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ADAPTIVE SIGNIFICANCE OF SPINATION IN ESTUARINE CRAB ZOEAE¹

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Abstract. Spines of zoeae of the mud crab *Rhithropanopeus harrisi* apparently have been selected primarily through predation by small fishes rather than by predatory invertebrates, and do not appear to have evolved either to stabilize the organism or to retard its sinking. The settling velocity and swimming and sinking behavior of spined zoeae vs. those with their spines removed were similar. Sinking slowed when the antennal spines were flared perpendicularly to their resting position, but zoeae do so only when molested. Only 1 of 10 planktonic and benthic invertebrates preyed on more despined than spined zoeae, but spines were effective against two fishes that predominate in upper estuaries of the east coast of the United States where larvae of *R. harrisi* develop. Spines limited the size at which planktivorous silversides, *Menidia menidia*, and opportunistic killifish, *Fundulus heteroclitus*, began preying on zoeae, but the effectiveness of spines in preventing predation appeared to diminish with each successive zoeal instar.

Gape-limited fishes apparently exert strong selective pressure for crab zoeae to produce spines rather than a large unarmed body. Not only do spines increase the size of the zoeae, but spines are noxious, enhance survival of attacked zoeae, regenerate quickly, and are effective when partially regenerated. Spined first-instar zoeae were preyed upon by silversides less often than despined second-instar zoeae, in much the same numbers as despined third-instar zoeae, and more often than despined fourth-instar zoeae. The sharp multiple spines of zoeae prevented fishes from manipulating their prey for easy ingestion, so that zoeae often lodged in the pharynxes of small fishes and sometimes killed them. *Rhithropanopeus harrisi* zoeae that were attacked by fishes had the same survival and time to metamorphosis as zoeae that were not attacked, whereas the shorter spines and larger bodies of zoeae of the marsh crab *Sesarma reticulatum* were less effective at preventing fatalities. Dorsal spines were broken most often during attacks. The partially regenerated spines of third-, but not fourth-, instar zoeae were as effective as unbroken spines in preventing predation by silversides.

The effectiveness of spines as an antipredatory adaptation is enhanced, because fishes apparently detected spines and quickly learned to prefer despined to spined zoeae. Zoeae did not attempt to evade or escape attacks by fishes, but instead relied on armor and postcontact antipredatory behaviors for their survival. The differential effectiveness of spines of marine and freshwater zooplankters at deterring predation by fishes and invertebrates is discussed.

Key words: antipredatory adaptations; body size; crab zoeae; estuaries; fishes; freshwater; invertebrates; predatory-prey interactions; regeneration; sinking; spines.

INTRODUCTION

Planktonic organisms possess an array of possible morphological, chemical, or behavioral antipredatory adaptations (Zaret and Suffern 1976, Kerfoot 1977a, Drenner et al. 1978, Cowden et al. 1984). Spines have been shown to serve an antipredatory function in freshwater plankton communities by deterring copepod predation on rotifers (Gilbert 1967) and cladocerans (Kerfoot 1977a, O'Brien et al. 1979). Although spination is a particularly prominent characteristic of many ma-

rine planktonic organisms, including diatoms, dinoflagellates, radiolarians, cladocerans, rotifers, trochophores, barnacle nauplii, stomatopod larvae, decapod zoeae and fish larvae, the effectiveness and mode of operation of this alleged antipredatory adaptation (Lebour 1919, Hardy 1956) has rarely been documented experimentally. Spines also have been hypothesized to retard sinking by plankters (Hardy 1956, Hutchinson 1967), and to stabilize the organism while swimming (Weldon 1889) or passively sinking (Fisher 1977).

Considering all plankters, freshwater and marine, spination is perhaps best developed among brachyuran zoeae. Crab zoeae are typically armed with rostral, antennal, dorsal, and lateral carapace, abdominal, and telson spines, some of which may be longer than the larva. To demonstrate that zoeal spines could have

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evolved in response to predation, one must (1) use sympatric predators and prey, (2) show that spines increase the fitness of zoeae, and (3) investigate other possible functions of spines to determine if they could have evolved for more than one purpose (Williams 1966, Gould and Lewontin 1979, Vermeij 1982). Furthermore a variety of common predators using different modes of feeding should be employed to test the relative effectiveness of spines. The encounter frequency, the severity of the interaction, and the ability of the predator and prey to learn to avoid or diminish the consequences of the encounter all may affect the rate of evolution of spines.

Here I provide evidence that (1) spines of crab zoeae probably have evolved to deter predatory fishes rather than to deter predatory invertebrates, to stabilize zoeae, or to retard sinking by zoeae; (2) spines rather than large body size probably have been selected to deter gape-limited fishes, because they are noxious, enhance survival of attacked zoeae, and are effective while partially regenerated; (3) fishes can detect zoeal spines and learn to avoid them; and (4) crab zoeae rely on armor and postcontact antipredatory behaviors rather than evasive maneuvers to survive encounters with fishes.

METHODS AND MATERIALS

Selection of experimental organisms

Zoeae of the mud crab *Rhithropanopeus harrisi* (Fig. 1) were fed to two fishes, the Atlantic silverside (*Menidia menidia*) and the killifish (*Fundulus heteroclitus*), and to 10 common and widely distributed invertebrates (Table 1). Mud crabs hatch from April to October in the Newport and Neuse River estuaries, North Carolina, and the zoeae are found primarily in the upper estuary in waters ranging between 0 and 25 g/kg salinity. Silversides are selective diurnal planktivores; they occur primarily in open waters ranging between 0 and 36 g/kg salinity (Bayliff 1950). Killifish feed opportunistically on a variety of prey, including armored prey (Kneib and Stiven 1978), and range throughout the estuary (Weinstein 1979). Furthermore, the breeding season of the fishes is concurrent with that of the crabs (Kneib and Stiven 1978, Middaugh 1981), so that zoeae would be subject to larval fish predation. Thus, both predators should encounter *R. harrisi* zoeae frequently.

General methodology

Ovigerous *R. harrisi* were lured by oyster shells into traps placed in the Neuse River estuary, North Carolina. Ovigerous marsh crabs, *Sesarma reticulatum*, were collected by digging their burrows along the North River estuary. Gravid *F. heteroclitus* were collected with a 4.6-m seine in tidal creeks at low tide. Gravid *M. menidia* were collected with a 15.3-m seine in high-salinity marshes at low tide in the Newport River estuary. All invertebrate predators were collected by hand from the Newport River estuary.

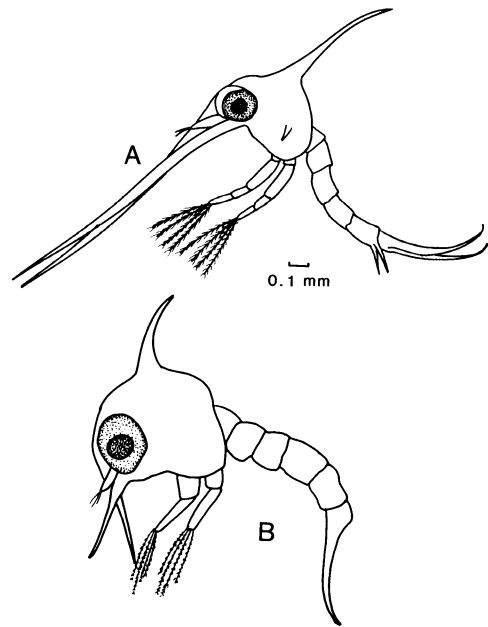


FIG. 1. First-instar zoeae of (A) *Rhithropanopeus harrisi* and (B) *Sesarma reticulatum*.

Eggs of crabs and fishes were hatched in the laboratory and reared on *Artemia* nauplii under a 12 h light : 12 h dark photoperiod. Crabs were hatched at 25°C and 25 g/kg salinity. Fishes were hatched at ambient temperatures and salinities in flowing seawater ($\approx 25^\circ$ and 30 g/kg). Predators were starved 1 d prior to experimentation, and fish were fed several drops of *Artemia* nauplii at the end of every feeding trial to determine if they were still hungry. Only actively swimming zoeae displaying normal behavior were used in experiments. The rostral, dorsal, and antennal spines of *R. harrisi* zoeae were amputated with a scapel under a dissecting microscope for experiments requiring "despined" zoeae. The naive predators and prey were used only once.

Adaptive significance of zoeal spines

Sinking and stabilization.—To determine if spines retard the sinking rate of zoeae, the settling velocity of first-instar *R. harrisi* zoeae with (1) their spines amputated, (2) antennal spines flared at right angles to the rostral spine, and (3) antennal spines collapsed alongside the rostral spine in the normal resting position was measured after placing them in a 45.7 × 6 × 7.5 cm plexiglass column. Zoeae descended 15.2 cm before the settling velocity was measured over the next 30.5 cm. All zoeae were killed by placing them for 1 min under a hot light, which caused many zoeae to flare their spines.

To determine if spines stabilize zoeae while swimming or passively sinking, the swimming and sinking behaviors of spined and despined zoeae were observed.

Invertebrate predation.—To determine if spines

TABLE 1. Conditions of feeding trials: size (mean, minimum, and maximum) of 10 planktonic and benthic invertebrate predators, diameter of culture dishes used for feeding trials, number of crab larvae fed of each species, and number of replicates.

