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Recruitment to adult habitats following marine planktonic development in the fiddler crabs, *Uca pugilator*, *U. pugnax*, and *U. minax*

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Abstract Three congeneric species of fiddler crabs, *Uca pugilator* (Bosc, 1802), *U. pugnax* (Smith, 1870), and *U. minax* (LeConte, 1855), co-occur in estuaries along the east coast of North America, from Cape Cod to northern Florida. Although *U. minax* adults are generally found at lower salinities than the other two species, the distributions of all three species overlap to some degree. The distribution of megalopae and juvenile fiddler crabs (from first crab stage to those with a carapace width of 3.0 mm) was examined at four sites along a salinity gradient (from $35.0 \pm 2.0\text{‰}$ to $3.0 \pm 3.0\text{‰}$; $\bar{x} \pm \text{SD}$) in the North Inlet Estuary, South Carolina, USA, in August 2002. A PCR-RFLP technique was developed to identify individuals from the genus *Uca* to species from first zoea through the early crab stages. An examination of the distribution of early life stages showed that *U. minax* reinvades low-salinity adult habitats at settlement, following planktonic larval develop-

ment in the coastal ocean. Also, juveniles of *U. pugilator* were found to occupy *Spartina alterniflora* stands, where adult conspecifics rarely occur. Species frequencies were different for adults compared to early life stages in low-salinity areas of the marsh, where populations overlap. Settlement and survival dynamics of early life-history stages in wet and dry years likely determine the distribution of adult *Uca* spp. populations along salinity gradients in estuarine ecosystems.

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Introduction

Many marine invertebrates undergo larval development in the plankton and settle into benthic adult habitats at metamorphosis. To accomplish this transition, water-borne larvae or postlarvae must reach adult habitats and recognize appropriate settlement sites. In the present study, we examined settlement patterns in the fiddler crabs, *Uca pugilator*, *U. pugnax*, and *U. minax*, all of which undergo planktonic larval development in the coastal ocean and live as adults on or near the banks of tidally influenced brackish and freshwater creeks, from Florida to Cape Cod, Massachusetts (Barnwell and Thurman 1984; Williams 1984). *U. pugilator* and *U. pugnax* adult habitats are generally found in higher salinity areas compared to those of *U. minax*; *U. pugilator* is typically found on open sandy substrata, while *U. pugnax* is found with marsh plants (especially *Spartina alterniflora*) in muddier areas (Teal 1958; Williams 1984). *U. pugilator* and *U. pugnax* have been shown to settle and metamorphose more quickly in the presence of conspecific odor cues than without these cues in the laboratory and in controlled field experiments, suggesting that direct settlement into adult habitats occurs in the field (e.g. Christy 1989; O'Connor and Gregg 1998). Adult *U. minax* are generally found in areas where salinity is $< 10\text{‰}$, and populations of this species can be found many kilometers inland, in tidally influenced

freshwater rivers and streams. There is no published work on the effect of potential settlement cues on megalopae of *U. minax*.

We collected and identified megalopal and juvenile fiddler crabs on the banks of Oyster Creek in North Inlet estuary, South Carolina. Sampling sites included an open area occupied by adult *U. pugilator*, a *S. alterniflora*-covered area dominated by adult *U. pugnax*, and two areas where all three species were present as adults. These four sampling sites were located along a salinity gradient. We determined if adult and recently settled juvenile crabs showed the same species frequencies at each site. We also determined if young *U. minax* enter the North Inlet estuary and settle directly into low-salinity adult habitats or if the transition from high- to low-salinity environments is accomplished gradually over the duration of megalopal and juvenile development.

To distinguish early life stages of the three fiddler crabs, we identified a restriction fragment length polymorphism (RFLP) that readily distinguishes among the three species, allowing us to easily identify recently settled crabs. The difficulty of distinguishing the early life stages of these three *Uca* species has previously hampered research into their movements and habitat preferences during their early life history. The RFLP technique we developed alleviates this problem, as it can be used to differentiate these three fiddler crab species from the time they hatch until they are large enough to be identified by their distinct morphologies.

