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## Daily, Monthly And Annual Settlement-Patterns By Callinectes-sapidus And Neopanope-sayi Megalopae On Artificial Collectors Deployed In The York River, Virginia - 1985-1988

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# DAILY, MONTHLY AND ANNUAL SETTLEMENT PATTERNS BY *CALLINECTES SAPIDUS* AND *NEOPANOPE SAYI* MEGALOPAE ON ARTIFICIAL COLLECTORS DEPLOYED IN THE YORK RIVER, VIRGINIA: 1985-1988

Jacques van Montfrans, Christopher A. Peery and Robert J. Orth

## ABSTRACT

Daily, monthly and annual settlement of dominant brachyuran megalopae on six replicate artificial settlement substrates (collectors) was examined at one site in the York River, Virginia, from mid-July or early August to early December during 1985-1988. *Callinectes sapidus* Rathbun, an exported estuarine species, and *Neopanope sayi* (Smith), a retained estuarine species, were the numerically dominant colonizers of collectors. *C. sapidus* settlement was highly episodic (1-3-day duration) and significantly associated with the full moon period (lunar day 15-22). The temporal mean of settlement for *C. sapidus* each year fell within a 12-day period (24 September-6 October) over the 4 years. *C. sapidus* megalopae settled over a broad range of temperatures (7-31°C) extending into the fall months when resident predators become inactive or migrate to deeper water. In contrast, *N. sayi* settled throughout the lunar month with no significant lunar or tidal periodicity. Settlement by *N. sayi* occurred over a narrower temperature range (12-31°C) than that for *C. sapidus*, and mean annual settlement for *N. sayi* occurred earlier within a 12-day period from 9-21 September. A behavioral and physiological mechanism is invoked to explain the observed pattern of *C. sapidus* settlement. We postulate that synchrony in settlement over a broad temperature range may reduce predation in *C. sapidus*.

Settlement processes in marine habitats partially regulate recruitment success and population structure (Connell, 1985; Roughgarden et al., 1985; 1988; Young, 1987; Clarke, 1988; Robertson, 1988; Robertson et al., 1988). Factors affecting settlement success include both biotic (fecundity, behavior, resource availability, predation) and abiotic (currents, temperature, salinity, lunar phase) components (Cameron, 1986; Scheltema, 1986; Sulkin and Van Heukelem, 1986; Epifanio, 1988; Robertson et al., 1988; Roughgarden et al., 1988). Estuarine-dependent species display various life-history strategies in response to many of these factors for assuring either population retention within the estuary or transport of one life-history stage from the estuary to oceanic environments for spawning or larval development. In Chesapeake Bay, for example, most resident decapods (*Neopanope sayi* (Smith), *Panopeus herbstii* H. Milne Edwards, *Hexapanopeus angustifrons* (Benedict and Rathbun)), complete their entire life cycle within the estuary (Johnson, 1982; 1985; Cronin and Forward, 1986; McConaughy, 1988). Larvae of these species display behavior in response to various physical factors or other stimuli to ensure retention (Forward, 1987; McConaughy, 1988). In contrast, the adults of many estuarine-dependent fish (*Leiostomus xanthurus* Lacepede, *Microgogonias undulatus* (Linnaeus), *Paralichthys dentatus* (Linnaeus)) exhibit annual offshore migrations to spawn in oceanic waters (Boehlert and Mundy, 1988; Lawler et al., 1988; and references therein). A two-phase recruitment mechanism has been proposed for these species, initially involving the return of progeny to the nearshore waters with subsequent estuarine reinvasion (Boehlert and Mundy, 1988). In each phase, different stimuli induce behavior that promotes return to estuarine habitats. A third life history mode is typified by the blue crab, *Callinectes*

*sapidus* Rathbun, fiddler crabs, *Uca* spp. and relatively few other species: spawning occurs within the bay, larvae are exported to the nearshore continental shelf where development takes place, and invasion of the estuary is believed to occur by postlarvae (megalopae) or juveniles (Sulkin and Epifanio, 1986; Sulkin and Van Heukelem, 1986; McConaughy, 1988; and references therein). It is likely that species exhibiting the latter life history mode utilize similar stimuli during estuarine invasion to those of estuarine-dependent fish spawned offshore. Each suite of species found within the estuary exhibits unique behavioral characteristics that promote the retention or return of estuarine-dependent life history stages which subsequently occupy appropriate habitats and in time contribute to adult populations.

Fisheries investigations of settlement and recruitment relative to physical factors have been a mainstream effort in attempting to understand fluctuations in commercial stocks (Sherman et al., 1983; Young, 1987). In marine decapod populations, relationships between availability of larvae (*Homarus americanus* H. Milne Edwards: Scarratt, 1973) and settlement of post-larvae (*Panulirus longipes* (Milne-Edwards): Chittleborough and Phillips, 1975; *P. cyngus* George: Morgan et al., 1982) show a positive relationship with commercial harvest. Data from natural settlement on collectors has been successfully applied to develop predictive models of commercial harvest in *Panulirus* spp. (Phillips, 1972; Witham et al., 1968) and to examine settlement and growth in *Cancer irroratus* Say (Beninger et al., 1986). This technique has also been used to describe lunar relationships in settlement patterns of *Panulirus* spp. (Witham et al., 1968; Serfling and Ford, 1975; Little, 1977) and to examine transport mechanisms via tidally forced internal waves (Shanks, 1983; in press) and wind-generated non-tidal volume flux events (Goodrich et al., 1989).

In the present study, we examine daily postlarval settlement of dominant brachyura (principally the portunid, *Callinectes sapidus*, and xanthid, *Neopanope sayi*) during July/August–December in the York River (Chesapeake Bay), Virginia, over a 4-year period (1985–1988). Postlarval settlement is defined as the period of transition from a largely pelagic existence to a predominantly benthic vagile lifestyle preparatory to the physiological and morphological changes associated with metamorphosis (Scheltema, 1974). Settlement patterns by *C. sapidus* and *N. sayi* were analysed by temporal, lunar and tidal components and compared. We provide the basis for conducting detailed studies of settlement processes on appropriate time scales for *C. sapidus* (Lipcius et al., in press; Olmi et al., in press) and examining relationships between settlement and year-class strength for this ecologically and commercially important species.