Predator	Taxon/common name	Predator size (mm)			Dish size (cm)	No. larvae	No. replicates
		Measure*	Mean	Min.–Max.			
Planktonic							
<i>Sagitta hispida</i>	Chaetognath	L:	7.5	7–8	6	10	19
<i>Eutima mira</i>	Hydromedusa	W:	5.2	5–8	6	10	15
<i>Mnemiopsis leidyi</i>	Ctenophore	L:	23.5	17–30	9, 19	20	8
Benthic							
<i>Styela plicata</i>	Tunicate	H:	43.3	31–67	19	25	10
		W:	23.1	21–26			
<i>Aiptasia pallida</i>	Anemone	BW:	8.1	4–12	9	25	10
		TW:	20.5	13–35			
<i>Balanus amphitrite</i>	Barnacle	BW:	12.7	10.0–16.0	6	20	14
		H:	8.0	7.2–11.4			
<i>Caprella penantis</i>	Amphipod	L:	5.1	3–8	6	20	18
<i>Palaemonetes pugio</i>	Grass shrimp	L:	27.2	22.0–30.0	9	40	20
<i>Rhithropanopeus harrisi</i>	Crab	W:	9.6	8.7–10.8	9	40	20
<i>Geukensia demissa</i>	Mussel	L:	56.0	48–75	9	40	10

* L = length, W = width, H = height, BW = base width, and TW = distance from tip of tentacle to opposing tentacle tip.

physically prevent predation by invertebrates, invertebrates (see Table 1) were placed in culture dishes and were allowed to adjust to laboratory conditions for at least 1 d prior to experimentation. Either 12 despined or 12 spined *R. harrisi* zoeae were fed to predators that were isolated in bowls. Half of the predators were fed despined zoeae the 1st d, and the other half were fed spined zoeae first. On the following day, these predators were fed 12 of the opposite type of zoeae. The numbers of zoeae remaining after 24 h were recorded each day. The size of the culture dishes and the number of larvae used in feeding trials depended on the size of the predators (Table 1).

Fish predation.—To determine if spines physically prevent predation by small fishes, despined and spined *R. harrisi* zoeae were fed separately (as described above for invertebrates) to silversides ranging in size from 6 to 20 mm standard length (SL) in 2-mm size class intervals. All four zoeal instars were used to determine the effectiveness of spines against predatory fishes as a function of prey size. In addition, 12 first-instar spined and 12 despined zoeae simultaneously were offered to killifish 6, 8, and 10 mm long for 24 h. Ten fishes of each size class were fed in 6 cm diameter bowls.

Spination vs. large body size as antipredatory adaptations

Spines vs. body size.—The effectiveness of spines vs. body size in preventing predation was determined by feeding (either separately or concurrently) despined second-, third- or fourth-instar *R. harrisi* zoeae with spined first-instar zoeae to silversides capable of feeding on both types of prey. Otherwise the protocol followed that previously described for other feeding trials.

Noxious properties of spines.—To determine if long spines can kill predatory fishes, silversides and killifish were fed 100 spined *R. harrisi* (long spines and small body size), 100 despined *R. harrisi*, 100 *S. reticulatum* (short spines and large body size), *Artemia* nauplii, or nothing for 8 d. Twelve replicates each were performed in 6-cm bowls for 18-mm silversides and 6- and 18-mm killifish. Five 40-mm silversides were offered prey in 10-L containers, but despined *R. harrisi* and *S. reticulatum* zoeae were not offered to fish. The number of fish surviving was monitored daily. Autopsies were performed on fish that died during the experiment.

Spine length, body size, and survival.—To determine if spine length is associated with increased survival and decreased larval development time for zoeae attacked by fish, *R. harrisi* zoeae, bearing long spines on a moderate-sized body, and *S. reticulatum* zoeae (Fig. 1), bearing short spines on a large body, were fed separately to 18-mm silversides. The total size (spine length plus body size) of each species was comparable, so that silversides were capable of ingesting both prey with some difficulty. Zoeae were removed with a pipet for rearing following initial attacks and prior to ingestion.

Larval survival and duration to megalopa were determined for 360 freshly hatched zoeae (120 from each of three hatches) of each species that had not been attacked by silversides, and compared with 360 that had. Fifty larvae also were taken from each hatch and were reared without being introduced to fish. The incidence of spine breakage was recorded for all zoeae on the 2nd d of the experiment.

Partially regenerated spines.—The effectiveness of partially regenerated spines (compared with normal ones) at preventing predation was determined by am-

putating spines of second-instar zoeae and rearing them to the third or fourth instar to enable spines to regenerate. Second-instar zoeae were operated on because first-instar zoeae are more sensitive. The partially regenerated spines of the third instar were shorter than the regenerated spines of fourth-instar zoeae. Zoeae with partially regenerated spines were fed to silversides with zoeae of the same hatch that had not had their spines removed, following the protocol previously described for similar feeding trials.

Detection and avoidance of spines by fishes

Feeding trials.—To determine if fishes can detect spines and learn to avoid them, feeding trials on (1) “fish predation,” (2) “spines vs. body size,” and (3) “partially regenerated spines” were repeated, but 12 despined and 12 spined *R. harrisii* zoeae were fed to silversides simultaneously rather than on consecutive days. However, feeding trials on fish predation were repeated only with first- and fourth-instar zoeae. If the co-occurrence of spined and despined zoeae results in fewer despined zoeae being consumed, while the number of spined zoeae eaten remains unchanged, then feeding is being inhibited because fish cannot distinguish between prey. If fish can distinguish between spined and despined zoeae then despined zoeae should be preyed upon in greater numbers when the prey are offered simultaneously rather than separately. If fish feed on similar numbers of spined and despined zoeae, regardless of whether or not they were fed the zoeae separately or concurrently, then fish are probably unable to discriminate between the two prey types.

Behavioral observations.—Fish-zoeal interactions were observed during the first 10 min of feeding trials on “fish predation” (except those involving second- and third-instar zoeae) to provide further evidence that fish can detect spines and learn to avoid them. The change in behavior of predator and prey was determined by comparing the frequency of behaviors in the first 5 min with those in the second 5 min. The behaviors of fishes were quantified using the following categories: avoidance, attack, capture, ingestion, and unusual behavior following capture, such as shuddering, loss of upright orientation, sinking, and mouthing and shaking the zoea.

Antipredatory behavior of zoeae

To determine if *R. harrisii* zoeae have behavioral antipredatory adaptations that complement their armor, zoeae were observed during the first 10 min of feeding trials while the behavior of fishes was being examined. Behavior of zoeae was categorized as evasion or spine flaring after an encounter, or escape or spine flaring after an attack.

Effects of spine amputation on zoeae

Despined zoeae were observed for abnormal swimming behavior, and two types of controls were em-

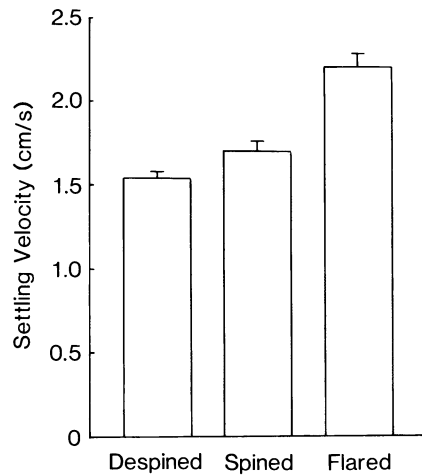


FIG. 2. Settling velocity of *Rhithropanopeus harrisii* with spines removed, resting in their normal position, or flared perpendicularly to their body. Error bars show ± 1 SE.

ployed to determine the effects of spine amputation on their survival. First, the survival of despined and spined zoeae that were placed either separately or together in bowls without fish was measured after 24 h for a total of 30 replicates from three different hatches. Second, a sham operation was performed by amputating an antennule. These zoeae were fed, separately and together with spined zoeae that had not undergone an operation, to 14-mm silversides. Ten replicates were performed with one hatch of larvae. Only first-instar zoeae were used for both control experiments because they are the most sensitive to stress.

Statistical analysis

All data that were a function of fish length were analyzed by orthogonal polynomial contrasts and the analysis of variance (Snedecor and Cochran 1980). Linear and quadratic regression lines were plotted when a significant regression existed, otherwise data points were simply connected. The experiment on “spines vs. body size” was unbalanced because zoeae were fed separately but not concurrently to the largest size class of fish. Therefore these last data points were plotted but not included in the contrasts.

Prey were not replaced during behavioral observation periods, so all behaviors were expressed as proportions in order to compare prey of differing vulnerability at the two time intervals. Thus, avoidances and attacks were expressed as a percentage of the number of pursuits made by the fish. Similarly, the ratios of captures and escapes to attacks, and ingestions and unusual behaviors to captures were calculated. Non-significant interaction terms from initial analyses of variance were omitted and the data were reanalyzed.

All data expressed as percentages were arcsine transformed prior to performing analyses of variance. Differences between the settling velocities of the different

TABLE 2. Analysis of variance comparing number of spined vs. despined *Rhithropanopeus harrisi* larvae surviving after exposure to invertebrate predation.

Predator	df	ms	F	P
<i>Sagitta hispida</i>	1,18	38.00	3.59	.07
<i>Eutima mira</i>	1,14	45.63	29.13	.0001
<i>Mnemiopsis leidyi</i>	1,7	49.00	0.45	.51
<i>Styela plicata</i>	1,9	26.45	4.16	.06
<i>Aiptasia pallida</i>	1,9	80.00	1.88	.19
<i>Balanus amphitrite</i>	1,13	5.89	0.13	.72
<i>Caprella penantis</i>	1,17	0.44	0.06	.80
<i>Geukensia demissa</i>	1,9	1.13	0.19	.67

types of zoeae were compared using the Student-Newman-Keuls multiple range test (SNK).

RESULTS

Adaptive significance of spines

Sinking and stabilization.—The elongate spines of *R. harrisi* zoeae did not slow sinking unless the antennal spines were flared perpendicularly to the rostral spine (Fig. 2). Despined zoeae did not sink more quickly than spined zoeae, but they did sink faster than those with their spines splayed (SNK: df = 2, 147; $t = 6.73$; $P < .05$).

Spines were not needed to stabilize *R. harrisi* zoeae while swimming or passively sinking. Despined and spined zoeae with their spines flared or in the resting position all sank upside down without oscillating sideways. Zoeae often swam erratically after their spines

were amputated, but they quickly regained normal orientation.