Materials and methods

Collection of recently settled crabs

Recently settled fiddler crab megalopae and juvenile crabs were collected along Oyster Creek in North Inlet estuary, South Carolina, from 6 to 29 August 2002. Four sampling areas were chosen along the bank of the creek, extending from a region of high salinity and ending inside the edge of a pine forest, where salinities were often < 5‰ during heavy rain (Fig. 1). The sites differed in salinity, cover, and the dominant adult fiddler crab species present. The first site (site A) was an oyster reef with high salinity, dominated by adult *Uca pugilator* (Bosc, 1802); the second site (site B) also experienced high salinity conditions and was covered with the marsh grass *Spartina alterniflora* and dominated by *U. pugnax* (Smith, 1870); the third site (site C) was a sandy patch in a low-salinity region on the border between marsh and pine forest, where all three species were present, but *U. pugilator* was most abundant; and the fourth site (site D) was a low-salinity site, located 100 m inside the forest from the marsh's edge, where *U. minax* (LeConte, 1855) was the dominant species. Fiddler crab megalopae and juveniles were collected from the first three sites on eight dates in the month of August, and from the forest site (site D) on the last four dates. On each date, 10–30

megalopae and juvenile crabs of carapace width ≤ 3 mm [approximately through juvenile crab stage IV or V (O'Connor 1990)] were collected from the exposed sediment at each site during the day-time low tide; individual specimens were spotted by the collector, retrieved from the sediment surface with a spoon, and preserved in 95% ethanol. Also, the first 20 full-sized adult crabs seen by the collector were identified to species to determine adult species frequencies. The surface salinity of Oyster Creek closest to the collection site was measured with an automatic, temperature compensating salinity refractometer (Aquafauna Bio-Marine, Hawthorne, Calif., USA).

