*, *S. reticulatum*, and *P. pugio* (Fig. 1). The larvae of all species hatch from April to September in the Newport and Neuse River estuaries, North Carolina, where the study was conducted. The six species of decapod zoeae vary in spine length and number as well as body size.

Decapod larvae were fed to two fish predators: the Atlantic silverside, *Menidia menidia*, and the striped killifish, *Fundulus heteroclitus*. Silversides are selective diurnal planktivores occurring primarily in open waters, ranging from 0–36‰ (Bayliff 1950). The killifish feeds opportunistically on a variety of prey, including armored prey (Kneib and Stiven 1978), and occurs throughout the estuary (Weinstein 1979). Thus, both of these wide-ranging predators should encounter the six species of decapod larvae in the estuary during the breeding season of the crabs. Furthermore, fishes hatch and develop in the estuary during spring and summer when crabs do (Kneib and Stiven 1978; Middaugh 1981), so that zoeae would be subject to larval fish predation.

General methodology and experimental design

Gravid *R. harrisii* were collected by using traps that lure crabs to oyster shells provided within. Gravid *S. reticulatum* and *U. minax* are semiterrestrial and were collected by digging up their burrows at low tide. *Callinectes sapidus* were collected in crab pots or by dipnetting at night while using a light to attract the crabs. *Pinnotheres ostreum* were obtained by opening oysters collected from intertidal oyster bars. Oviparous *P. pugio* and *F. heteroclitus* were collected with a 5 m seine in tidal creeks at low tide. Gravid *M. menidia* were collected with a 15 m seine in high salinity marshes at low tide.

Eggs of crabs and fishes were hatched in the laboratory and reared under a 12 h light: 12 h dark photoperiod. Decapods were hatched at 25° C and from 20–30‰ depending on the species. Fishes were hatched at ambient temperatures and salinities in flowing seawater (approximately 25° C and 28–33‰). Thus, naive predators and prey were used during experiments. Predators and prey were used only once. Larvae were reared on *Artemia* nauplii. Predators were starved at least one day prior to experimentation, and fish were fed several drops of *Artemia* nauplii following the conclusion of the feeding trial to determine if they were still hungry. Only actively swimming zoeae displaying normal swimming behavior were used in experiments.

Specific methodology and experimental design

The following experiments were done to determine whether 1) spines physically prevent predation by small size classes of fishes, 2) spine length, body size or total size (spines plus body size) of the six species of zoeae are more likely to prevent predation by small fishes, and 3) large-mouthed killifish are better able to prey on zoeae than are small-mouthed silversides.

The six species of zoeae were fed separately to silversides in 6 cm bowls for 24 h and the number of surviving larvae was counted. Fish from 6–16 mm standard length in 2 mm size/class increments were fed first instar zoeae. *Uca minax* and *R. harrisii* also were fed separately to killifish (6, 8, 10 mm SL) in 6 cm bowls. Silversides 20 and 40 mm long were fed *R. harrisii*, *S. reticulatum*, *P. ostreum*, and *U. minax* zoeae together to determine the vulnerability of zoeae to predation by large fish during a 15 min period.

The behavioral interactions of predator and prey were observed for ten minutes (two consecutive five minute intervals) following the introduction of the zoeae into the bowl with the fish, to determine 1) if antipredatory behavior by zoeae was evident, 2) if fish experienced more difficulty

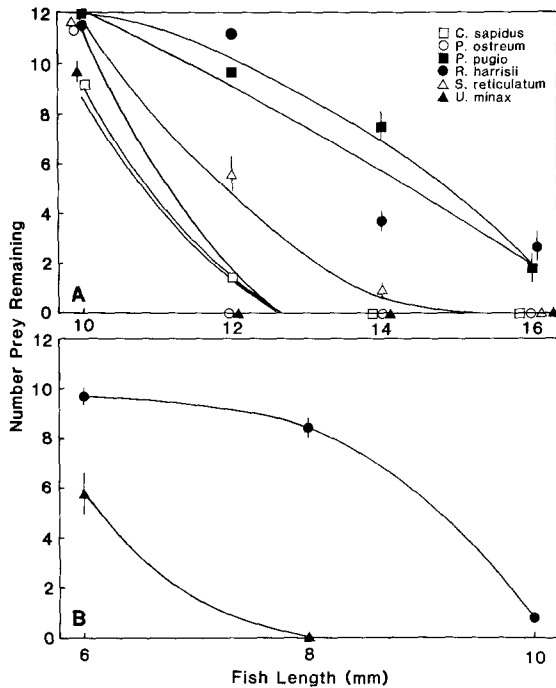


Fig. 2A, B. Number of zoeae remaining after 24 h in the presence of A) *M. menidia* 10–12 mm long and B) *F. heteroclitus* 6–10 mm long