## METHODS AND MATERIALS

Daily settlement of megalopae on artificial settlement substrates (collectors) was examined at the Virginia Institute of Marine Science in the York River, Virginia (Fig. 1), from mid-July or early August to early December (the period of primary ingress by *Callinectes sapidus* into Chesapeake Bay) over 4 years (1985–1988). Collectors measuring 47·39·1 cm were made of commercial “hogshair” air conditioner filter material consisting of a synthetic fiber matrix. Six replicate collectors were weighted at the bottom and suspended from floats such that each maintained a vertical position within 10 cm of the water column surface with an orientation perpendicular to the prevailing current. Surface associated collectors were shown to be colonized by significantly greater numbers of megalopae than bottom associated collectors in a preliminary study conducted during new and full moon. Collectors were deployed midway between a pier and an adjacent parallel row of pilings to prevent contact with these obstructions during tidal fluctuations. Water depth was approximately 1.5 m at mean low water. Each collector was sampled daily, principally between 0800 and 1000, using a long handled dipnet (0.5 × 0.75-mm mesh). At the same time, replacement collectors were deployed, thereby maintaining a soak

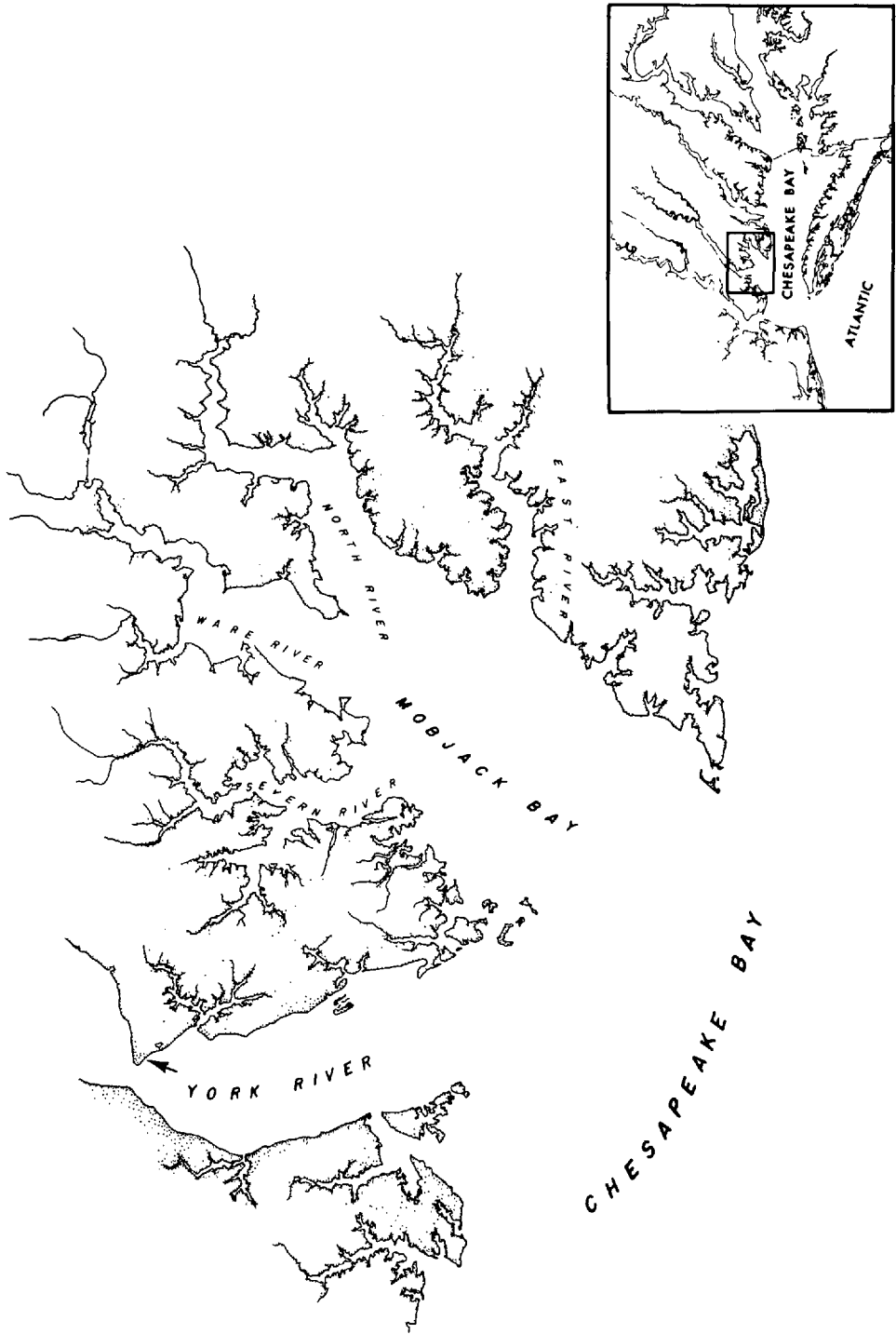


Figure 1. Location of study site (arrow) at the Virginia Institute of Marine Science near the mouth of the York River.

time for each collector of approximately 24 ( $\pm 1$ ) h throughout the study period. Dipnet contents and collectors were placed in individual 19-liter buckets and collectors were further processed for colonizing fauna. Processing involved soaking collectors in 19-liter buckets filled with fresh water for 20 min and subsequently rinsing each one with a moderate spray of fresh water into two additional 19-liter buckets. Rinse water from this process was then decanted through nested 3.0-mm and 0.5-mm mesh-sieves and the sieve contents were identified and enumerated. This process was 98% effective in removing colonizers as determined by an analysis of the cumulative number of individuals found in six successive 19-liter rinses per filter ( $N = 6$ ). Temperature and salinity were measured with a stem thermometer and refractometer, respectively, and recorded daily.