RFLP analysis—identification of unknown species

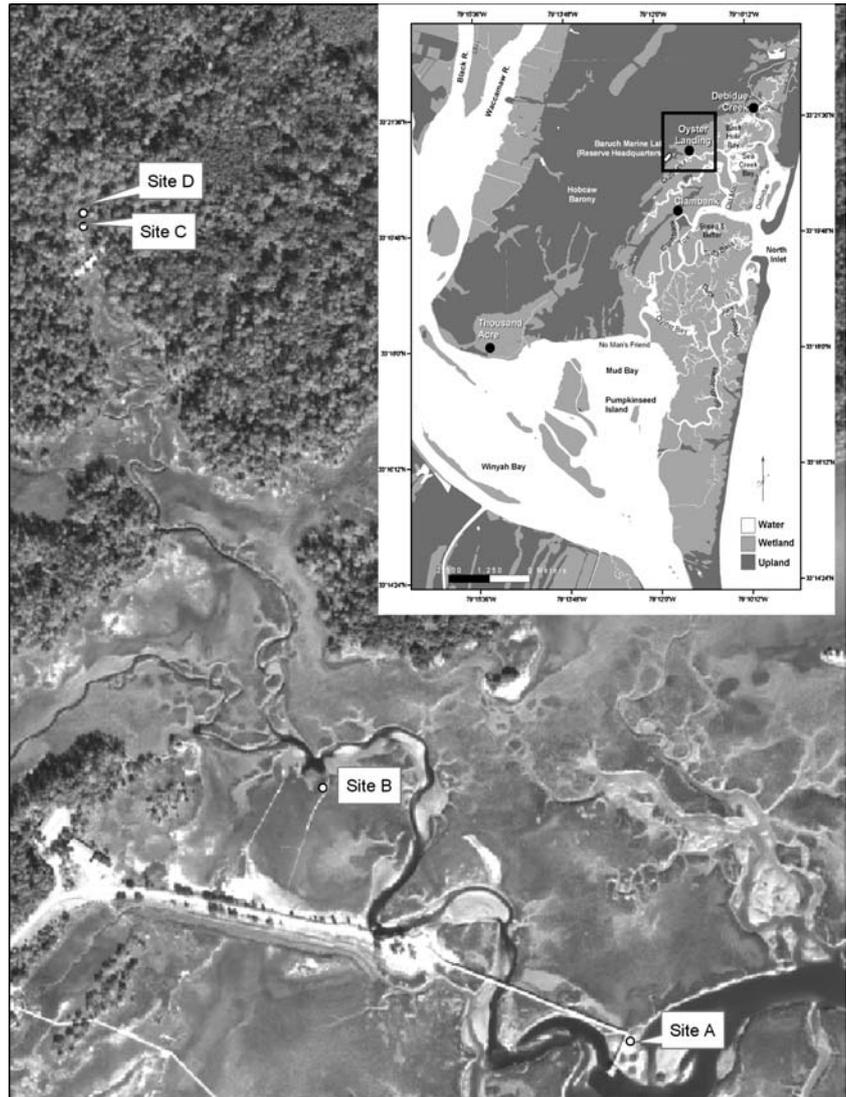
Whole, ethanol-preserved megalopal or juvenile crab stages were individually ground with disposable micro-tube pestles and extracted using the DNeasy protocol (QIAGEN, Valencia, Calif., USA) and eluted in a final buffer volume of 100 μ l (for megalopae) or 200 μ l (for all crab stages). Small aliquots of extracted nucleic acids (typically 1 μ l) were used as templates for polymerase chain reaction (PCR) amplification (Saiki et al. 1988). Amplifications of the internal transcribed spacer region I (ITS-1) used the following conditions: 50 mM KCl, 10 mM Tris-HCl, pH 8.3, 3.0 mM MgCl₂, 200 μ M dNTP (Pharmacia), 5 pmol forward and reverse primer, and 1 U *Taq* DNA polymerase (Promega) in 20 μ l total volume, including 1 μ l of the eluted template. Amplifications used the primers ITS-1F (CAC ACC GCC CGT CGC TAC TAC CGA TT) and ITS-1R (ATC GAC CCA TGA GCC GAG TGA TC) described by Schizas et al. (1999). Template DNA and negative controls were initially denatured at 96°C for 3 min, followed by 25 cycles of 94°C for 15 s, 55°C for 45 s, and 72°C for 60 s. Then, 6 μ l of each 20- μ l PCR product was used directly in a restriction digest (1 U *Hpa*II in 15 μ l total volume), which was incubated for 2.5 h at 37°C. Restriction fragments (RFLPs) for each individual were resolved in a 3% agarose gel and photoarchived. Distinctive patterns were easily identified (Fig. 2). Anomalous banding patterns (i.e. those differing from the stereotypical patterns in Fig. 2) were not observed.

Statistical analysis

A Chi-squared goodness-of-fit test was performed, using juvenile and adult species frequencies for each site to determine whether relative species abundances for juveniles reflected those seen for the adults.

A univariate logit analysis was performed to examine how well salinity predicted the presence or absence of juvenile *U. minax*. Logit analysis can be used to model a dichotomous response variable as a function of categorical or continuous predictor variables by transforming the dichotomous data into linear functions (logits) from which regressions are computed (Sokal and Rohlf

Fig. 1 Sampling locations along Oyster Creek, North Inlet estuary, South Carolina