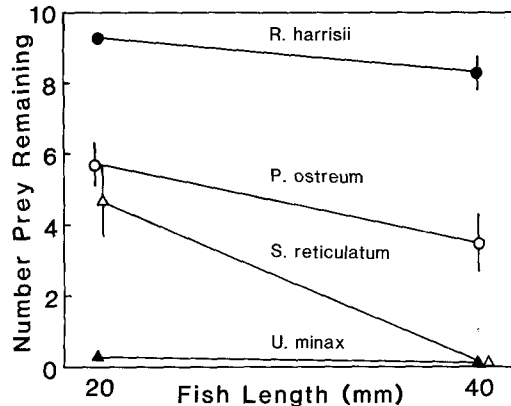


Fig. 3. Number of zoeae remaining after 15 min in the presence of *M. menidia* 20 and 40 mm long

with some zoeae than others, and 3) if fish learned to avoid some zoeae and not others. The behavioral interactions of the fish were quantified using the following categories: attacks, avoidances, captures, mouthings, ingestion, and unusual behavior following capture or ingestion. Unusual behavior indicating that the fish was experiencing difficulty with the prey included shaking the zoeae, shuddering, and sinking while attempting to swallow the zoeae. Zoal behavior was categorized as evasion before and escape after attack. Orthogonal polynomial contrasts of behavioral data were analyzed by the analysis of variance.

Results

Callinectes sapidus, *U. minax* and *P. ostreum* zoeae were most susceptible to predation by silversides less than 16 mm long, and *R. harrisii* and *P. pugio* were least vulnerable to predation (Fig. 2A). *Sesarma reticulatum* demonstrated an intermediate susceptibility to predation by small silversides. Small killifish also consumed more *U. minax* than *R. harrisii* zoeae (Fig. 2B). Large silversides continued to prefer *U. minax* to *R. harrisii* zoeae, but preferred *S. reticulatum* to *P. ostreum* (Fig. 3). Zoeae were consumed increasingly as silversides and killifish increased in length (Figs. 2, 3).

A comparison of behavioral interactions between 12 mm silversides (*M. menidia*) and the six species of zoeae revealed that *P. ostreum* and *U. minax* were avoided significantly less often than were other zoeae (Table 1). All species of zoeae were attacked with similar frequency. *Pinnothereos ostreum* zoeae were captured most often, followed by *C. sapidus* and *U. minax* zoeae. *Sesarma reticulatum*, *R. harrisii* and *P. pugio* zoeae were captured least often. *Uca minax* and *C. sapidus* zoeae were ingested more often than were other species. *Uca minax* zoeae also were mouthed more often than other species, and *S. reticulatum* were shaken more often. All zoeae attempted to evade attacks with similar frequency, but *P. pugio* most often attempted to escape following attack.

A comparison of interactions between 6–8 mm killifish (*F. heteroclitus*) and *R. harrisii* and *U. minax* zoeae showed that *R. harrisii* zoeae were avoided more frequently, and captured, mouthed, shaken and ingested less often than *U. minax* zoeae (Table 1). *Rhithropanopeus harrisii* zoeae attempted to escape following attack more often than did *U. minax* zoeae.

Table 1. Analysis of variance and Student Newman Keuls tests of fish and zoal interactions between six species of zoeae fed to 12 mm *M. menidia*, *df*=5,54 and between *R. harrisii* and *U. minax* zoeae fed to 6 and 8 mm *F. heteroclitus* *df*=5,34 (Cs=*C. sapidus*, Po=*P. ostreum*, Pp=*P. pugio*, Rh=*R. harrisii*, Sr=*S. reticulatum*, and Um=*U. minax*)