Megalopal settlement data were analyzed for temporal (annual, monthly and daily) patterns. The timing of settlement was statistically characterized following techniques described by Mundy (1982) for both short-term events and annual settlement. Short term settlement periods were arbitrarily defined as being delimited by at least 5 successive days where total daily settlement did not exceed 0.005% of the annual total. Daily settlement was expressed as a proportion of either the short term or annual total settlement (Mundy's time density) and daily proportional settlement was progressively summed as the cumulative time density for the settlement period in question. Thus, the temporal mean of settlement ( $\bar{t}$ ; i.e., central date of settlement) during time interval "t" over the period of "m" days based on the daily proportion of the total number of individuals that settled annually ("P") was determined as:

$$\bar{t} = \sum_{i=1}^{i=m} tP_i$$

The variance (i.e., the dispersion of settlement around this mean) was further calculated as:

$$S_{t^2} = \sum_{i=1}^m (t - \bar{t})^2 P_i$$

Settlement patterns by *Neopanope sayi* and *Callinectes sapidus* were examined for lunar influences over 3 complete and successive lunar months (calendric time period from August to November) for each of the 4 years. For the purpose of this analysis, lunar quarters were defined as new moon (first quarter; lunar day 1–7), waxing half moon (second quarter; day 8–14), full moon (third quarter; day 15–22), and waning half moon (fourth quarter; day 23–30). Daily settlement was expressed as a percentage of the total settlement for each lunar month (data were square root arcsine transformed when necessary to meet the assumptions for analysis of variance, ANOVA; Sokal and Rohlf, 1981) and compared. A multiple range test (Student-Newman-Keuls) distinguished relationships when significant differences in settlement by lunar quarter were detected. Detailed annual patterns of settlement around the full moon period (lunar day 15–22) were examined for *C. sapidus* only by normalizing settlement as the mean of proportional settlement per lunar day for each year. A log-linear model (Sokal and Rohlf, 1981) was then used to examine whether settlement patterns around full moon differed between years, months of each year and lunar day within months. Furthermore, settlement was cross-correlated with maximum daily tidal range measured in situ at an adjacent pier to also examine tidal relationships in settlement patterns.

## RESULTS

At least 10 brachyuran megalopal taxa colonized collectors throughout the 4-year study period. Of these, *Callinectes sapidus* and *Neopanope sayi* made up 93%, *Uca* spp. and *Panopeus herbstii* combined to constitute 6%, while all other species together contributed only 1% of the total abundance (Table 1).

Settlement by *Uca* spp. and *P. herbstii* was low early in the study period (August–December) each year and ceased during early October (Fig. 2) when temperatures decreased to approximately 16 and 18°C for each species, respectively (Fig. 3). In contrast, large numbers of *C. sapidus* and *N. sayi* settled during August and September each year with settlement by *C. sapidus* extending farther into the fall (late November vs. mid October; Fig. 2) and occurring over a broader range of temperatures (6–31 vs. 12–31°C; Fig. 3) than in *N. sayi*. Salinity values over the 4 years ranged from 16 to 24‰ and were similar between years. Water temperature decreased from 31°C in July/August to 5°C in early December.

Table 1. Annual numerical composition (and %) of megalopal taxa which colonized collectors during the study

Species	1985 (%)	1986 (%)	1987 (%)	1988 (%)	Total (%)
<i>Neopanopae sayi</i>	1,661 (53)	8,237 (8)	7,253 (72)	4,513 (57)	21,664 (69)
<i>Callinectes sapidus</i>	882 (28)	1,482 (15)	2,228 (22)	2,920 (36)	7,512 (24)
<i>Uca</i> spp.	304 (10)	185 (2)	312 (3)	236 (3)	1,037 (3)
<i>Panopeus herbstii</i>	234 (8)	185 (2)	241 (2)	212 (2)	872 (3)
<i>Rhithropanopeus harrisi</i>	12	5	8	9 (1)	34
<i>Libinia dubia</i>	2	11	12	0	25
<i>Pinnixa</i> spp.	12	3	0	3	18
<i>Eurypanopeus depressus</i>	2	0	6	9 (1)	17
<i>Sesarma</i> spp.	0	5	3	5	13
<i>Libinia emarginata</i>	0	0	1	1	2
Unknown	18	9	17	10	54
Total	3,127	10,122	10,081	7,918	31,248

Total daily settlement on all six collectors by *C. sapidus* was continuous at low levels (1–20 megalopae per day) over broad time periods (1 to 2 weeks) with episodic peaks (order-of-magnitude increases) occurring on shorter time scales (1 to 3 days; Fig. 4). *C. sapidus* settlement increased from 1985 to 1988 by a factor of 3.3 (Table 1) and settlement events of greatest magnitude occurred during different times each year (1985: early November; 1986: late October; 1987: early September; 1988: early November; Fig. 4). A plot of cumulative proportional settlement (Fig. 5) illustrates a relatively consistent step-like pattern for all 4 years with the central date of annual settlement (mean settlement time density) occurring on 24 September in 1985, 6 October in 1986, 25 September in 1987, and 29 September 1988 (Fig. 5). Sixty eight percent (i.e., 1 SD) of all settlement occurred within 25–27 days of these means each year.