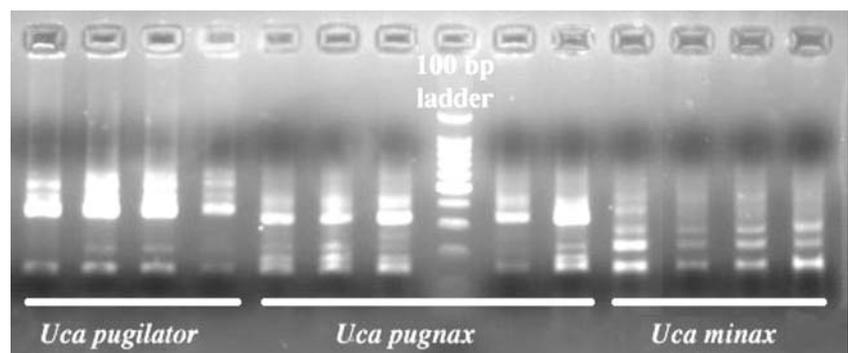


1995; Floyd 2001). *U. pugnax* and *U. pugilator* were used as reference species so that each juvenile crab collected during the course of the sampling period was scored as either 1 (*U. minax*) or 0 (*U. pugnax* or *U. pugilator*) to obtain the value for the dependent variable. Salinity measurements were those taken at the surface of the creek adjacent to the exposed sediment where the juvenile crabs

were collected. In this analysis, the binomial response variable was the presence or absence of *U. minax* and the predictor variable was salinity (continuous).

We performed a time-series analysis, and found that the distribution of juvenile fiddlers across our sampling sites was not influenced by sampling date; hence, data from all of the sampling dates were pooled for the

Fig. 2 *Uca* spp. Restriction fragment length polymorphisms of the ITS-1 gene digested with *Hpa*II restriction endonuclease



Chi-squared analysis and sampling date was not included as a variable in the logit analysis.

Results

Distribution of juvenile *Uca pugilator*, *U. pugnax*, and *U. minax*

Populations of the three fiddler crab species—*U. pugilator*, *U. pugnax*, and *U. minax*—lined the banks of the Oyster Creek study site (Fig. 1; Table 1). Adult *U. pugilator* dominated open sand and oyster bed habitats along most of the length of the creek, becoming less abundant where the creek entered the forest and salinity was lower. *U. pugnax* was the dominant species in high-salinity areas with plant cover (especially *Spartina alterniflora*), and also became less abundant where the creek entered the forest. *U. minax* populations first appeared in the forest and continued along the banks of Oyster Creek until it ended. A total of 144, 130, 165, and 57 megalopae and juvenile fiddler crabs were identified from sites A, B, C, and D, respectively (Table 2). Fourteen specimens were not successfully identified with PCR-RFLP, and were excluded from the analysis which follows.

Species proportions for juveniles and adults were statistically identical only on the high salinity oyster reef (site A), where *U. pugilator* comprised 95% of the adult fiddler crab population and 93% of the post-larval and juvenile crab population (Fig. 3; $\chi^2=0.5$, $P=0.48$, $df=1$). Of the eight megalopae found at this site, seven belonged to *U. pugnax*; however, only 3 out of 136 juveniles identified from this site were *U. pugnax*. For the high-salinity *S. alterniflora* site (site B), where 96% of the adult population was comprised of *U. pugnax* and the remainder of *U. pugilator*, the species proportions were different for the juvenile population, which was comprised of 75% *U. pugnax* and 24% *U. pugilator* (Fig. 3; $\chi^2=26.9$, $P<0.001$, $df=1$). The two low-salinity forest sites also showed differences between the species proportions of adult and postlarval/juvenile populations. At the forest pool (site C), *U. pugilator* dominated the adult stages (64%), while *U. minax* (29%) and *U. pugnax* (7%) were less abundant. At the postlarval and juvenile stages, *U. minax* was more abundant than

Table 1 *Uca* spp. Characteristics of four sampling sites along Oyster Creek, North Inlet estuary, South Carolina, in August 2002. Surface salinity measurements were taken at low tide after megalopae and juvenile crabs were collected on exposed sediment at each site ($n=8$ measurements for sites A–C; $n=4$ measurements for site D)

Site	Habitat type	Most common adult species present	Salinity (mean ± SD)
A	Oyster reef	<i>U. pugilator</i>	35.0 ± 2.0
B	<i>Spartina alterniflora</i>	<i>U. pugnax</i>	34.0 ± 4.0
C	Forest bank	<i>U. pugilator</i> and <i>U. minax</i>	8.5 ± 5.0
D	Forest interior	<i>U. minax</i>	3.0 ± 3.0

Table 2 *Uca* spp. Number and identity of early life stages of *Uca* spp. found along Oyster Creek. Juvenile crabs were 0.90–3.09 mm in carapace width