Invertebrate predation.—Spines were not effective in deterring predation by most invertebrates. Of the 10 invertebrates tested, only the medusa of the hydrozoan *Eutima mira* preyed on significantly fewer spined than despined zoeae (Fig. 3, Table 2).

Fish predation.—Spines prevented silversides and killifish from preying on *R. harrisi* zoeae (Figs. 4 and 5, Table 3). Silversides 6 mm long were incapable of feeding on either despined or spined first-instar zoeae; 12-mm fish consumed all despined zoeae presented, but consumed few spined zoeae. Nearly all spined and despined zoeae were eaten by 16-mm fish. Similar patterns resulted from feeding later stage zoeae to slightly larger silversides, but the effectiveness of spines progressively decreased for each subsequent instar (Fig. 4). Killifish were smaller than silversides when they consumed all despined and spined first-instar zoeae offered (Fig. 5).

Spination vs. large body size as antipredatory adaptations

Spines vs. body size.—Spines can be more effective than larger body size at preventing predatory fishes from preying on *R. harrisi* zoeae. Spined first-instar zoeae were consumed by silversides less often than despined second-instar zoeae, in numbers similar to despined third-instar zoeae, and more often than fourth-instar zoeae (Fig. 6, Table 3).

Noxious properties of spines.—Spines can kill small

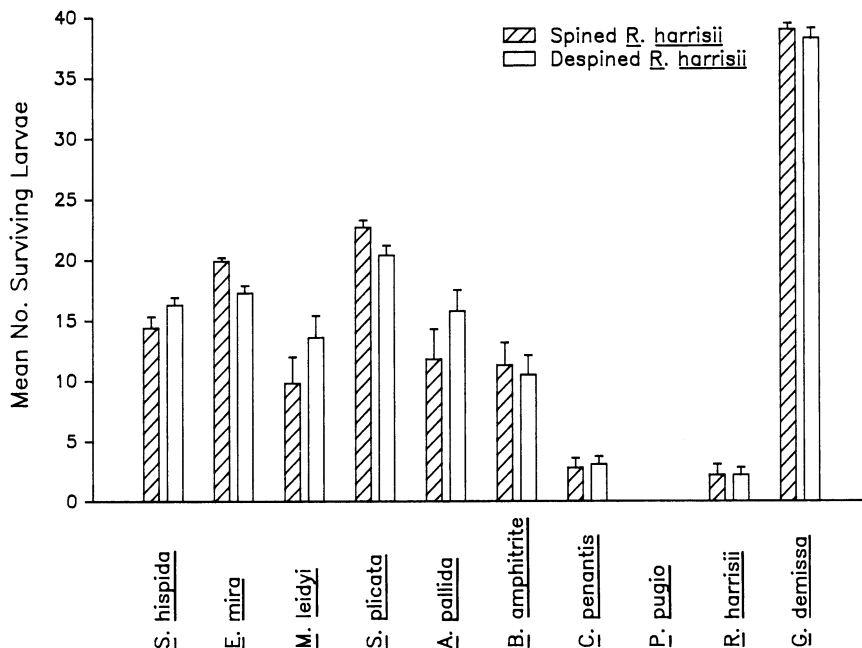


FIG. 3. Number of spined and despined *Rhithropanopeus harrisi* zoeae surviving after exposure to 10 planktonic and benthic invertebrate predators. Error bars show ± 1 SE.

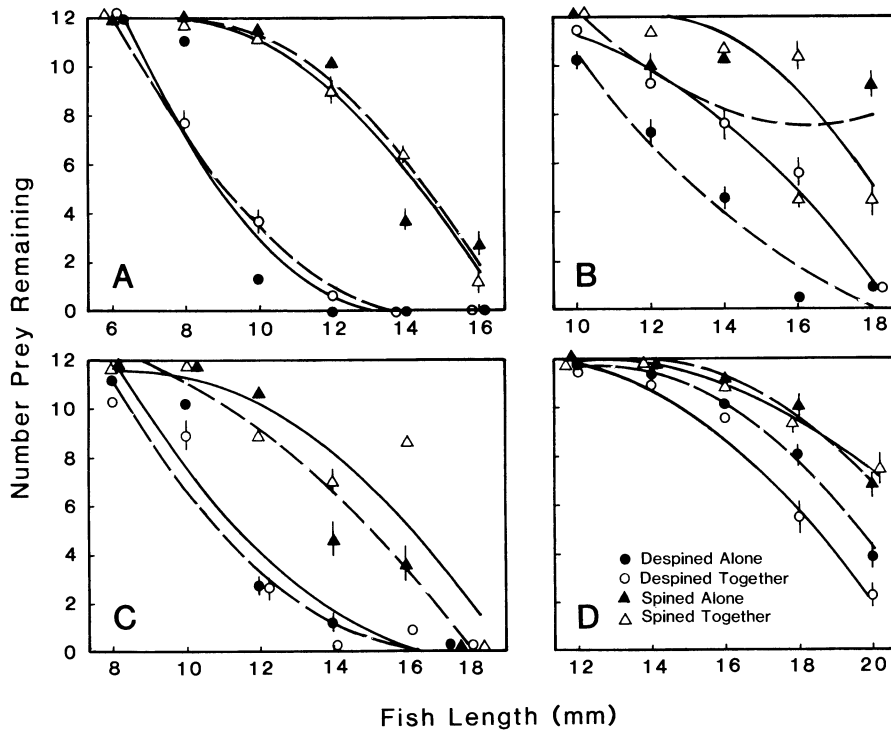


FIG. 4. Number of first- (A) to fourth- (D) instar despined and spined *Rhithropanopeus harrisii* zoeae remaining after 24 h when the two prey types were fed to *Menidia menidia* either separately or together. Error bars show \pm 1SE.

fishes attempting to ingest zoeae. All 12 18-mm silversides that were fed *R. harrisii* zoeae died within 8 d, whereas all fish that were fed despined *R. harrisii* zoeae, *S. reticulatum* zoeae, or *Artemia* nauplii survived. Only one starved fish died (on the last day of the experiment). However, spines did not kill killifish or 40-mm silversides.

Spine length, body size, and survival.—Crab zoeae often survived attacks by juvenile fishes, but small zoeae bearing long spines were more likely to survive than were large zoeae with short spines. Survival to post-larva of *R. harrisii* zoeae was similar regardless of whether or not they had been attacked by small silversides ($df = 2, 6; F = 0.12; P = .89$) (Fig. 7). *Sesarma reticulatum* zoeae have shorter spines and a larger body than *R. harrisii* zoeae, and did not survive as well when attacked by silversides ($df = 2, 6; F = 12.01; P = .008$). The larval development time of attacked zoeae was not extended for either species (*Rhithropanopeus*: $df = 2, 6, F = 2.55, P = .16$; *Sesarma*: $df = 2, 6, F = 1.07, P = .40$).

Crab zoeae that were attacked by fishes were most likely to suffer broken dorsal spines. The long spines of *R. harrisii* zoeae were broken more often than the short spines of *S. reticulatum* zoeae, although long spines protected zoeae better (Table 4). None of the 360 *R. harrisii* zoeae attacked by fish was mangled whereas 21 *S. reticulatum* zoeae were.

Partially regenerated spines.—The partially regen-

erated spines of third-, but not fourth-, instar *R. harrisii* were as effective as unbroken spines at preventing predation by small silversides (Fig. 8, Table 3).

Detection and avoidance of spines by fishes

Feeding trials.—The results of feeding despined and spined zoeae separately or concurrently to fishes do not

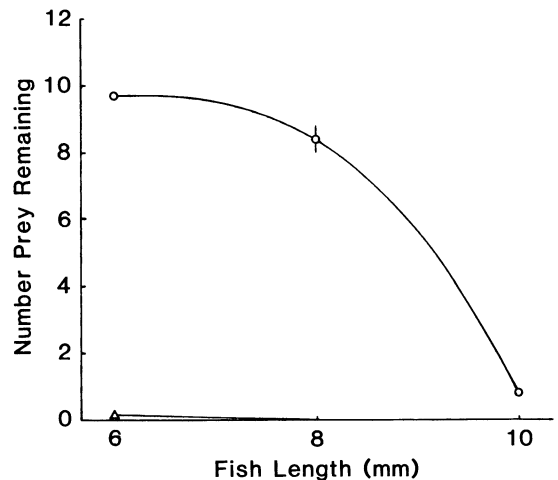


FIG. 5. Number of first-instar despined (circles) and spined (triangles) *Rhithropanopeus harrisii* zoeae remaining after both prey types were fed together to *Fundulus heteroclitus* 6–10 mm long for 24 h. Error bars show \pm 1 SE.

TABLE 3. Analyses of variance of number of spined (S), despined (D), or partially regenerated (R) *Rhithropanopeus harrisi* zoeae of the indicated instars (Prey) fed either alone or together (Treatment) to *Menidia menidia* of various lengths.