Settlement (natural log, ln) by *C. sapidus* was significantly ( $P \leq 0.05$ ) cross-

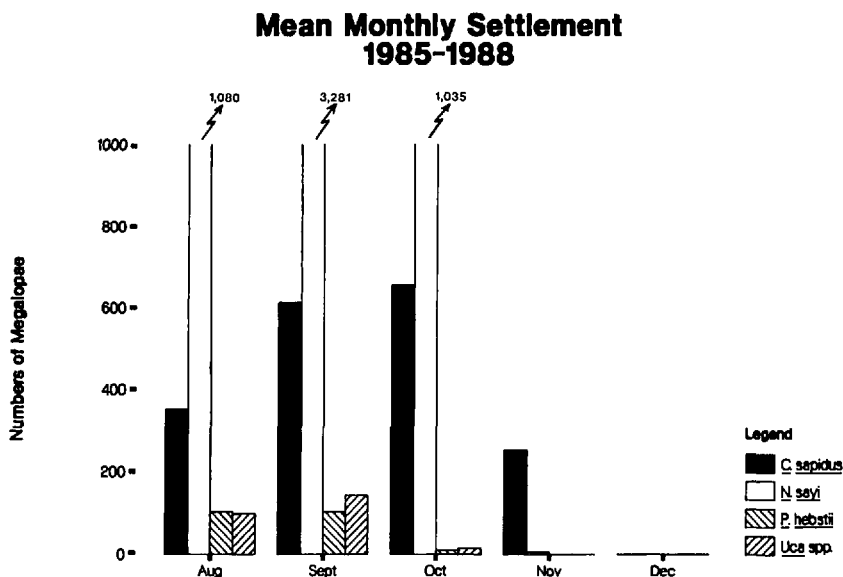


Figure 2. Mean monthly settlement for the four most numerous decapods on collectors (all years combined).

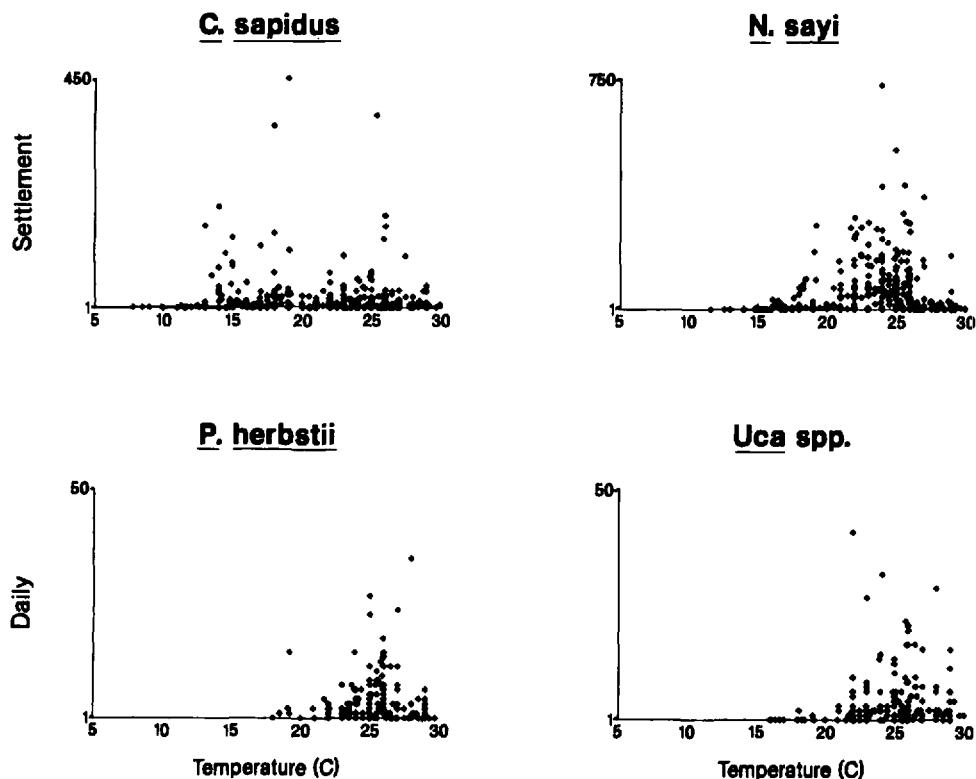


Figure 3. Settlement vs. temperature plots for the four numerically dominant species of decapods on collectors (1985–1988). Note that values on the y-axis begin with 1. Thus, only days when at least one megalopa settled are shown.

correlated with maximum tidal range but only during full moon periods (Fig. 6). Settlement was significantly affected by lunar period (ANOVA;  $P \leq 0.01$ ) with greatest settlement during the third lunar quarter (on and immediately following full moon; Table 2). Log-linear analysis of settlement patterns during the full moon period across years, months and lunar days indicated that all three- and two-way interactions were significant ( $P \leq 0.05$ ; Table 3). Thus, although the central date of settlement (and SD) for all 4 years was similar, detailed settlement patterns during the full moon period were variable, differing across years, months and lunar days.

The magnitude of annual *N. sayi* settlement differed each year as follows: 1986 > 1987 > 1988 > 1985 (Table 1; Fig. 4). Settlement occurred over more protracted periods (weeks to months) with few distinctly episodic peaks (Fig. 4). Monthly patterns (Figs. 2, 4) indicated that greatest settlement occurred during September of 1986, 1987 and 1988 and September/October, 1985. A plot of cumulative proportional settlement (Fig. 5) indicated a step-like pattern illustrating two settlement events in 1985 and relatively continuous settlement following a normal distribution during 1986, 1987 and 1988. In 1985 and 1986, settlement began in August, approximately 1 month earlier than in 1987 and 1988 when substantial settlement started in September (Fig. 4). No significant correlation of settlement to maximum tidal range or lunar period was evident for *N. sayi* (Fig. 6, Table 2).