Developmental stage	Site A			Site B			Site C			Site D		
	<i>U. pugilator</i>	<i>U. pugnax</i>	<i>U. minax</i>	<i>U. pugilator</i>	<i>U. pugnax</i>	<i>U. minax</i>	<i>U. pugilator</i>	<i>U. pugnax</i>	<i>U. minax</i>	<i>U. pugilator</i>	<i>U. pugnax</i>	<i>U. minax</i>
Megalopae	1	7	0	0	0	0	0	0	0	0	0	0
Juvenile crabs	133	3	0	31	98	1	91	6	68	9	1	47

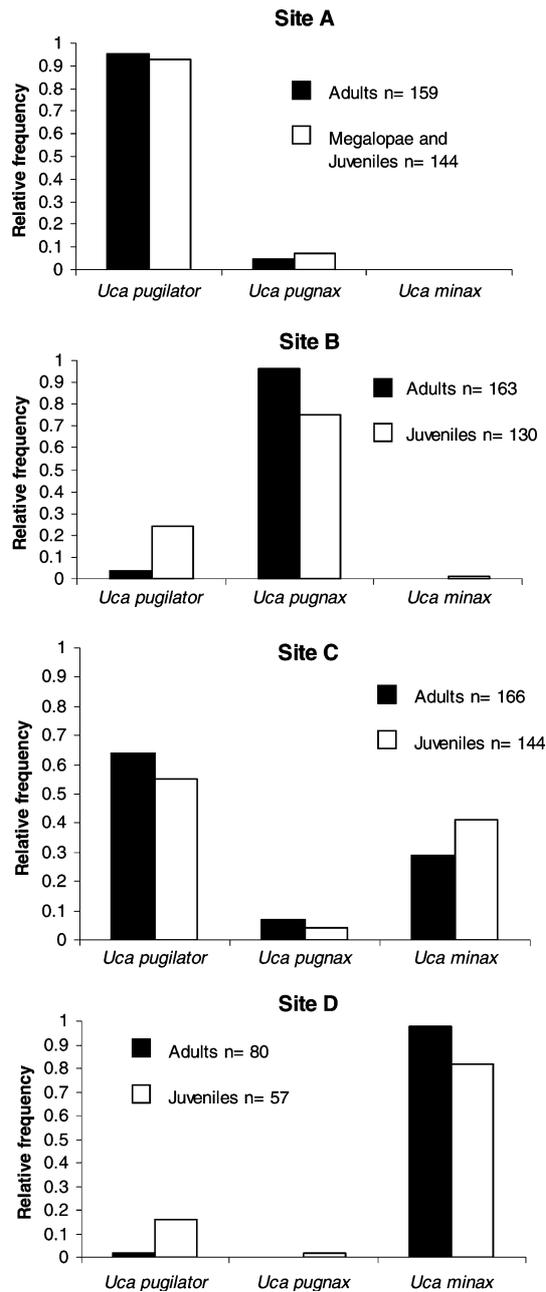


Fig. 3A–D *Uca* spp. Species frequencies for adults versus early life stages of *U. pugilator*, *U. pugnax*, and *U. minax*: **A** site A, cyster reef; **B** site B, *Spartina alterniflora* flat; **C** site C, forest edge; **D** site D, forest interior

expected given the adult proportions, comprising 41% of this population, while *U. pugilator* and *U. pugnax* made up 55% and 4%, respectively (Fig. 3; $\chi^2 = 6.6$, $P = 0.037$, $df = 2$). The forest interior site (site D) was dominated by *U. minax*, which comprised 98% and 82% of the adult and juvenile populations, respectively, though the number of juvenile *U. pugilator* (16% of the population) was greater than expected given adult numbers (Fig. 3; $\chi^2 = 8.2$, $P = 0.004$, $df = 1$). *U. pugnax* was not present at the adult stage, and comprised only about 2% of the juveniles at the deep forest site.