Behavior	<i>M. menidia</i>		SNK	<i>F. heteroclitus</i>		
	MS	F		MS	F	
Avoids/Pursuit	51.56	8.82***	<i>Sr Pp Rh Cs</i> > <i>Po Um</i>	98.10	10.43***	Rh > Um
Attacks/Pursuit	34.39	2.49*	<i>Po Um Rh Pp</i> ≥ <i>Cs Um</i>	0.23	0.01	
Captures/Attack	186.54	30.51***	<i>Po</i> > <i>Cs Um</i> > <i>Sr Rh Pp</i>	223.11	16.29***	Rh < Um
Ingestions/Capture	150.40	46.82***	<i>Cs Um</i> > <i>Po Sr Rh Pp</i>	264.13	35.73***	Rh < Um
Mouthings/Capture	92.47	12.60***	<i>Um</i> > <i>Sr Rh Po Cs Pp</i>	430.05	43.24***	Rh < Um
Shakes/Capture	29.57	5.21***	<i>Sr</i> > <i>Pp Cs Rh Um Po</i>	242.43	18.40***	Rh < Um
Evasions/Attack	0.80	0.79	<i>Rh Po Cs Um Sr Pp</i>	12.37	1.74	
Escapes/Attack	11.05	2.97*	<i>Pp</i> > <i>Um Rh Sr</i> ≥ <i>Cs Po</i>	82.42	15.99***	Rh > Um

