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Adaptive significance of hatching rhythms and dispersal patterns of estuarine crab larvae: avoidance of physiological stress by larval export?

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Abstract: Estuarine crabs commonly display two larval dispersal patterns in which larvae are either exported from or retained within estuaries. The semiterrestrial fiddler crab *Uca minax* (LeConte, 1855) hatches on nocturnal spring high tides in the upper estuary and larvae are rapidly transported downstream. The mud crab *Rhithropanopeus harrisii* (Gould, 1841) hatches on nocturnal high tides of any amplitude and larvae are retained behaviorally in the upper estuary throughout development. If larvae are exported from the estuary to avoid environmental stress, then exported larvae should be less tolerant of high temperatures and low salinities than retained larvae. Larvae of these two species of estuarine crabs were hatched at 20‰ and 25 °C and subjected to salinities of 0, 5, 10, 20, and 30‰, temperatures of 25 and 35 °C, and exposure times of 2, 6, 12, and 48 h. Larvae of both species reared at 30 or 20‰ survived well, while those reared in fresh water all died within 2 h regardless of temperature. Mud crab larvae reared at 5 and 10‰ survived better at the lower temperature (25 °C), higher salinity, and shorter exposure times. There was no significant effect of temperature or salinity on the survival of fiddler crab larvae, although survival decreased with increasing exposure time. Thus, the hypothesis that fiddler crab larvae are exported into stable coastal waters to reduce physiological stress is not supported. However, fiddler crab larvae may have evolved to be very tolerant of extreme temperature and salinity stress because they, unlike mud crabs, often release their larvae into shallow creeks. Most fiddler crab larvae are released on nocturnal spring high tides, which facilitates dispersal from tidal creeks. However, freshwater runoff and heat transferred from the marsh surface to flooding waters may still create stressful conditions for larvae soon after they are released. Larval release on spring high tides may facilitate dispersal from tidal creeks.

Key words: Larva; Dispersal; Temperature; Salinity; Hatching; Estuary

INTRODUCTION

Most marine organisms have a complex life cycle in which the larval phase disperses from the adult habitat to develop in the plankton before returning to the habitat and metamorphosing. Organisms inhabiting estuaries along the eastern coast of the U.S. commonly display two larval dispersal patterns in which larvae are either exported from or retained within estuaries. Estuarine organisms that retain their larvae in estuaries include some species of molluscs, barnacles, decapods, and fishes (Bousfield, 1955;

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Wood & Hargis, 1971; Sandifer, 1973; Goy, 1976; Cronin, 1982; Ouellet & Dodson, 1985; Weinstein *et al.*, 1980), whereas other species of barnacle nauplii and decapod larvae are exported into coastal waters (Bousfield, 1955; Dudley & Judy, 1971; Sandifer, 1973; Christy & Stancyk, 1982; Truesdale & Andryszak, 1983).

Selection could favor export of larvae from estuaries if (1) spreading larvae over several estuaries dampens variation in survival and reproduction of an individual's descendents (Strathmann, 1974), or (2) survival or growth of larvae is greater outside the estuary (Christy, 1982; Strathmann, 1982). Simulation models of the consequences of larval dispersal on different spatial scales and under different patterns of environmental variation revealed that there is no advantage to spreading larvae among estuaries when the carrying capacities or probabilities of invading an estuary differ consistently (Palmer & Strathmann, 1981). Furthermore, adaptation to local conditions and homing by organisms provide indirect evidence against the hypothesis that spatial and temporal variability of estuaries has selected for dispersal of larvae among estuaries (Strathmann, 1982).

However, larvae may be exported from the estuary if starvation, predation or physiological stress reduces the probability of survival or growth in the estuary. Estuaries are generally at least as productive as coastal waters (Ryther, 1959; Malone, 1977; Ferguson *et al.*, 1980), so that it is unlikely that larvae will find more food offshore. However, the greater productivity of estuaries does support more predators (Weinstein, 1979), and therefore, predation may be less in coastal waters. Strathmann (1982) compiled the instantaneous mortality rates of copepods in estuarine and coastal waters and found that mortality rates were greater in estuaries.