Source	df	ss	Source	df	ss
S1, D1	6	5757.73	S1, D2	7	1739.88
Prey	1	1810.47***	Prey	1	429.03***
Treatment	1	1.67	Treatment	1	1.63
Length	1	3763.04***	Length	1	864.61***
(Length) ²	1	4.95	(Length) ²	1	14.50
P × L	1	48.89**	P × L	1	43.51*
P × L ²	1	623.16***	P × L ²	1	44.20*
Error	233	1020.52	P × T	1	70.53**
S2, D2	7	4881.21	Error	112	1020.03
Prey	1	969.41***	S1, D3	5	796.10
Treatment	1	1.84	Prey	1	40.83
Length	1	3760.72***	Treatment	1	24.30
(Length) ²	1	8.80	Length	1	588.61***
P × L ²	1	323.48***	(Length) ²	1	82.84**
T × L	1	28.60*	P × L	1	59.51*
P × T	1	31.54*	Error	114	1343.60
Error	232	1464.08	S1, D4	5	706.15
S3, D3	7	2564.99	Prey	1	294.53***
Prey	1	662.48***	Treatment	1	12.03
Treatment	1	243.63***	Length	1	281.25***
Length	1	1482.25***	(Length) ²	1	4.27
(Length) ²	1	2.06	P × L	1	72.20*
P × L	1	139.24***	Error	114	1283.72
T × L ²	1	140.00***	S3, R3	3	330.27
P × T	1	35.28*	Prey	1	4.27
Error	192	1431.89*	Length	1	193.60***
S4, D4	5	1512.72	(Length) ²	1	0.30
Prey	1	190.13***	Error	53	506.80
Treatment	1	21.13*	S4, R4	5	301.50
Length	1	1095.61***	Prey	1	20.83*
(Length) ²	1	109.83***	Treatment	1	145.20***
P × L	1	96.04***	Length	1	94.61***
Error	194	926.63	(Length) ²	1	3.04
			T × L	1	37.81**
			Error	114	500.20

* $P < .05$, ** $P < .01$, *** $P < .001$.

support the hypothesis that fish can detect zoeal spines. If fishes can detect spines, then they should have eaten more despined than spined zoeae when prey were fed concurrently rather than separately. This result was obtained in only 1 of 8 feeding trials (Figs. 4, 6, and 8, Table 3). Despined zoeae were eaten less often than spined zoeae in two trials, and in similar numbers in the remaining five trials.

Behavioral observations.—Nevertheless, silversides and killifish both preferred despined to spined *R. harrisi* zoeae (Figs. 9–11, Tables 5–7), and therefore they must be able to discriminate between the two prey types. Silversides were more likely to avoid first- and fourth-instar spined zoeae, and to capture, ingest, and mouth despined zoeae (Figs. 9 and 10, Tables 5 and 6). First-instar despined zoeae were attacked more than spined zoeae, but only long silversides shook despined zoeae more frequently. Fourth-instar despined zoeae were not attacked more often than spined zoeae, but they were shaken more often. Silversides feeding on spined zoeae occasionally shuddered, lost their upright orientation, and sank motionless to the bottom of the

dish with their mouths locked open. Silversides often shuddered violently several times before they were able to dislodge the zoeae and resume swimming.

Killifish attacked, captured, ingested, and mouthed despined zoeae more than spined ones, although they did not avoid them less (Fig. 11, Table 7). Killifish shook spined zoeae more frequently than despined zoeae, which further indicated that they posed greater difficulties.

Killifish generally experienced less difficulty preying on spined zoeae than did silversides. Killifish attacked ($df = 1, 118; F = 27.98; P < .001$), captured ($df = 1, 118; F = 79.47; P < .001$), ingested ($df = 1, 118; F = 5.6; P = .02$), mouthed ($df = 1, 118; F = 16.28; P < .001$), and shook ($df = 1, 118; F = 16.48; P < .001$) more first-instar zoeae than silversides, but they also avoided them more ($df = 1, 118; F = 12.53; P < .001$).

Small silversides and killifish avoided spined and despined first-instar zoeae less often than did large fishes, whereas the numbers of captures, mouthings, ingestions, and shakings were greater for larger fishes (Figs. 9 and 11, Tables 5 and 7). Intermediate-sized silver-

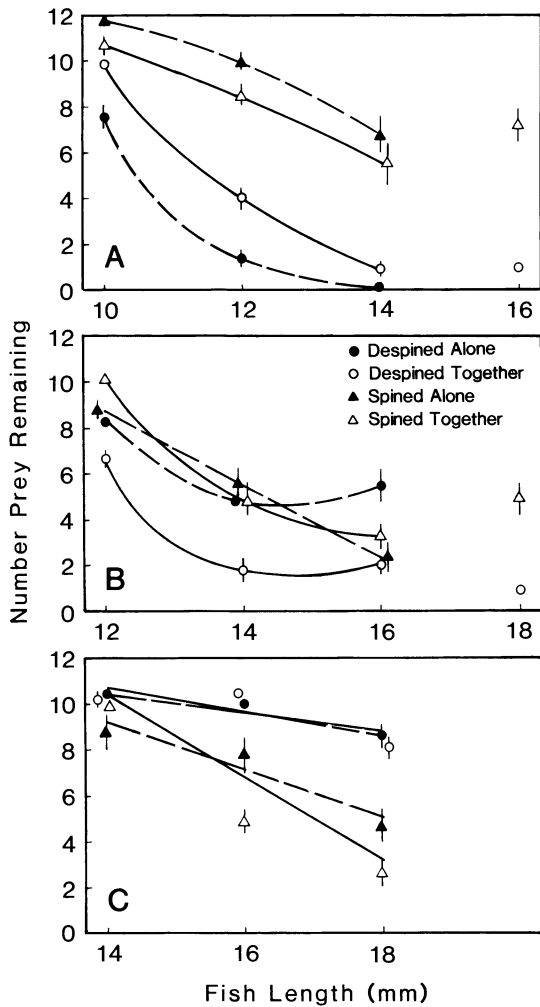


FIG. 6. Number of spined first-instar zoeae remaining after 24 h when fed to *Menidia menidia* either separately or together with despined (A) second-instar, (B) third-instar, and (C) fourth-instar *Rhithropanopeus harrisii*. Error bars show ± 1 SE.

sides attacked first-instar zoeae (Fig. 9, Table 5), and large silversides shook fourth-instar zoeae, most often (Fig. 10, Table 6).

Silversides and killifish did not increase their preference for despined zoeae from the first to the second half of the observation periods, but instead they learned to avoid both types of zoeae (Tables 5-7). Fish generally avoided, attacked, captured, mouthed, and swallowed zoeae less often during the second than the first half of the observation period (Figs. 5-7). Fishes were very hungry at the conclusion of the observation period, but zoeae always remained uneaten.

Antipredatory behavior of zoeae

Rhithropanopeus harrisii zoeae rarely attempted to evade or escape attacks by silversides and killifishes (Figs. 9-11, Tables 5-7), but they did display antipred-

atory behaviors that complemented their armor. Following vigorous attacks, zoeae increased their size by flaring their antennal spines and flexing their abdomens back over the carapace. A pair of spines on the fifth abdominal somite also became erect when zoeae arched backwards. Zoeae remained motionless in this position until fish lost interest, whereupon they collapsed their spines and resumed swimming.

The frequency of evasion ($df = 1, 118; F = 2.02; P = .16$) and escape ($df = 1, 118; F = 0.54; P = .46$) from silversides and killifish was similar, but zoeae fed to killifish flared their spines more often ($df = 1, 118; F = 49.7; P < .001$). First-instar zoeae attempted escapes and flared their spines more when attacked by fishes of intermediate size classes, but fourth-instar zoeae evaded and escaped small silversides more often than large ones (Figs. 9-11, Tables 5-7). Despined zoeae did not attempt to evade or escape attacks more often than spined zoeae. Zoael behavior did not change during the observation period.

Effects of spine amputation on zoeae

Both types of controls and behavioral observations indicated that spine amputation did not significantly affect the survival or swimming of *R. harrisii* zoeae. Survival was not significantly different between spined and despined zoeae regardless of whether they were placed in bowls separately or together ($df = 3, 44; F = 0.59; P = .627$). Nor was survival of zoeae that had an antennule removed significantly different from those that were not operated on and fed to 14-mm silversides ($df = 1, 26; F = 0.03; P = .862$). Finally, fish quickly consumed all *Artemia* nauplii that were offered at the conclusion of every feeding trial, indicating that fish were still hungry even though zoeae remained.

DISCUSSION

Adaptive significance of zoeal spines

Spines of crab zoeae appear to have been selected primarily to prevent predation by small fishes rather

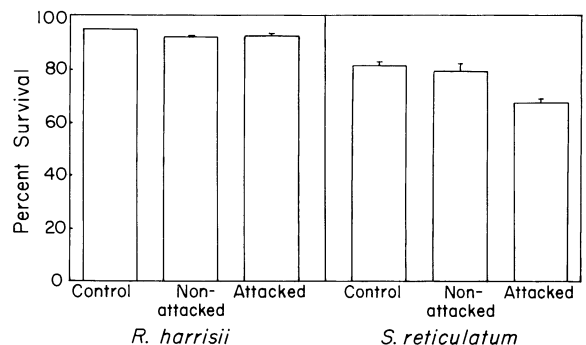


FIG. 7. Percent survival to metamorphosis of *Rhithropanopeus harrisii* and *Sesarma reticulatum* zoeae that were attacked by *Menidia menidia*, exposed to fish but not attacked, or not exposed to fish. Error bars show ± 1 SE.

TABLE 4. Occurrence of damage to 360 *Rhithropanopeus harrisia* and 360 *Sesarma reticulatum* zoeae not offered to *Menidia menidia*, of zoeae offered but not attacked, and zoeae attacked by fish.

Damage	Control	Not attacked	Attacked
<i>R. harrisia</i>			
Damaged spines	8	7	39
Dorsal	8	7	25
Rostral	0	0	4
Antennal	0	0	10
Mangled bodies	0	0	0
<i>S. reticulatum</i>			
Damaged spines	0	0	11
Dorsal	0	0	7
Rostral	0	0	1
Antennal	0	0	3
Mangled bodies	0	0	21

than by predatory invertebrates, and do not appear to have evolved to stabilize the organism or retard its sinking. Spines can slow sinking when flared, but I have seen *R. harrisia* zoeae splay their spines only when attacked. Trochophores and rotifers also appear to flare their spines only after attack (Gilbert 1967, Cowden et al. 1984, Pennington and Chia 1984). Furthermore, cladocerans with helmets and longer spines actually sink faster than nonexuberant forms (Dodson 1984), so that spines of crustacean zooplankters do not appear to have evolved to resist sinking.