* = 0.05, ** = 0.01, *** = 0.001

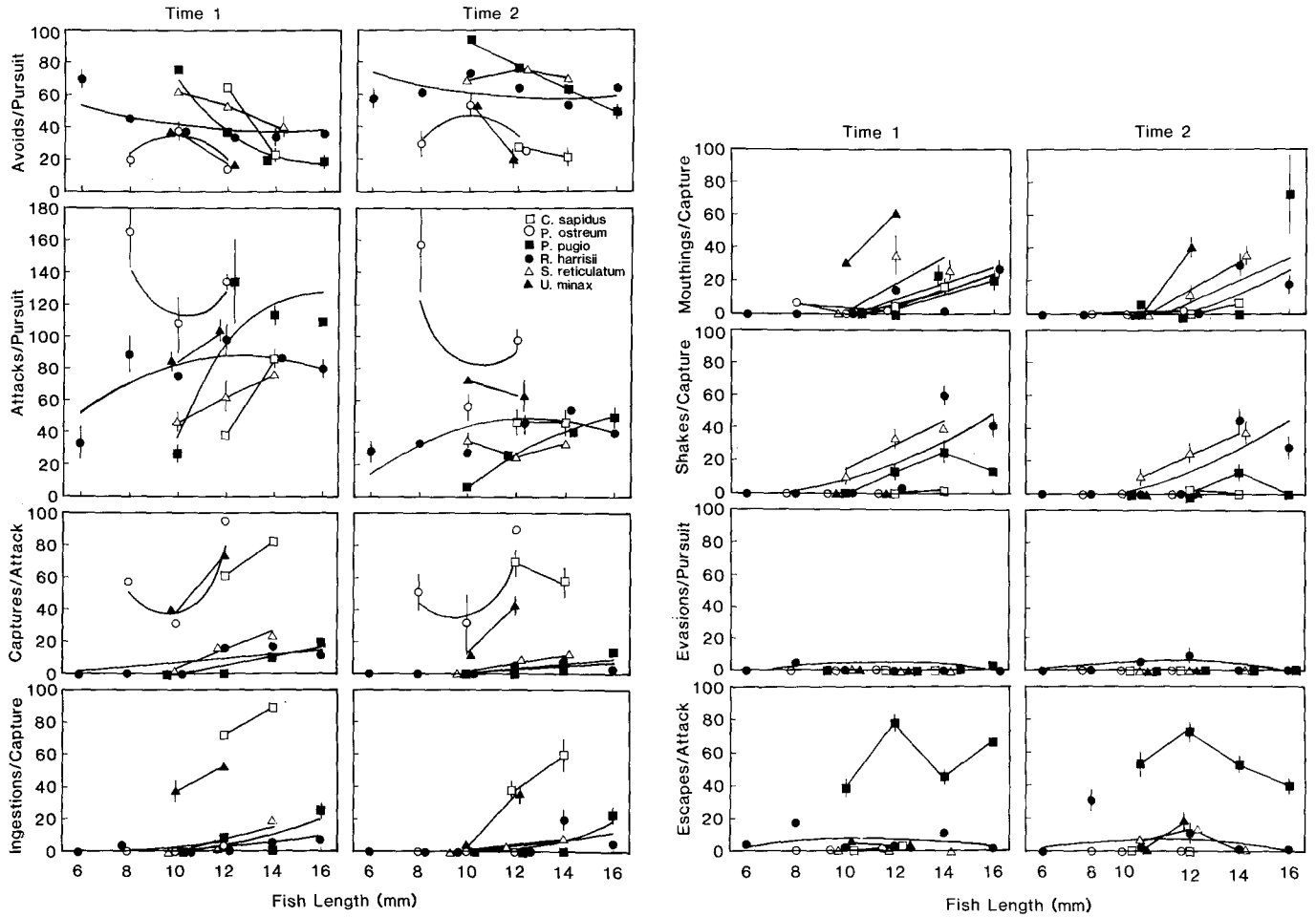


Fig. 4. Behavioral interactions between six species of zoeae and *M. menidia* 6–16 mm long during two consecutive 5 min observation periods

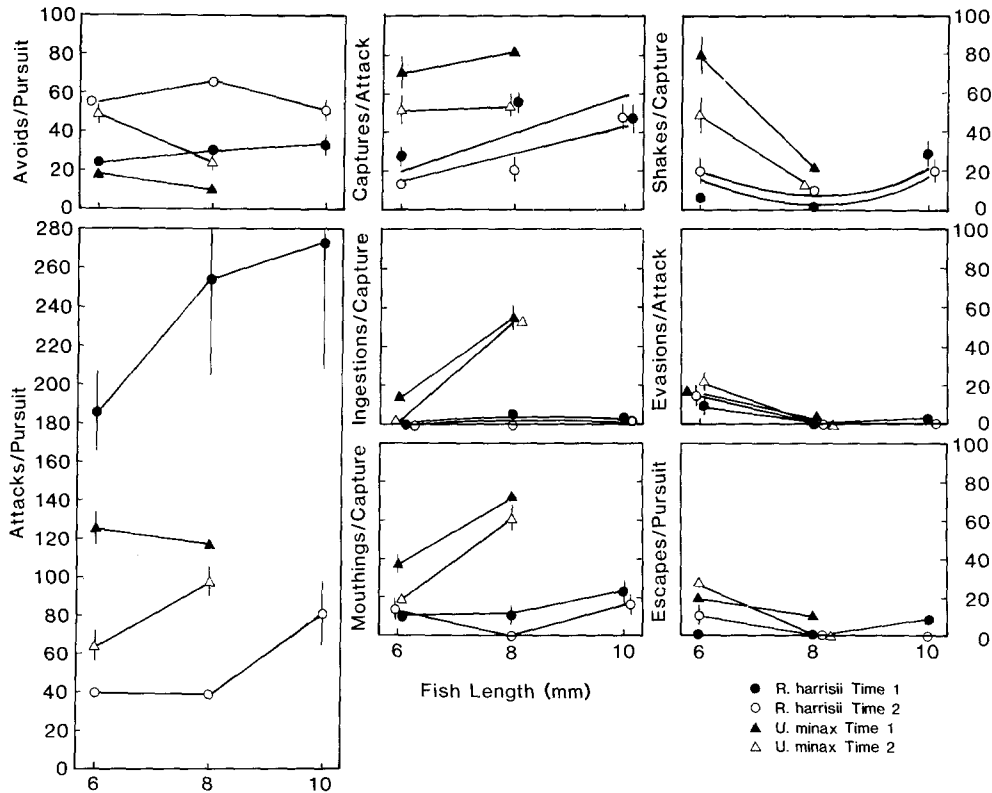


Fig. 5. Behavioral interactions between *R. harrisi* and *U. minax* zoeae and *F. heteroclitus* 6–10 mm long during two consecutive 5 min observation periods

Table 2. Analysis of variance of fish and zoeal behavioral interactions with increasing exposure time and fishlength. Cs = *C. sapidus*, df = 24; Po = *P. ostreum*, df = 30; Pp = *P. pugio*, df = 77; Rh = *R. harrisi*; *M. menidia* df = 120, *F. heteroclitus* df = 58; Sr = *S. reticulatum*, df = 60; and Um = *U. minax*; *M. menidia* df = 38, *F. heteroclitus* df = 40