There is also evidence to support the hypothesis that hatching rhythms and larval behaviors may have evolved to reduce physiological stress. Semiterrestrial crabs often release their larvae into waters of shallow tidal creeks, which may have salinities of 0‰ and temperatures exceeding 40 °C during the day (Dollard, 1980). At 40 °C and 10‰, 50% of newly hatched larvae of the fiddler crabs *Uca minax* die in 1 h of exposure (Vernberg & Vernberg, 1975). Thus, some species of semiterrestrial crabs release their larvae on nocturnal spring high tides when the water volume is greatest in the upper estuary, and consequently the larvae are swept rapidly downstream on ebbing spring tides. Such seaward dispersal presumably minimizes the exposure of larvae to low salinities and high temperatures (Wheeler, 1978; Saigusa, 1981; Christy, 1982).

If newly hatched larvae that are rapidly transported from the estuary avoid environmental stress, then exported larvae should be less tolerant of high temperatures and low salinities than are retained larvae. To test this hypothesis, I selected two species of crabs which coexist at the heads of estuaries in salinities of 0–25‰. Larvae of the semiterrestrial fiddler crab hatch on nocturnal spring high tides and are exported from the estuary (De Coursey, 1979; Christy & Stancyk, 1982; Truesdale & Andryszak, 1983; Salmon *et al.*, 1986). In contrast, larvae of the subtidal mud crab *Rhithropanopeus harrisii* hatch within several hours of sunset on high tides of any amplitude (Forward *et al.*, 1986), and remain in the upper estuary behaviorally (Cronin, 1982; Lambert & Epifanio, 1983).

The experiment was designed to determine the larval survival of both species following exposure to high temperatures and low salinities for various durations, and to simulate the most physiologically stressful situation estuarine larvae are likely to encounter.

METHODS AND MATERIALS

Ovigerous *U. minax* (LeConte, 1855) and *R. harrisii* (Gould, 1841) were collected during July and August from the North and Neuse Rivers, North Carolina, respectively. Water temperatures at the collection sites ranged from 25 to 35 °C, and the salinities ranged from 15 to 22‰. Crabs were placed individually in 20‰ water contained in 19-cm culture dishes several days before their eggs hatched. All ovigerous females were held at 25 °C. Adults and larvae were maintained at a photoperiod of 12 h light: 12 h dark.

Following hatching, larvae were removed from 20‰ water and subjected to lower salinities for various durations. Larvae were either continuously exposed to these low salinities or reintroduced into high-salinity waters. The experiments were conducted at moderate and high temperatures. Thus, larvae from four females of each species were subjected to salinities of 0, 5, and 10‰, temperatures of 25 and 35 °C, and exposure times of 2, 6, 12, and 48 h. Survival of these larvae were compared with those reared at the same temperatures but more favorable salinities: 20‰ for mud crab larvae (Costlow *et al.*, 1966), and 20 and 30‰ for fiddler crab larvae (Vernberg & Vernberg, 1975). Seawater was diluted with deionized water and allowed to stand for at least one day prior to use in experiments. Larvae were introduced shortly after hatching into waters of appropriate temperature, but were allowed to acclimate for $\approx$20 min at intermediate salinities if the change in salinity was > 10‰. Larvae that were exposed for 2, 6, or 12 h were reintroduced to 20‰ seawater following their exposure to lower salinities. Larvae undergoing changes > 10‰ while being reintroduced to 20‰ seawater, again were allowed to acclimate to intermediate salinities. Fifty larvae, 10 in each of five 4-cm culture dishes, were reared at each combination of temperature, salinity, and exposure time. Larvae were fed *Artemia* (Great Wall brand) nauplii and provided with clean water daily. Survival was recorded 48 h after the beginning of the experiment. The experiment was terminated after 2 days, before larvae began to molt to the second instar. Survival data were arcsine-transformed, and orthogonal polynomial contrasts were analyzed by the ANOVA.