Like the spines of crab zoeae, the setae of trochophores and the frontal horns of barnacle nauplii did not deter predation by filter-feeding mussels and tunicates (Cowden et al. 1984). Ctenophores have been reported to coexist with high densities of crab zoeae while the copepod population was being decimated (Cronin et al. 1962, Burrell and Van Engel 1976), indicating that they do not exert a strong impact on larval populations. However, the shadow response of crab zoeae (Forward 1986) rather than their spines limits predation by ctenophores.

The fitness of zoeae clearly is increased because spines prevent predation by fishes. The size of first-instar *R. harrisia* zoeae, from the tips of the dorsal to the rostral spines, is 2 mm, but without spines the body size is only 0.4 mm. Thus, spines quintuple the size of zoeae. Even a small increase in prey size will greatly decrease the profitability of the prey to a small fish, but will increase the handling costs to large fish only slightly (Werner 1974, Durbin 1979, Hunter 1980, Unger and Lewis 1983). Indeed, the effectiveness of zoeal spines in preventing predation appeared to diminish with each successive instar, despite the constant ratio of spine length to body size throughout development. However if alternative prey are available, even adult silversides and killifish strongly avoid *R. harrisia* zoeae (Morgan 1986, 1987).

Spination vs. large body size as antipredatory adaptations

Fishes select the largest manageable prey (Zaret 1980a). The elongate spines of *R. harrisia* zoeae increase their size in all directions without greatly increasing their visibility to fishes, as would a substantial increase in body size. Once detected, spines are more effective than a large body at deterring predation by gape-limited fishes, because they not only increase the size of the zoeae but are noxious. The zoeae are defended by multiple sharp spines so that fishes cannot manipulate the prey for easy ingestion. Zoeae frequently became lodged in the pharynx of small fish and sometimes killed the fish, as has also been observed by Lebour (1919). Only juvenile silversides died while preying on zoeae, presumably because the large mouths of killifish and adult silversides are better able to handle armored prey.

Long spines absorb the brunt of attacks by fishes and may break, but otherwise leave the bodies of *R. harrisia* zoeae undamaged. Zoeae were sometimes attacked over 30 times in quick succession but still swam away. *Rhithropanopeus harrisia* zoeae that were attacked had the same survival and duration to metamorphosis as did zoeae that had not been attacked, whereas the short spines and large body of *S. reticulatum* were less ef-

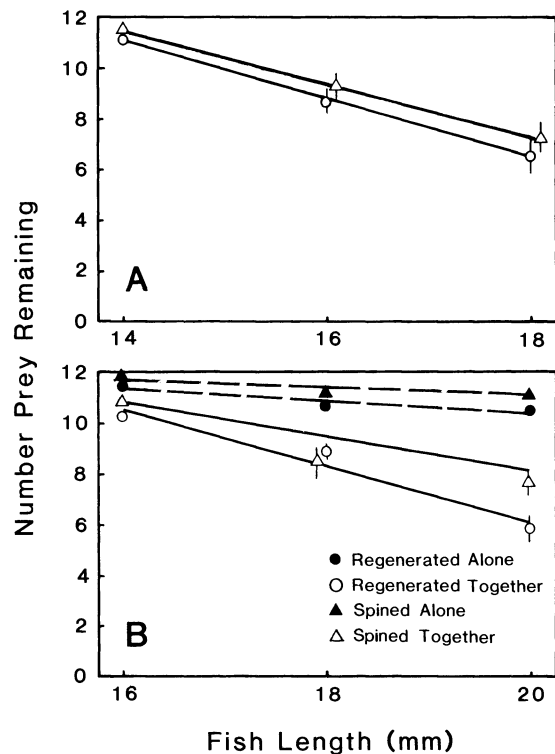


FIG. 8. Number of third-instar (A) and fourth-instar (B) *Rhithropanopeus harrisia* zoeae with partially regenerated or normal spines surviving after being fed either separately or together to small *Menidia menidia*. Error bars show ± 1 SE.

TABLE 5. Analyses of variance of behavioral interactions between spined and despined first-instar *Rhithropanopeus harrisi* zoeae (Prey) and *Menidia menidia* 6–16 mm long (Length), when the two prey types were fed to the fish either alone or together (Treatment) during two consecutive 5-min periods (Time).

Source	df	ss	Source	df	ss
Avoids per pursuit	7	1140.30	Mouthings per capture	9	369.75
Prey	1	227.45***	Prey	1	549.86***
Treatment	1	0.71	Treatment	1	31.58*
Time	1	134.50***	Time	1	79.01***
Length	1	588.02***	Length	1	1806.75***
(Length) ²	1	0.02	(Length) ²	1	25.88
P × L	1	167.32***	P × L	1	445.77***
Time × L ²	1	33.16*	P × L ²	1	35.47*
Error	472	3175.96	Trt × L ²	1	46.93*
Attacks per pursuit	7	2310.63	P × Time	1	39.90*
Prey	1	87.01**	Error	470	3327.76
Treatment	1	132.11***	Shakes per capture	8	1122.72
Time	1	588.20***	Prey	1	5.56
Length	1	1118.06***	Treatment	1	14.26
(Length) ²	1	184.57***	Time	1	24.21
Trt × L ²	1	68.44*	Length	1	755.00***
Time × L ²	1	85.28**	(Length) ²	1	42.93*
Error	472	5425.64	P × L	1	114.64***
Captures per attack	9	3075.56	P × L ²	1	84.17***
Prey	1	761.93***	Time × L	1	37.08*
Treatment	1	13.32	Error	471	3076.69
Time	1	102.28***	Evasions per pursuit	5	24.08
Length	1	1633.15***	Prey	1	0.05
(Length) ²	1	1.93	Treatment	1	5.03
P × L	1	476.29***	Time	1	2.55
Trt × L ²	1	18.39*	Length	1	5.01
Time × L	1	60.76***	(Length) ²	1	11.43*
P × Trt	1	20.49*	Error	474	1010.64
Error	470	1744.79	Escapes per attack	5	80.49
Ingestions per capture	9	3275.55	Prey	1	18.45**
Prey	1	895.91***	Treatment	1	26.65**
Treatment	1	26.53*	Time	1	0.19
Time	1	37.38**	Length	1	6.79
Length	1	1370.19***	(Length) ²	1	28.43***
(Length) ²	1	81.89***	Error	474	1213.10
P × L	1	784.75***	Flares per attack	7	30.93
Trt × L ²	1	43.04***	Prey	1	10.77***
Time × L	1	22.57*	Treatment	1	6.88***
P × Time	1	39.77**	Time	1	1.30
Error	470	2159.94	Length	1	0.68
			(Length) ²	1	2.72*
			P × L ²	1	6.88***
			Error	472	247.84

fective at preventing fatalities. Thus small zoeae defended by long spines are more likely to survive encounters with fishes than large-bodied zoeae that are unprotected or protected by short spines. However, spine length may be correlated with exoskeleton thickness or rigidity, as it is in cladocerans (Dodson 1984), which may partially account for the greater survival of *R. harrisi* than *S. reticulatum* zoeae.

Prey that survive attacks often suffer broken spines (Kerfoot 1977a, Murtaugh 1981, Strathmann 1981, Vermeij 1982). Dorsal spines were broken most often during attacks, but they can be entirely regenerated by *R. harrisi* zoeae within two molts (Freeman 1983 and S. G. Morgan, *personal observation*) even though larval development includes only four molts over a 12-d period at 25°C (Costlow et al. 1966). When all spines

were removed, they did not regain their initial length but could be as effective as undamaged spines in preventing fish predation. Thus zoal spines quickly regenerate, are effective while partially regenerated, and may cost little to produce because they are composed only of epidermis, hemolymph, and cuticle (Freeman 1983).

Jacobs (1967, cited in Riessen 1984) has calculated that the cost of growing helmets and spines to cladocerans also is slight. The decreased survival, fecundity, and growth rates of cyclomorphic cladocerans (Kerfoot 1977b, O'Brien et al. 1980, Riessen 1984) may not be due to the energy allocated to the production of spines and helmets as much as to the concurrent lateral compression of the body, which results in smaller brood chambers and decreased feeding efficiency (Riessen