Only one juvenile *U. minax* was found in a high-salinity area where no adults were found; the remaining 116 juvenile *U. minax* were found at low-salinity sites C and D, where conspecific adults also occurred. *U. minax* juveniles were far more likely to be found in areas of low salinity compared to juveniles of *U. pugnax* and *U. pugilator* (Table 3). There was a strong negative correlation between the presence of adult *U. minax* and salinity (Spearman's correlation coefficient $r_s = -0.80$, $P < 0.0001$ for salinity and the presence of *U. minax* adults; $N = 486$). *U. minax* juveniles could have settled in response to conspecific adult odors and not low salinity.

Discussion

After undergoing larval development in the coastal ocean, *Uca* spp. megalopae return to the mouths of estuaries, possibly in deep shoreward currents (Dittel and Epifanio 1982; Johnson 1985; Epifanio 1988), and actively swim during nocturnal flood tides to move up-estuary towards adult habitats (DeVries et al. 1994; Christy and Morgan 1998; Forward et al. 2003). This phenomenon, generally termed “selective tidal stream transport” (STST), is a common recruitment strategy of many estuarine species that develop in coastal waters, including many fishes and estuarine invertebrates (Wood and Hargis 1971; McCleave and Kleckner 1982; McCleave and Wippelhauser 1987).

The PCR-RFLP technique we developed to distinguish among *U. pugilator*, *U. pugnax*, and *U. minax* makes broad-scale field investigations of the early life stages of these fiddler crab species logistically feasible for the first time. The scope of past field work has been limited because these species are morphologically identical during their larval and early juvenile stages; however, with a molecular genetic approach, large numbers of individual crabs at any life stage can be collected and preserved immediately for identification. In this first assessment of *Uca* spp. megalopal settlement and juvenile recruitment by molecular methods, we found that juvenile fiddler crabs occurred in the same habitats as their adult conspecifics; however, juvenile and adult species frequencies were dissimilar at all of the sites, except the high-salinity, oyster reef site (site A). Here, *U. pugilator* dominated both the adult and juvenile stages. *U. pugilator* occupies oyster reefs throughout the North Inlet area (authors' personal observations) and may

Table 3 *Uca minax*. Logit analysis showing that juveniles were far more likely to be found at lower salinities compared to *U. pugilator* and *U. pugnax* juveniles. Proportion of predicted to observed values = 88.4% (a goodness-of-fit measure); total $n = 486$ ($n = 117$ for *U. minax* and $n = 369$ for *U. pugnax* and *U. pugilator* combined)

	Estimate	Error	Chi-squared	Pr > Chisq
x-variable intercept	1.6344	0.2417	45.7103	< 0.0001
Salinity	-0.1801	0.0197	83.9124	< 0.0001

congregate in these open areas to increase their mating encounters (Croll and McClintock 2000). Also, these nutrient-rich environments probably provide highly favorable deposit-feeding conditions for fiddlers, which do best on water-saturated sediment with high organic content (Reinsel and Rittschof 1995).

U. pugnax was the most abundant fiddler crab on the *Spartina alterniflora* flat (site B) at the adult stage, and comprised the greatest proportion of juvenile crabs there. However, *U. pugilator* juveniles appeared in greater frequencies than expected (24% of juvenile crabs) given their low representation in the adult crab population (4% of adult crabs). This discrepancy shows that *U. pugilator* has a different distribution across the marsh landscape during the juvenile stages than it does as an adult. If stands of *Spartina* spp. are good habitat for young *U. pugilator* and they have not settled there by mistake, then biological factors are probably responsible for this discrepancy: adult *U. pugilator* may be excluded from *Spartina*-covered areas by adult *U. pugnax*, which are more aggressive (Aspey 1971), but these competitive dynamics may not be as strong for juvenile crabs. In addition, adult *U. pugilator* have specialized mouthparts for processing sediment with large particle sizes and may avoid *Spartina*-covered areas where the sediment tends to be muddy (Miller 1961; Robertson and Newell 1982; O'Connor 1990). Small juveniles of both *U. pugnax* and *U. pugilator* may be better able to process detritus in *Spartina*-covered areas.