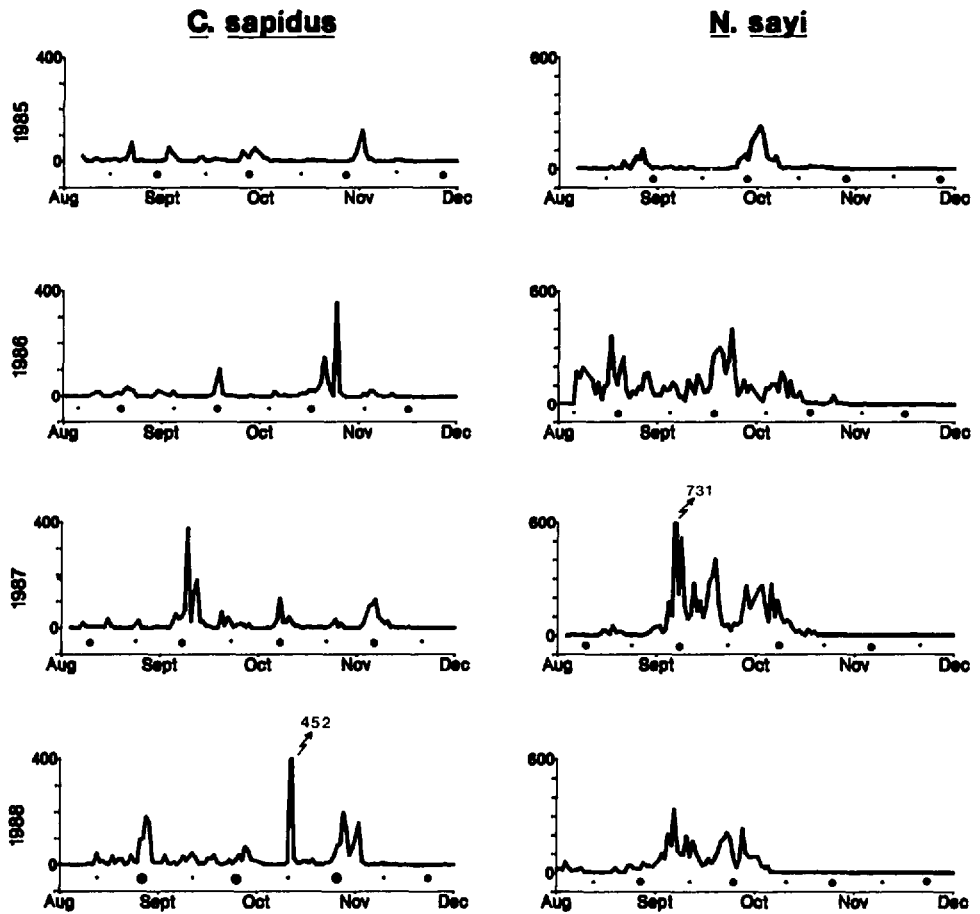


Figure 4. Daily settlement records for *Callinectes sapidus* and *Neopanope sayi* from August to December 1985–1988. Large dots along the X-axis denote full moon whereas small dots signify new moon. Note the highly episodic settlement by *C. sapidus* in contrast to the more continuous daily settlement by *N. sayi*.

## DISCUSSION

The megalopae of several decapod species settled on collectors during the study, but only two (*Neopanope sayi* and *Callinectes sapidus*) were numerous enough for data analysis. Together, *Panopeus herbstii* and *Uca* spp. contributed only 6% of the total individuals collected and will be discussed only briefly.

It is not known when *Uca* spp. or *P. herbstii* settlement began because of the limited seasonal duration of our study; however, spawning information and larval abundance data from Chesapeake Bay (Sandifer, 1973) relative to data on developmental time to the first crab (Costlow et al., 1962) suggest that settlement may be occurring earlier in the summer. Spawning in most species of *Uca* is synchronized with neap tides (Wheeler, 1978; Berge, 1981; Christy, 1978; 1982) and overall developmental time to the first crab is approximately 6–8 weeks (Hyman, 1920; Christy, 1982; 1986). Sandifer (1973) found the larvae of *Uca* spp. to be the most numerous decapod in Chesapeake Bay with larvae first appearing in June, peak abundances occurring in July and larvae disappearing from