Behavior	<i>M. menidia</i>						<i>F. heteroclitus</i>	
	Cs	Po	Pp	Rh	Sr	Um	Rh	Um
Avoids/pur	66.42	51.07	346.65	745.32	45.37	88.33	100.11	103.96
Time	24.95	5.19	141.85***	123.43***	39.34**	3.78	70.01**	57.90*
Length	41.47*	0.07	175.35***	588.02***	5.62	84.55**	13.58	45.06*
Length ²	—	22.22*	11.21	0.20	0.42	—	12.64	—
T × L ²	—	—	18.17*	33.16*	—	—	—	—
Error	151.61	142.47	270.97	3570.93	214.35	293.54	436.78	327.89
Attacks/pur	9.90	97.04	730.36	2108.94	92.26	74.44	147.65	80.44
Time	7.95	25.32	393.09***	703.10***	70.55**	73.58*	116.20**	72.33**
Length	1.95	7.92	247.77***	1118.06***	20.12	0.85	2.09	8.11
Length ²	—	63.80*	89.50**	184.57***	1.58	—	3.54	—
T × L ²	—	—	—	85.28**	—	—	—	—
Error	233.01	345.63	690.50	5627.34	442.53	551.94	537.88	336.46
Captures/att	14.37	195.11	142.27	1798.51	152.36	213.43	151.12	86.68
Time	14.36	0.29	22.09**	102.28***	28.08**	121.23***	2.53	80.07*
Length	0.01	78.71*	119.21***	1633.15***	117.85***	92.19**	123.69*	6.61
Length ²	—	116.11*	0.91	1.93	6.43	—	11.07	—
T × L	—	—	—	60.76**	—	—	—	—
Error	225.15	406.52	213.20	3021.86	134.65	284.59	760.00	407.90
Ingestions/cap	61.80	11.90	152.02	1512.70	75.81	203.07	278.68	247.72
Time	56.53*	5.87	1.02	37.38*	6.49	97.94**	37.87*	44.72*
Length	5.27	0.15	98.50***	1370.19***	60.36***	105.12**	90.21*	203.00***
Length ²	—	2.94*	52.50***	81.89**	8.97	—	147.91**	—
T × L ²	—	2.94*	—	—	—	—	—	—
Error	183.95	14.31	279.25	3922.79	175.80	344.44	715.70	274.85
Mouthings/cap	14.84	10.69	230.22	1940.85	188.33	289.46	272.97	172.68
Time	7.51	3.43	0.89	79.01**	5.99	97.19**	197.00**	49.24*
Length	7.32	0.60	192.15***	1806.75***	182.27***	192.27***	25.44	123.44*
Length ²	—	6.66*	37.19	25.88	0.07	—	28.69	—
Error	109.58	23.10	781.00	6628.76	611.27	319.90	1103.75	322.92
Shakes/cap	0.17	0	82.66	867.29	175.57	0.68	267.75	194.47
Time	0.08	0	36.47*	24.21	14.54	0.32	114.28**	71.95*
Length	0.08	0	23.53	755.00***	159.34**	0.36	74.23*	122.52**
Length ²	—	—	22.67	42.93*	1.68	—	—	—
T × L	—	—	—	37.08*	—	—	—	—
Error	17.76	0	476.15	2140.81	799.14	11.28	786.42	519.02
Evasions/att	0	0	1.23	20.57	0	0	0	58.48*
Time	0	0	0.01	2.55	0	0	0	0.01
Length	0	0	0.02	5.01	0	0	0	58.47**
Length ²	—	—	1.20	11.43*	—	—	—	—
Error	0	0	46.11	1014.15	0	0	0	260.53
Escapes/att	0	0.34	81.40	37.89	18.39	34.29	1.38	66.74
Time	0	0.11	3.69	0.19	4.87	1.43	0.29	5.49
Length	0	0	55.89***	6.79	11.08	32.87**	0.41	61.26**
Length ²	—	0.23	0.06	28.42**	2.49	—	0.14	—
T × L	—	—	21.77*	—	—	—	—	—
Error	0	29.8	245.58	1255.70	184.73	167.96	14.99	217.12

* = 0.05, ** = 0.01, *** = 0.001

att attack, pur pursuit, cap capture

Behavioral observations also indicated that large silversides and killifish generally captured, ingested and mouthed *P. pugio*, *R. harrisi*, *S. reticulatum* and *U. minax* zoeae more often and avoided these zoeae less frequently than did small fish (Figs. 4, 5; Table 2). Only *P. pugio* and *R. harrisi* zoeae were attacked more often as fish length increased, and only *R. harrisi*, *S. reticulatum* and *U. minax* zoeae were shaken more frequently.