RESULTS

Both fiddler crab and mud crab larvae reared at control salinities (20, 30‰) survived well (*U. minax*: 30‰ = 98.5 $\pm$ 0.96%, 20‰ = 99.5 $\pm$ 0.50%; *R. harrisii*: 20‰ = 99.1 $\pm$ 0.58%), whereas all larvae died within 2 h when reared in deionized water. Fiddler crab larvae survived significantly better at extreme temperatures and

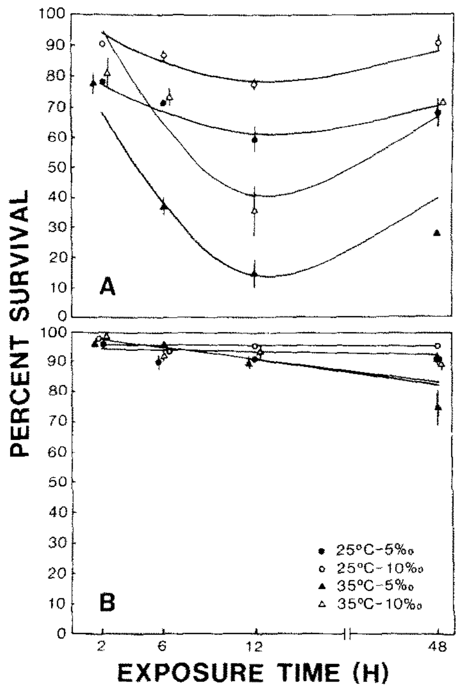

Fig. 1. Percent survival (±1 SE) of (A) *R. harrisii* and (B) *U. minax* zoeae reared under different combinations of temperature, salinity, and exposure time. Note: each data point is a result of a separate experiment and not the survival rate of a single cohort at different times.

salinities than did mud crab larvae (Fig. 1, Table I). Significantly more first instar mud crab larvae survived at the lower temperature (25 °C) and the higher salinity (10‰) than at the higher temperature (35 °C) and lower salinity (5‰). Mud crab larvae exposed to stressful temperatures and salinities survived better as exposure time decreased, except for those continually exposed (48 h) to only one salinity. There was no significant effect of temperature or salinity on the survival of fiddler crab larvae, although survival decreased with increasing exposure time.

Discussion

Selection for export or retention of estuarine larvae does not appear to be due to differential mortality of larvae exposed to extremes of estuarine temperatures and salinities. Although fiddler crab larvae are exported from the estuary, they can tolerate high temperature and low salinity better than mud crab larvae, which are retained within the estuary.

Previous investigators have found that mud crab larvae acclimatized to high-salinity waters and introduced to lower salinities survived less well than those released and

TABLE I

Results of 3-way ANOVA of temperature, salinity, and exposure time effects on *R. harrisii* and *U. minax* larvae. Exposure = linear effect of exposure time; $(\text{Exposure})^2$ = quadratic effect of exposure time.

R. harrisii Source	df	SS	*F* value	*P* value
Model	6	4.5788	18.79	0.001
Temperature	1	1.4475	35.64	0.001
Salinity	1	1.1027	27.15	0.001
Exposure	1	1.1037	27.18	0.001
$(\text{Exposure})^2$	1	1.4087	34.69	0.001
Temp. × Exp.	1	0.4326	10.65	0.01
Temp. × $(\text{Exp.})^2$	1	0.3701	9.11	0.01
Error	56	1.9404		
Total	62	6.8530		

U. minax Source	df	SS	*F* value	*P* value
Model	4	0.2867	2.62	0.05
Temperature	1	0.0188	0.69	NS
Salinity	1	0.0743	2.72	NS
Exposure	1	0.1719	6.28	0.05
$(\text{Exposure})^2$	1	0.0210	0.77	NS
Error	59	1.6138		
Total	63	1.9010		

reared at low salinities. Costlow *et al.* (1966) determined that > 90% of first instar mud crab larvae hatched and reared at 5‰ and 25 or 30 °C survived; whereas Christiansen & Costlow (1975) found that only 50 and 6% of first instar mud crab larvae reared at 5‰ survived when hatched at 10‰ and 25–30 or 30–35 °C. Similarly, mud crab larvae hatched at 10‰ and 20–25 or 30–35 °C and reared at 5‰ did not survive the first molt (Rosenberg & Costlow, 1979). Only 40% of mud crab larvae hatched at 20‰ and 25–30 °C and acclimated to 5‰ over 2 days survived to the second instar (Rosenberg & Costlow, 1979). Thus, fluctuating salinities are more stressful than prolonged exposure to low salinities for mud crab larvae.