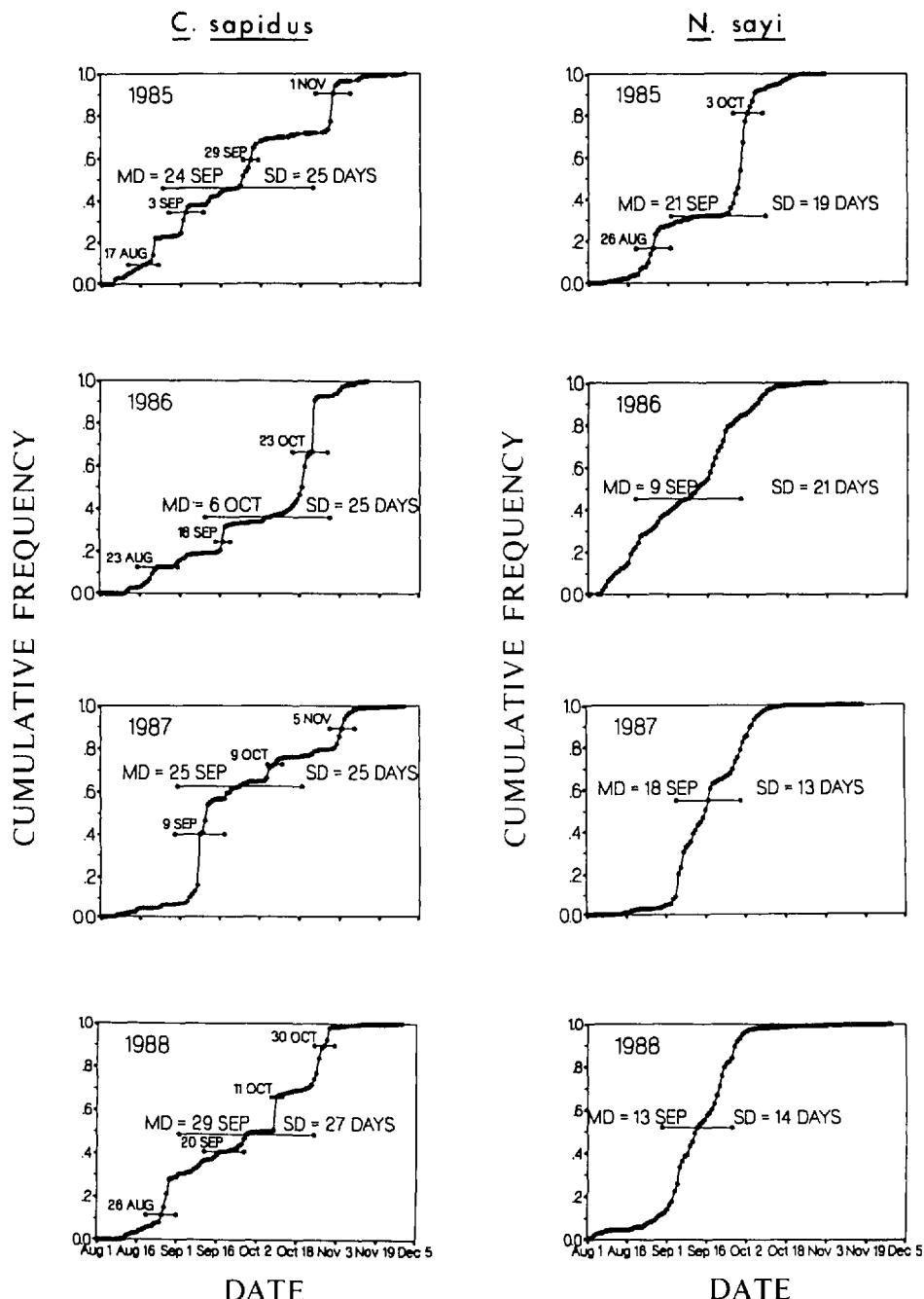


Figure 5. Cumulative proportional settlement by *Callinectes sapidus* and *Neopanope sayi* during each year. Means and standard deviations for each short-term settlement event and for total annual settlement are indicated. Short term settlement events were delimited by periods of at least 5 consecutive days when daily settlement did not exceed 0.005% of the annual total.

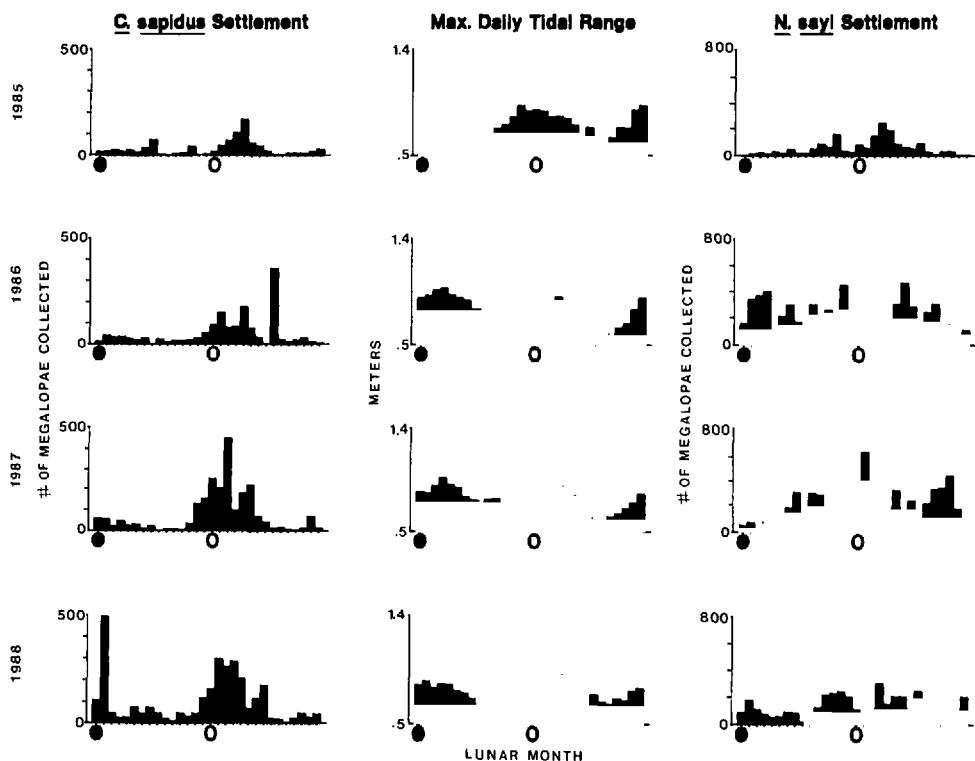


Figure 6. Combined settlement by *Callinectes sapidus* and *Neopanope sayi* and mean daily tidal range for all days of the lunar month. Open circles denote full moon whereas solid circles indicate new moon.

Table 2. One-way analysis of variance and Student-Newman-Keuls multiple comparison results of *Callinectes sapidus* and *Neopanope sayi* settlement by lunar quarter for 1985–1988. Settlement by lunar quarter was calculated as the proportion of each lunar month total and appropriate transformations were made on 1985 and 1988 data for *N. sayi* only to meet the assumptions of ANOVA. Lunar quarters were divided as follows: 1st quarter (new moon: day 1–7; 2nd quarter (waxing half moon): day 8–14; 3rd quarter (full moon): day 15–22; 4th quarter (waning half moon): day 23–30

Year	Lunar quarter	<i>Callinectes sapidus</i> (settlement)	<i>Neopanope sayi</i> (settlement)
1985	1		
	2	$P = 0.004$	$P = 0.61$
	3	$3 > 2 = 1 = 4$	$2 = 3 = 1 = 4$
	4		
1986	1		
	2	$P = 0.005$	$P = 0.748$
	3	$3 > 4 = 1 = 2$	$1 = 3 = 2 = 4$
	4		
1987	1		
	2	$P = 0.000$	$P = 0.807$
	3	$3 > 1 = 2 = 4$	$3 = 2 = 1 = 4$
	4		
1988	1		
	2	$P = 0.000$	$P = 0.6384$
	3	$3 > 1 > 2 = 4$	$3 = 2 = 4 = 1$
	4		

Table 3. Log-linear analysis of megalopal settlement patterns between lunar days 15–22

Interaction	df	Partial Chi-sq.	P
Yr. $\times$ Mo. $\times$ Lun. D.	54	430.688	.000
Yr. $\times$ Mo.	6	455.122	.000
Yr. $\times$ Lun. D.	18	336.770	.000
Mo. $\times$ Lun. D.	27	403.669	.000

the plankton in October. Similarly, larvae (principally first zoeae) of *P. herbstii* are most abundant during July to August at the York River mouth (Sandifer, 1973) and based on calculations from developmental times (18–52 days; Costlow et al., 1962), settlement most likely begins in July and continues through the fall (Williams, 1984). Peak settlement in these two species may be occurring slightly earlier than in *C. sapidus* and *N. sayi* although settlement can potentially continue throughout the earlier portion covered in our study. Thus, the apparent termination of settlement in these species may be a function of the timing of spawning in conjunction with developmental times, but may ultimately be regulated by a decrease in water temperature at about 15°C. Alternatively, both *Uca* spp. and *P. herbstii* may settle into lower salinity areas of tributaries or may not exhibit comparable thigmotaxis relative to the two most abundant species collected.