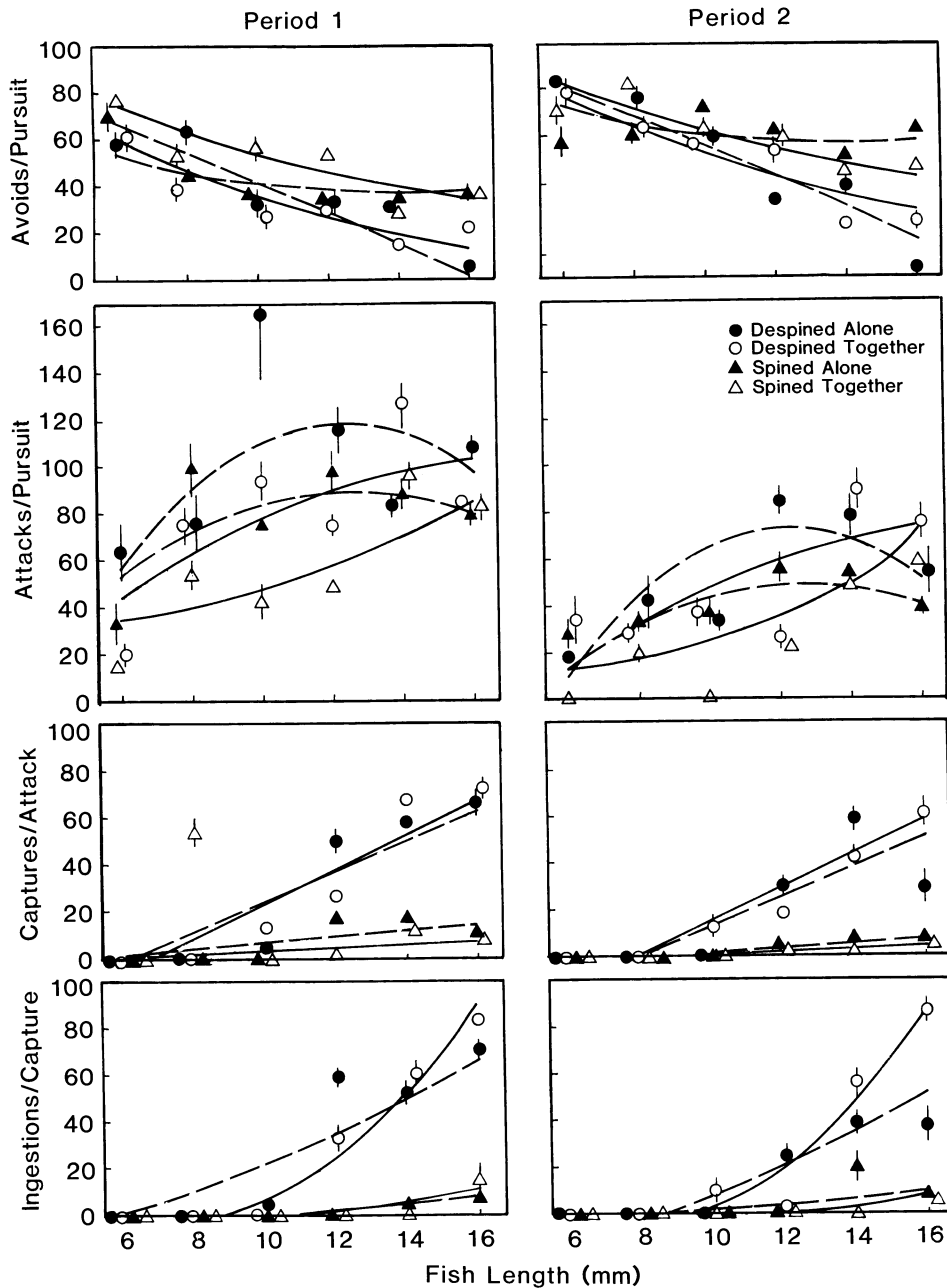


FIG. 9. Percent occurrence of behaviors resulting from feeding trials with *Menidia menidia* 6–16 mm long confined with despined and spined first-instar *Rhithropanopeus harrisi* zoeae during two consecutive 5-min periods. Spined and despined zoeae were fed to fish either separately or together. Error bars show ± 1 SE.

1984). However, the asymmetrical growth of the posterior spines of cyclomorphic rotifers may indicate that there is a cost to spine production, provided one spine is as effective as two in deterring predation (Gilbert and Stemberger 1984).

Detection and avoidance of spines by fishes

Although the visual acuity of larval fish is poorer than that of adults (Durbin 1979, Li et al. 1985, Hair-

ston et al. 1982, Breck and Gitter 1983, Unger and Lewis 1983, Neave 1984), small fishes can detect zoeal spines and rapidly learn to avoid them. Fishes quickly established a preference for despined zoeae, so that their behavior during the first half of the observation period was not significantly different from that of the second half. Feeding trials designed to test further the discriminatory behavior of fish were inconclusive, perhaps because despined and spined prey merely differ

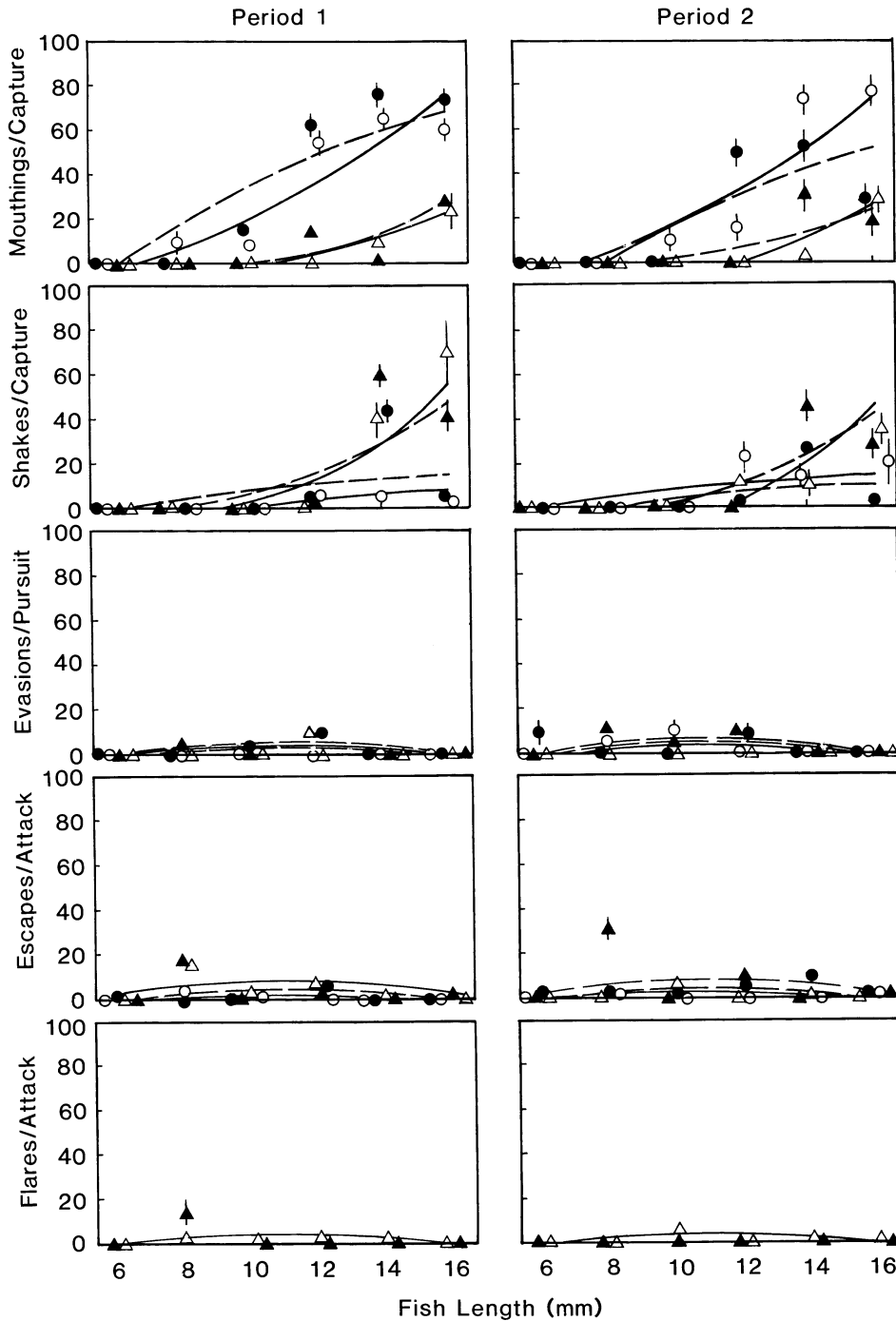


FIGURE 9. Continued.

in the extent of their unpalatability to fishes; the experimental design may be more effective when preferred prey are used in opposition to noxious prey.

Fish larvae are apparently capable of detecting spines and learning to avoid crab zoeae in the field as well as the laboratory. Alvarino (1980) surveyed the coastal waters of California for 3 yr and discovered that the abundance of anchovy larvae was positively correlated

with patches of zooplankton containing their prey (copepods, euphausiids), but was negatively correlated with patches containing crab zoeae. Furthermore, menhaden, herring, and redfish larvae did not feed on crab zoeae even though the zoeae often were very abundant and similar in size to their prey (Mulkana 1966, Marak 1974, Hunter 1980). Aggregations of zooplankters often may be encountered in patchily distributed plankton