All three fiddler crab species were found at the two inland woods sites (sites C and D), but again juvenile and adult species frequencies were dissimilar. A higher proportion of juvenile *U. minax* were found at the first inland site (site C) than expected and a higher proportion of *U. pugilator* were found at the second inland site (site D) than expected given adult frequencies. Oyster Creek was narrower, shallower, and more heavily influenced by terrestrial runoff at these inland sites, where salinity can plummet from 25‰ to 0‰ during a rainstorm and remain low for several days following the rain event (authors' unpublished data). Given the stochastic nature of these salinity changes, it is not surprising that adult and juvenile frequencies do not match. Adult *U. pugnax*, *U. pugilator*, and *U. minax* have a wider salinity tolerance range than younger conspecifics based on laboratory investigations (Vernberg et al. 1973; Vernberg and Vernberg 1975; O'Connor and Epifanio 1985; Epifanio et al. 1988), field distributions (Thurman 2003a, 2003b), and field survival data for megalopae and juveniles (Emord and Brodie, unpublished data), meaning that the relative species frequencies for adults may have been reflective of differential settlement and survival dynamics from past years and that the species proportions of early life stages a consequence of that season's current physical conditions. Alternatively, because only 20 adult crabs were identified with a quick visual check during each visit to the field sites, adult species proportions may not have been accurately assessed if there were species-specific differences in how

the adult crabs responded to the human observer (e.g. if one of the species tended to remain in its burrow longer than the others or was more likely to leave the area altogether). This was much less of a concern for the two high-salinity sites (sites A and B), where one species clearly dominated at each site, than it was for the two forest sites, where populations of the three species overlapped. The three fiddler crab species appear to have the same spawning season (generally, May–September in the North Inlet estuary; DeCoursey, personal communication and Brodie, personal observation), so we have assumed that juvenile frequencies are not influenced by differences in the timing of settlement among species.

Finally, we found that *U. minax* recruits directly into adult habitats: 115 out of the 116 juvenile crabs that were identified to this species were found inland in the low-salinity areas where adult *U. minax* also occurred (sites C and D). Mean salinity was a very good predictor of the presence or absence of juvenile *U. minax* in this study; however, adult presence (i.e. the presence of an odor cue) and salinity were highly negatively correlated and always will be in nature. Although conspecific odor cues have not been identified as accelerators or inducers of metamorphosis in *U. minax*, both *U. pugilator* and *U. pugnax* have been found to settle and metamorphose more quickly when conspecific odors are present than when they are absent (Christy 1989; O'Connor 1991, 1993; O'Connor and Judge 1997, 1999; O'Connor and Gregg 1998). *U. minax* may use adult odors to locate appropriate adult settlement sites like its congeners, and salinity may also function as a metamorphic cue, with either the low-salinity conditions or the salinity fluctuations that occur during the tidal cycle speeding metamorphosis. Laboratory experiments in which salinity and conspecific odor cues are separated would illuminate whether one or both of these potential cues induce settlement and metamorphosis.

There is a great deal of interest in the ecology, behavior, and physiology of the three fiddler species investigated in this study. Studies of early life stages have typically involved laboratory-reared specimens observed in the laboratory or transplanted back into the field so that the *Uca* species under investigation was known. There has only been one previous study on early life stage *Uca* spp. in the field where the individuals were identified to species. Molecular methods were not used for this earlier investigation; instead, field-collected specimens were reared in the laboratory until they were large enough to be distinguished morphologically (O'Connor 1993). O'Connor found juvenile *U. pugnax* and *U. pugilator* distributed along an intertidal gradient, with juveniles occurring in the same habitats as their conspecific adults. Our results support this finding, but furthermore show that juvenile *U. pugilator* occupy habitat types not typical of conspecific adults and that species frequencies in areas where *U. pugnax*, *U. pugilator*, and *U. minax* occur together are different for adults compared to early life stages, possibly reflecting their different physiological tolerances to the prevailing physical conditions in the high estuary.

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