In this study, larvae were acclimatized to high-salinity waters and quickly introduced to lower salinities, or acclimatized to high-salinity waters, introduced to lower salinities, and returned to the high salinity. The survival of mud crab larvae may improve relative to fiddler crab larvae if both were reared under less stressful conditions. However, the survival of mud crab larvae probably could not surpass that of fiddler crab larvae given the already high survival of the latter under demanding circumstances.

Fiddler crab larvae may have evolved a greater tolerance of extreme temperatures than mud crab larvae because, unlike mud crabs, fiddler crabs often release their larvae into shallow tidal creeks. *U. minax* are more abundant along creeks than the river because they prefer substrates of higher organic content for feeding and perhaps burrow construction (Whiting & Moroshi, 1974). Fiddler crab larvae released in creeks may suffer exposure to high temperatures or low salinities, even though peak hatching occurs on nocturnal spring high tides. Freshwater runoff may greatly reduce the salinities of shallow tidal creeks even during spring high tides. Temperatures also may remain high during evening spring high tides, because shallow waters heated throughout the day may become warmer as heat is transferred from the marsh surface to flooding waters.

Larvae that are stranded in pools as the tide ebbs would be particularly susceptible to physiological stress. Thus, fiddler crabs may hatch on spring high tides not only to reduce the risk of releasing larvae into fresh or very warm water, but to facilitate transport into deeper channels where environmental conditions are generally less severe. Corks used to simulate larvae all accumulated in tidal pools when released at spring low tide, whereas they were carried out to sea when released on a spring high tide (Saigusa, 1981). Furthermore, Saigusa (1981) found that two species of *Sesarma* (another genus of semiterrestrial crabs) which are less tolerant of fresh water hatch in closer synchrony with the nocturnal spring tides than does a third species which is more tolerant.

Fiddler crab larvae would be able to withstand salinity fluctuations over a series of tidal cycles unless they hatched in fresh water. However, if fiddler crab larvae were acclimatized to fresh water, then probably they would be able to survive stranding in freshwater tidal pools at least until the next high tide. Two species of *Sesarma* larvae hatched and reared in either spring water or tap water died in <48 h, and a third species died in <70 h (Saigusa, 1981).

Mud crab larvae may be less tolerant of physiological stress and hatch on nocturnal high tides of any amplitude, because they hatch subtidally and are much less likely to become stranded in tidal pools. Furthermore, mud crab larvae can regulate their horizontal position in the estuary, so that they can avoid physiological stress and congregate in areas most conducive to their development (Cronin, 1982).

Fiddler crab larvae may have evolved to be very tolerant of extreme temperature and salinity and hatch on nocturnal spring high tides to facilitate survival in and dispersal from tidal creeks. However, semilunar hatching and subsequent rapid seaward dispersal may also have evolved to facilitate larval escape from predation. Young planktivorous fishes are most abundant in low-salinity waters where fiddler and mud crabs hatch (Weinstein, 1979). Fiddler crab larvae are more vulnerable to fish predation than mud crab larvae, because they are smaller and have shorter spines (Morgan, in press). Peak release of fiddler crab larvae may occur on spring high tides to disperse the larvae quickly from tidal creeks and the upper estuary where predation could be greatest (Christy, 1982).

Mud crabs hatch subtidally, regulate their horizontal position in the upper estuary, and are well-defended against fish predation, so they may hatch on any nocturnal high tide. In fact, Forward *et al.* (1986) has determined that larval release occurs on high tides only when they occur between 2 h after sunset and 3–5 h before sunrise. When high tide occurs after 0300, larvae are hatched soon after sunset regardless of the tidal phase.

Therefore, hatching early in the evening is more important than hatching on high tide, and so reducing vulnerability to predators is probably more important than avoiding physiological stress or promoting initial seaward transport.

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