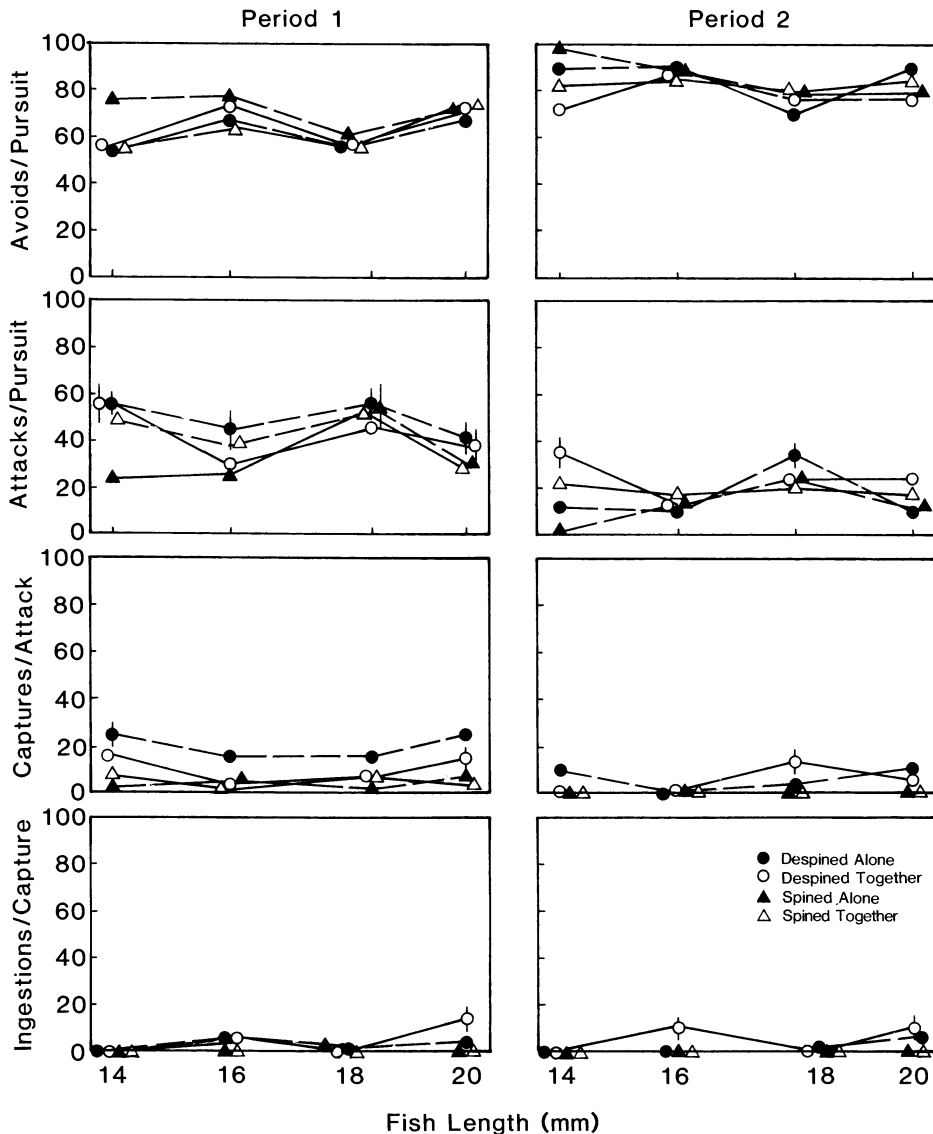


FIG. 10. Percent occurrence of behaviors resulting from feeding trials with *Menidia menidia* 14–20 mm long confined with despined and spined fourth-instar *Rhithropanopeus harrisii* zoeae during two consecutive 5-min periods. Spined and despined zoeae were fed to fish either separately or together. Error bars show ± 1 SE.

communities, and could hasten learning by fish to avoid noxious prey or to take advantage of palatable prey (Bohl 1982, Dill 1983, Bronmark et al. 1984).

Adult fish also can detect spines, because they have been observed to nip off the extremely elongate rostral spine of porcellanid zoeae in the field before ingesting the zoea (S. Stancyk, *personal communication*). They also learn to avoid spined (Hoogland et al. 1957) and distasteful prey (Kerfoot et al. 1980, Bronmark et al. 1984).

Antipredatory behavior of zoeae

Rhithropanopeus harrisii zoeae do not attempt to evade or escape attacks by fishes, but instead rely on armor and complementary behavioral adaptations for

survival. Spine flaring and arching backwards further increase the size of the zoeae, making it more difficult for fishes to ingest them. Zoeae remain motionless while in their defensive posture until fish lose interest. Lindstrom (1955) also found that fish quickly lose interest in motionless prey, and other organisms also erect spines (Cowden et al. 1984, Pennington and Chia 1984), arch backwards (Magnahagen and Wiederholm 1982), and remain motionless when attacked (Cowden et al. 1984, Magnahagen 1985).

Summary of selective pressures for zoeal spines

Zoeal spines were demonstrated in this study to be effective against two fishes that predominate in upper estuaries of the east coast of the United States (Mc-

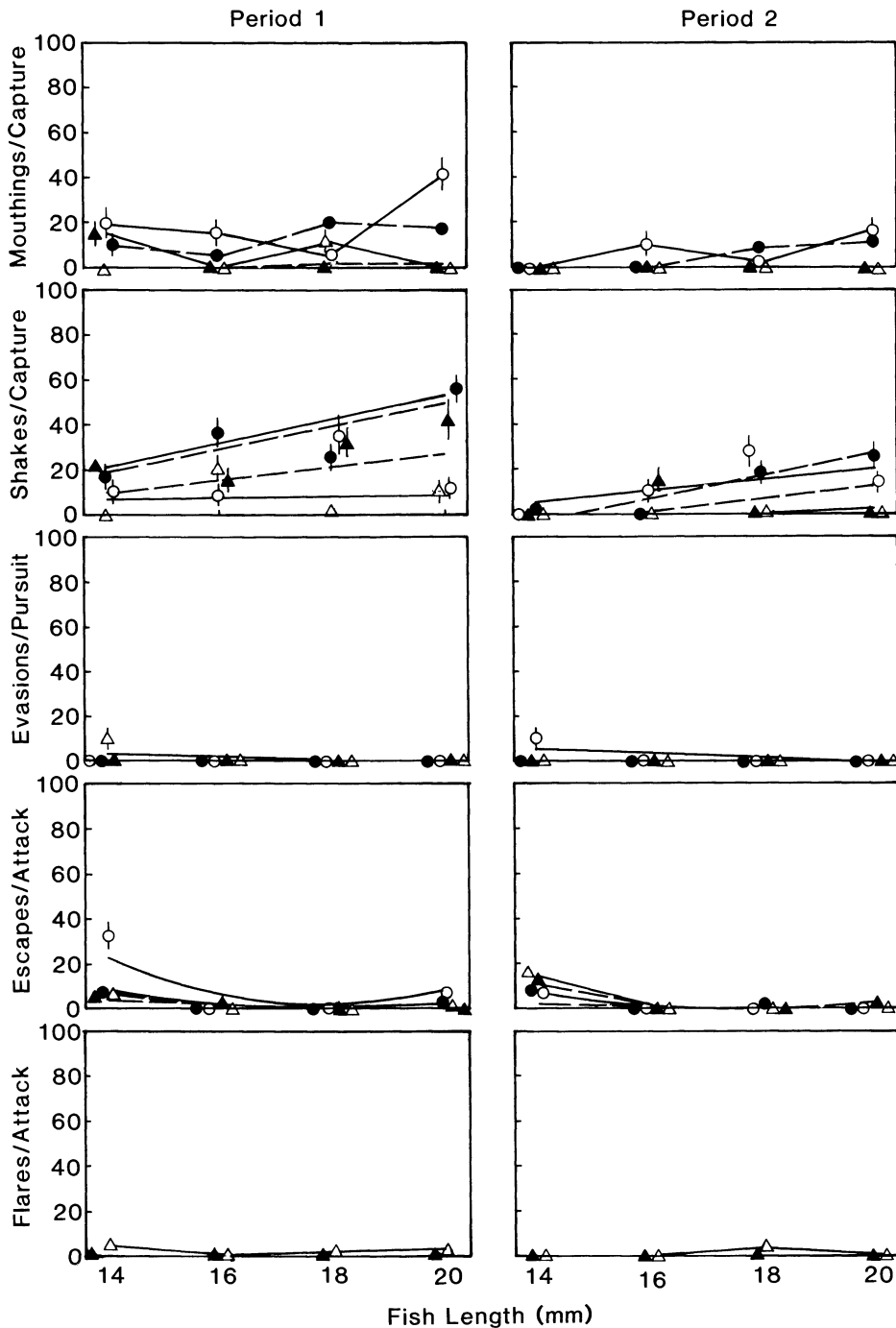


FIGURE 10. Continued.

Erlean et al. 1972, Subrahmanyam and Drake 1975, Hillman et al. 1977, Weinstein 1979, Boesch and Turner 1984), where larvae of *R. harrisii* develop. Planktivorous fishes apparently exert strong selective pressure for crab zoeae to produce spines rather than a large unarmed body. Spines are noxious, enhance survival of attacked zoeae, regenerate quickly, are effective while partially regenerated, cost relatively little to produce, and do not greatly increase the visibility of zoeae.

Fishes apparently can detect spines and quickly learn to avoid them, which increases the effectiveness of spines as an antipredatory adaptation and the rate of evolution of the trait.

Selection for spines in freshwater vs. marine plankters

Rotifers produce elongate spines and cladocerans form helmets and tail spines during summer when pre-