Silversides and killifish generally avoided *P. pugio*, *R. harrisi*, *S. reticulatum*, and *U. minax* more as the time of exposure increased, and zoeae were attacked and captured less often (Figs. 4, 5; Table 2). Fish mouthed and ingested fewer of these zoeae with time, or their behavior did not change.

The behavior of silversides towards *C. sapidus* and *P. ostreum* zoeae generally did not change in a manner that

would indicate that large fish were becoming more proficient at handling the zoeae. However, large fish avoided *C. sapidus* zoeae less than smaller ones, and more *P. ostreum* were captured by large fish (Fig. 4, Table 2). The behavior of silversides towards either of these zoeae generally did not change as exposure time increased, although the number of *C. sapidus* zoeae eaten decreased with time.

Zoeal behavior generally did not change during the course of the observation period (Figs. 4, 5; Table 2). In the presence of large silversides or killifish, zoeal behavior either did not change significantly, or the frequency of escape attempts decreased.

Discussion

Decapod zoeae which develop entirely within estuaries appear to have evolved better antipredatory adaptations than have those that are exported to coastal waters, where the risk of fish predation is predictably less. Feeding trials and behavioral observations both demonstrated that small silversides preferred small zoeae that are exported from the estuary (*C. sapidus* and *U. minax*) to large zoeae that are retained within estuaries (*R. harrisi*, *S. reticulatum*, and *P. pugio*). Behavioral observations also revealed that zoeae that complete their development in the lower estuary (*P. ostreum*) have better defenses against fish predation than the two species of larvae which develop in coastal waters.

Mud crab zoeae flared their spines following attacks and sometimes flexed their abdomens up over their carapace following attacks. Other crab zoeae bearing spines also can flare their antennal spines, but the spines were too short to observe them do so during the course of the ten-minute observation periods. However, mud crab zoeae, unlike other zoeae observed, possess a pair of abdominal spines that become erect when the abdomen is reflexed, further increasing their unpalatability. Zoeae did not evade attacks, but occasionally attempted to escape following attacks. Escape attempts were largely unsuccessful. Thus, zoeae primarily rely on their armor for protection.

Grass shrimp zoeae possess only a short rostral spine to deter attacks, but are much more effective than crab zoeae at escaping from fish. Shrimp zoeae, like crab zoeae, do not evade attack but rely on their spines and armor to survive initial attacks. Once released, shrimp zoeae can either swim very quickly in unpredictable loops or flex their abdomen to quickly traverse short distances. Because shrimp zoeae were initially difficult to handle, and because they can be difficult to recapture repeatedly, fish often appeared to lose interest. The combination of the very large body, short rostral spine and flexion response of *P. pugio* zoeae are as effective at preventing predation by small fishes as are the multiple spines of *R. harrisi* zoeae.

Zooplankters frequently have been described as either being evasive or armored. Copepods and some rotifers have light flexible exoskeletons or lorica and rely entirely on evasion for survival (Kerfoot 1978; Gilbert and Williamson 1979; O'Brien 1979; Vinyard 1980). Armored rotifers and cladocerans rely on postcontact defenses (e.g., spines, impenetrable and rigid protective carapaces and lorica, and passive sinking) for survival (Gilbert and Williamson 1979; Gilbert and Stemberger 1984; Havel and Dodson 1984). However, helmeted cladocerans have been reported to have increased evasive capabilities relative to nonhelmeted forms

(O'Brien and Vinyard 1978; Grant and Bayly 1981; Barry and Bayly 1985; Mort 1986). Shrimp zoeae are intermediates between the dichotomy of evasion versus armor that has arisen in the literature. They rely on armor to survive initial encounters and escape to prevent further interactions.