Both *C. sapidus* and *N. sayi* were abundant colonizers of collectors with total annual abundances of *N. sayi* always greater than *C. sapidus* by a factor of 1.5 to 5.5. *C. sapidus* is an exported estuarine species whereas *N. sayi* is an estuarine retained species (McConaugha, 1988). Factors affecting the transport of planktonic life-history stages and behavior of larvae and postlarvae in response to these factors differ considerably between the two species. *C. sapidus* is spawned within Chesapeake Bay, but undergoes larval development on the continental shelf and may rely on prevailing southwesterly winds (Epifanio et al., 1984; Johnson et al., 1984; Johnson, 1985; McConaugha, 1988) and possibly internal waves (Shanks, 1983; in press) for late larval and megalopal population maintenance near the bay mouth. Strong easterly winds (Goodrich et al., 1989) or use of deep residual inflowing currents (Sulkin and Epifanio, 1986) coupled with megalopal behavioral changes (Sulkin and Van Heukelem, 1986) are postulated mechanisms for reinvasion. Ultimately, the magnitude of potential recruits within the estuary is determined by: (1) stochastic events that appear to control the dispersal of the early life history stages (McConaugha, 1988), (2) biological processes (i.e., nutritional state, Sulkin, 1975; 1978; Anger and Dawirs, 1981; Welch and Sulkin, 1974; predation, E. J. Olmi III, unpubl. data; J. van Montfrans and R. J. Orth, unpubl. data; larval behavior: Sulkin et al., 1980; Sulkin and Van Heukelem, 1986) and

Table 4. Duration in days of various developmental stages in the life history of *Callinectes sapidus* and *Neopanope sayi*, both of which are reproductive in Chesapeake Bay from June–Sept. (Data compiled from Sulkin and van Heukelen, 1986; Costlow, 1967; Costlow and Bookhout, 1959; Chamberlain, 1957; 1961; Kurata, 1970; Swartz, 1972)

	<i>Callinectes sapidus</i>			<i>Neopanope sayi</i>		
	Minimum	Mean	Maximum	Minimum	Mean	Maximum
Embryonic (egg) phase	12	15	17	8	11	17
Zoeal (larva) phase	30	39	60	12	18	27
Megalopal (post-larval) phase	15	36	95	7	?	13
Total planktonic duration	45	75	155	19	?	40
Total time to first crab	57	90	172	27	?	57

(3) more predictable wind events (Goodrich et al., 1989) and internal waves (Shanks, in press) associated with transport towards and entry into Chesapeake Bay. By contrast, *N. sayi* remains within the estuary through vertical migration in response to tides for the duration of its development (Maris, 1986) and is not subjected to the large-scale transport processes experienced by *C. sapidus*. It is therefore not surprising that *C. sapidus* and *N. sayi* exhibited different patterns of settlement observed in this study.

*Callinectes sapidus* megalopae are more eurythermal than those of *Neopanope sayi*. Although the upper ambient temperatures at which settlement occurred ( $\sim 30\text{--}31^\circ\text{C}$ ) were similar, lower temperatures ( $6$  and  $12^\circ\text{C}$ , respectively) differed by  $6^\circ\text{C}$ . Settlement patterns did not appear to be an artifact of reproductive timing since neither species exhibited hatching in relation to tide or lunar phase (Salmon et al., 1986) and both species could potentially extend settlement beyond the time they colonized collectors (Table 4). Substantial settlement of *C. sapidus* occurred at considerably lower temperatures (between  $14\text{--}18^\circ\text{C}$ ) than was exhibited by *N. sayi*. Although survival and metamorphosis of *C. sapidus* to the first crab under laboratory conditions was greatly reduced at temperatures of  $15^\circ\text{C}$  and salinities of  $20\text{--}40\text{‰}$  (Costlow, 1967), it is not known how survival and metamorphosis are affected under natural conditions. Settlement of *C. sapidus* during cold temperatures can also be inferred from a 10-year study by Williams (1971) reporting the presence of megalopae throughout the year in plankton samples from North Carolina estuaries.

Swartz (1972) reported that *N. sayi* ceased spawning early in September because zoea hatched after September would not survive temperature decreases from  $23\text{--}15^\circ\text{C}$  in October. Costlow et al. (1962) suggested that temperature limits on larvae reduce the productive spawning period in another xanthid, *Panopeus herbstii*. Survival in both *C. sapidus* and *N. sayi* megalopae is probably also adversely affected by lowered temperatures, but *C. sapidus* may be more tolerant of reduced temperatures as indicated by settlement down to  $7^\circ\text{C}$ .

Settlement in *C. sapidus* was highly episodic (1–3 day duration) with greatest settlement occurring during and immediately after full moon. Mean cumulative proportional settlement for each year occurred at surprisingly similar times (24 September–6 October) and standard deviations around these means (25–27 d) were similar, further illustrating the broadly similar and predictable annual patterns; however, within the principal settlement period (lunar day 15–22) patterns of daily settlement varied across months or years. Thus, the precise timing of daily settlement during each month varied annually. Although such variability is partially accounted for by the fact that the lunar cycle within each month will vary from year to year, it also may reflect differences in the availability of megalopae which are competent to settle. Processes associated with the settlement of *C. sapidus* can nonetheless be examined over short intervals between August and November during the period surrounding full moon (Olmi et al., in press). Furthermore, the possibility exists that the relatively few episodic peaks of settlement in *C. sapidus* may have a strong influence on population size in this commercially important species, especially if these peaks occur during periods of lowered water temperature when predation rates could be reduced.