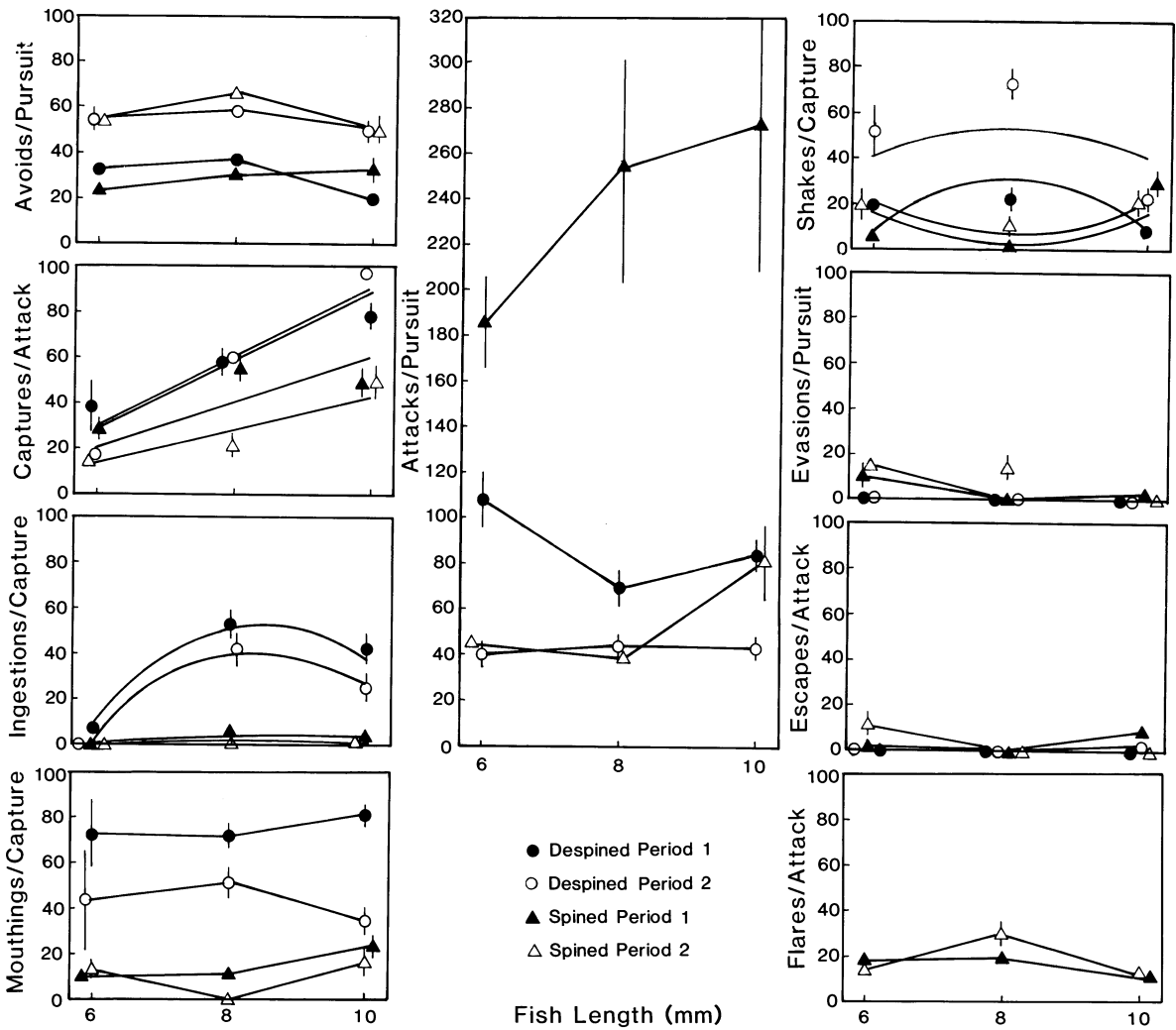


FIG. 11. Percent occurrence of behaviors resulting from feeding trials with *Fundulus heteroclitus* 6–10 mm long confined with despined and spined first-instar *Rhithropanopeus harrisi* during two consecutive 5-min periods. Error bars show ± 1 SE.

dation by invertebrates intensifies in freshwaters. Helmets and spines increase the hydrodynamic efficiency of cladocerans, and thereby increase their evasive capabilities (O'Brien and Vinyard 1978, Grant and Bayly 1981, Barry and Bayly 1985, Mort 1986). However, if the organism is captured, helmets (especially those equipped with a horn; Kreuger and Dodson 1981, Havel and Dodson 1984) and tough, inflexible carapaces (Kerfoot et al. 1980, Williamson 1983, Dodson 1984, Havel 1985) make it difficult for predatory invertebrates to manipulate their prey, which may escape. Rotifers that rely entirely on spines, a rigid lorica, and postcontact antipredatory behaviors frequently survive attacks by predatory invertebrates, whereas those that rely on evasive maneuvers do not (Szlauer 1965, Gilbert and Williamson 1979, Gilbert and Stemberger 1984).

Although the helmets and spines of cladocerans deter

predation by copepods, notonectids, midge larvae, and mysids, they are ineffective against fishes (Dodson 1974, Kerfoot 1977a, O'Brien 1979, Kerfoot et al. 1980, O'Brien et al. 1980, Zaret 1980b, Murtaugh 1981, Bohl 1982). Kerfoot (1977a) implicated fish fry in the removal of large, long-spined cladocerans from the littoral zone of a lake, permitting the return of small, fecund, nonexuberant forms. Many other studies have documented that fishes prefer large cladocerans to smaller plankters (Zaret 1980a). Only Jacobs (1966, cited in O'Brien and Vinyard 1978) has reported that helmeted forms suffer less predation by fishes than nonhelmeted forms, although he did not identify whether helmets increased their evasive capabilities or made them more difficult to swallow.

Why do spines appear to be primarily effective against invertebrates in freshwaters, and against fishes in marine systems? The answer lies in differences in the size

TABLE 6. Analyses of variance of behavioral interactions between spined and despined fourth-instar *Rhithropanopeus harrisi* zoeae (Prey) when the two prey types were fed to the fish either separately or together (Treatment) and *Menidia menidia* 14–20 mm long (Length), during two consecutive 5-min periods (Time).

Source	df	ss	Source	df	ss
Avoids per pursuit	6	140.50	Shakes per capture	6	571.42
Prey	1	8.29*	Prey	1	138.49***
Treatment	1	11.87*	Treatment	1	103.14***
Time	1	117.02***	Time	1	135.07***
Length	1	0.06	Length	1	77.46**
(Length) ²	1	0.96	(Length) ²	1	1.83
Trt × L	1	8.03*	Trt × Time	1	58.09*
Error	312	571.19	Error	312	2803.74
Attacks per pursuit	7	576.59	Evasions per pursuit	6	8.24
Prey	1	14.97	Prey	1	0.00
Treatment	1	4.85	Treatment	1	2.61*
Time	1	477.64***	Time	1	1.26
Length	1	10.54	Length	1	3.37*
(Length) ²	1	15.11	(Length) ²	1	1.26
Trt × L	1	40.06**	Error	312	189.92
Trt × L ²	1	20.27*	Escapes per attack	9	223.66
Error	311	1598.27	Prey	1	0.45
Captures per attack	5	320.00	Treatment	1	0.07
Prey	1	136.35***	Time	1	13.55*
Treatment	1	16.44*	Length	1	151.63***
Time	1	140.40***	(Length) ²	1	84.00***
Length	1	0.20	P × L	1	19.30**
(Length) ²	1	14.37	P × L ²	1	11.18*
Error	313	1252.41	Trt × L	1	21.07**
Ingestions per capture	5	36.08	Trt × L ²	1	15.91**
Prey	1	20.53***	Error	309	643.60
Treatment	1	0.00	Flares per attack	5	2.53
Time	1	1.04	Prey	1	5.53***
Length	1	3.56	Treatment	1	5.48***
(Length) ²	1	0.66	Time	1	1.34
Error	313	517.94	Length	1	0.13
Mouthings per capture	5	220.38	(Length) ²	1	0.26
Prey	1	5.53***	Error	313	12.65
Treatment	1	5.48***			
Time	1	1.34			
Length	1	0.13			
(Length) ²	1	0.26			
Error	313	1624.94			

and diversity of invertebrate predators, plankton morphology and behavior, and the focus of research in the two systems.

First, all but one of the marine invertebrates tested by Cowden et al. (1984) and in this study were sufficiently large to prey on spined larvae. In contrast, freshwater invertebrate predators are relatively small in comparison with their zooplankton prey, so that a slight increase in the size of the prey provided by helmets or longer spines is effective at deterring predation.

Second, marine invertebrates are more diverse and have a wider array of feeding modes, many of which may readily manage spined zooplankters.

Third, important planktivores in freshwaters appear to be unimportant in marine waters. Of the predominant invertebrate planktivores in freshwaters (copepods, rotifers, cladocerans, corixids, notonectids, aquatic insect larvae, and mysids), only mysids and copepods are abundant in marine waters. Furthermore, predaceous copepods and mysids simply may be too small to prey upon zoeae. Although mysids do not prey

on zoeae (Fulton 1982), it is still conceivable that zoeae without spines would be vulnerable to predation. Predaceous copepods are capable of preying on soft-bodied fish larvae (Lillelund and Lasker 1974, Turner et al. 1985), although they may not be able to handle the armor of zoeae.

Fourth, the multiple spines of crab zoeae are more effective at deterring predatory fishes than the single fixed spine and helmet of freshwater cladocerans, because they preclude the possibility of manipulating the zoea so it can be swallowed easily and painlessly. Although the small body size of rotifers renders them unattractive to adult fishes, their multiple spines may deter larval fishes because they operate like zoeal spines. Like zoeae, rotifers flare spines upon attack, lodge in pharynxes of predatory rotifers, passively sink with spines flared once rejected, and then collapse their spines and resume swimming.

Fifth, the spines of freshwater cladocerans may deter predation by young fishes even though they are ineffective against adult fishes. Bluegill fry in lakes select

TABLE 7. Analyses of variance of behavioral interactions between spined and despined first-instar *Rhithropanopeus harrisi* zoeae (Prey) and *Fundulus heteroclitus* 6–10 mm long (Length), when the two prey types were fed the fish during two consecutive 5-min periods (Time).

Source	df	ss	Source	df	ss
Avoids per pursuit	4	190.04	Attacks per pursuit	5	1086.45
Prey	1	0.56	Prey	1	193.94**
Time	1	161.52***	Time	1	739.98***
Length	1	5.67	Length	1	1.11
(Length) ²	1	21.95	(Length) ²	1	0.56
Error	113	848.34	P × T	1	139.93*
Captures per attack	4	361.64	Error	112	2882.88
Prey	1	117.01**	Ingestions per capture	6	554.04
Time	1	36.86	Prey	1	263.96***
Length	1	194.30***	Time	1	36.61*
(Length) ²	1	7.29	Length	1	73.39**
Error	113	1596.51	(Length) ²	1	78.74**
Mouthings per capture	4	754.01	P × L	1	31.12*
Prey	1	562.14***	P × L ²	1	70.64**
Time	1	150.94**	Error	111	801.09
Length	1	33.14	Shakes per capture	5	275.38
(Length) ²	1	1.19	Prey	1	207.24***
Error	113	1761.00	Time	1	47.94
Evasions per attack	4	19.28	Length	1	2.46
Prey	1	8.10	(Length) ²	1	7.03
Time	1	0.03	P × L ²	1	96.18*
Length	1	6.30	Error	112	1574.98
(Length) ²	1	4.55	Escapes per attack	4	9.45
Error	113	24.97	Prey	1	4.30
Flares per attack	4	346.42	Time	1	0.36
Prey	1	329.21***	Length	1	0.38
Time	1	2.31	(Length) ²	1	4.28
Length	1	2.93	Error	113	207.40
(Length) ²	1	11.78			
Error	113	360.65			

Bosmina spp. and avoid *Daphnia* spp. (Werner 1969, Siefert 1972, Beard 1982). However, despite the considerable attention devoted to predation in freshwaters, the effectiveness of spines of freshwater zooplankters against larval fishes apparently has not been determined.

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