Unlike most crab zoeae, *P. ostreum* do not bear spines and rely primarily on behavioral rather than morphological defenses to deter fish predation. Pea crab zoeae are small, darkly pigmented, and have a smooth, brittle carapace. Behavioral observations revealed that *P. ostreum* zoeae tuck their abdomen closely beneath their cephalothorax following an attack and then remain motionless. Silversides captured the zoeae repeatedly during the ten-minute observation period but did not consume them more often than other retained species. Pea crab zoeae may be rejected by fish because they resemble suspended inorganic particles in appearance, behavior and texture. After 24 h fish consumed as many pea crab zoeae as the two exported species of zoeae. Thus, passive sinking is about as effective as the spines of other crab zoeae or the flexion response of *P. pugio* during brief encounters, but not when fed for an entire day to starved fish.

Behavioral observations also revealed that the effectiveness of the antipredatory adaptations diminished for mud crab, marsh crab, fiddler crab and grass shrimp zoeae as fishes increased in length. Small fishes are generally less able to capture and handle prey than are large ones (Durbin 1979; Hunter 1980; Unger and Lewis 1983). However, small silversides generally did not have any more difficulty capturing and ingesting pea crab zoeae than did large fish larvae. The lack of spines and small body size permitted even the smallest fish examined to prey on pea crab zoeae. Larger silverside larvae also did not become more proficient at handling blue crab zoeae. Observations were conducted only on two size classes of silversides, both of which were capable of feeding on all blue crab zoeae presented within 24 h, whereas other zoeae were fed to fish which could not consume all zoeae offered. Thus fish did not experience as much difficulty preying on blue crab zoeae as on other zoeae. Furthermore, the similarity in body size and spine length of blue and fiddler crab zoeae would have probably otherwise resulted in similar behavioral responses of the fish towards the zoeae.

Fishes quickly learned to avoid spined prey, which not only increases the effectiveness of spines as an antipredatory trait, but may also increase the rate of evolution of the character. Noxious prey are attacked less often by predators that can learn to avoid them. Therefore prey should be damaged and killed less frequently by predators capable of learning, which would enhance selection for the antipredatory adaptation. Zooplankton are patchily distributed, which favors short-term learning by fish to avoid noxious prey (Dill, 1983; Bronmark et al. 1984). Longterm memory of noxious prey also has been exhibited by fish (Kerfoot et al. 1980), so that spines may continue to reduce the attack frequency upon zoeae even if they have not been encountered recently. Silversides did not learn to avoid pea crab and blue crab zoeae for the same reasons that both large and small fish could readily prey on the zoeae (discussed above).

Silversides 20 and 40 mm long continued to show similar preferences for zoeae during 15-minute feeding trials as did smaller silversides during 10-minute feeding trials. Thus, the relative effectiveness of the antipredatory adaptations

of the four species of crab zoeae is similar for larval and juvenile fish.

The antipredatory adaptations of mud crab zoeae also were more effective at preventing predation by larval killifish than were those of fiddler crab zoeae. Killifish were better able to capture and ingest both species of zoeae than were silversides of the same length, indicating that the larvae of large-mouthed demersal fishes may be best able to handle large, armored prey. Larval killifish are large upon hatching and were able to prey on fiddler crab zoeae immediately. Larval killifish occur in large numbers in salt marshes where fiddler crabs release their larvae and could have a considerable impact on their hatching rhythms. Zoeae which are not effectively dispersed from tidal creeks would become subject to predation by killifish and shrimp which together number over 5000/m² in tidal pools at low tide (Kneib 1984). Thus, fiddler crab zoeae as well as other semiterrestrial crabs may hatch on nocturnal spring tides when the tidal volume in the upper estuary is the greatest to reduce stranding in tidal creeks (Saigusa 1981; Christy 1982).

Conclusions

Larval killifish, larval silversides and juvenile silversides all preyed more readily on zoeae that are exported from the estuary than those that are retained within the estuary throughout their larval development. It is highly likely that those larvae remaining in estuaries have evolved morphologies and behavioral responses that enable them to withstand the intense predation pressure applied by the great abundance of fishes inhabiting estuaries. Zoeae that are vulnerable to fish predation morphologically have evolved behaviorally to undergo extensive horizontal migrations from the estuary into coastal waters where the risk of fish predation is reduced. The large size of many retained zoeae may make them more obvious to fishes, but large size in combination with an armored exoskeleton and spines also makes them less palatable and more capable of surviving repeated attacks. Furthermore, fish quickly learn to avoid noxious prey and appear to be able to distinguish them from palatable prey which enhances the effectiveness of their antipredatory adaptations.

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