The significantly greater settlement of *C. sapidus* following full moon was particularly noteworthy. Synchrony (i.e., reduction in variability) in the timing of settlement is contrary to the apparent absence of any tidal or lunar periodicity in hatching (Salmon et al., 1986), the variability in duration of egg (12–17 d), larval (30–60 d) and megalopal (15–95 d) stages (Table 4) during early development, and the stochastic processes that influence the dispersal of larvae and postlarvae.

It has been suggested that variability in developmental times of *C. sapidus* evolved to assure the proximity to desirable habitats of at least some megalopae for metamorphosis to the first crab (Sulkin and Van Heukelem, 1986). It seems likely that settlement and subsequent metamorphosis to the first crab is influenced by cues associated with the full moon because the processes presently postulated to drive the ingress of megalopae into Chesapeake Bay are not expected to occur with any lunar (full moon) periodicity and settlement is not related to tidally generated water movements. We saw a six-fold increase in settlement during full moon periods vs. new moon periods when tidal amplitudes were similar. In the absence of any lunar-related physical processes to explain the observed settlement patterns in *C. sapidus*, we invoke behavioral and physiological explanations and postulate that characteristics of estuarine habitats (possibly reduced salinity, increased turbulence, increased tactile stimuli, habitat quality, or other unknown cues) stimulate the onset of pre-molt with settlement ultimately timed to occur during the following full moon.

Settlement patterns in a variety of marine species have been described as episodic and were related to diverse phenomena. Settlement maxima for both the intertidal decapod, *Pachygrapsus crassipes* Randall (Shanks, 1983) and barnacle cyprids, *Chthamalus* spp. (Shanks, 1986) were positively correlated with the period immediately preceding maximum spring tides. These patterns were thought to relate to transport processes via internal waves that concentrated and increased the supply of potential settlers (Shanks, 1983; 1986; in press). Several tropical reef-dwelling fishes with a short pelagic larval existence exhibited lunar or semilunar settlement, but patterns actually reflected lunar- or semilunar-influenced spawning activity (see Johannes, 1978 for an early review and Doherty, 1983; McFarland et al., 1985). One species (the bluehead wrasse, *Thalassoma bifasciatum* (Bloch)), spawned continuously, but settled in sporadic peaks loosely associated with new moon (Victor, 1986). In the latter case, broad-scale settlement patterns into 24 reefs within 1,000 km<sup>2</sup> correlated with exposure to onshore currents implicating large-scale oceanographic events. In all of these investigations, settlement was attributed to physical factors influencing the supply of settlers or to reproductive periodicities in the breeding population.

The movement or settlement of decapods has also been correlated with lunar phases. Pink shrimp, *Penaeus duorarum* Burkenroad, appear to move into nursery habitats during new and first quarter lunar periods (Roessler and Rehner, 1971). Postlarval (pueruli) settlement into floating artificial habitats also occurred principally during new and first quarter moon in the spiny lobster, *Panulirus argus* (Latreille), off Florida (Little, 1977) and the western rock lobster, *Panulirus longipes cygnus* George of Western Australia (Phillips, 1972). Patterns of settlement in these species occurred during the darkest phases of the moon when predation was expected to be minimal, whereas settlement of *C. sapidus* occurred predominantly during and immediately after the full moon when night-time light intensities were greatest. Since most piscivorous predators on megalopae are likely to rely on visual detection of prey, synchronous settlement during full moon when predators could be active (Hobson et al., 1981) seems counterintuitive from the standpoint of survival. Although reasons for such patterns in association with full moon remain unclear, the temporal partitioning of a highly vulnerable activity like settlement (and subsequent metamorphosis) may overwhelm predators and reduce predation effects even during full moon. Additionally, the extended presence of *C. sapidus* megalopae into colder months of the year (October, November) in these temperate latitudes enables settlement when most piscivorous predators are becoming inactive or are migrating out of prime settlement habitats. This fact,

coupled with the dilution of predation through lunar-related episodic settlement may enhance overall survival in *C. sapidus*.

Settlement and subsequent metamorphosis to the juvenile phase in *C. sapidus* is a period of high vulnerability and intense predation (van Montfrans and Orth, unpubl. data). The selective advantages of synchronous molting in adult crustaceans (stomatopods) to reduce predation have been reviewed by Reaka (1976). Natural populations of large juvenile and sub-adult blue crabs in lower Chesapeake Bay (Ryer et al., in press) and in South Carolina estuaries (Bishop et al., 1984) undergo increased ecdysis in relation to full moon and the consensus of commercial soft crab shedders in Chesapeake Bay is that most crabs in shedding floats also molt during this period (Oesterling, 1988). Thus, the influence of full moon on ecdysis in *C. sapidus* may begin relatively early (i.e., during megalopal settlement) and may serve to minimize predation throughout its life cycle.

Patterns of settlement in *N. sayi* differed considerably from those of *C. sapidus*. Except during 1985 when two distinct settlement periods were evident, *N. sayi* exhibited somewhat continuous presence on collectors until mid-October. Settlement did not occur in relation to lunar phase and was continuous across all lunar quarters. Because of the relatively short developmental period in this species and the somewhat continuous settlement annually between August and October above temperatures of 16°, we concur with Salmon et al. (1986) that spawning may also be continuous and unrelated to lunar period.

If *C. sapidus* megalopae are preferentially preyed upon over *N. sayi* megalopae by benthic predators then a selective advantage of synchronous settlement may exist for *C. sapidus*. Whether predation on *N. sayi* megalopae is relatively lower than on *C. sapidus* is not known. A comparison of relative predation levels on the two species may serve as a test of the synchronous vs. continuous settlement concept. Alternatively, the patterns of settlement observed in the present study imply that species with short development may not have time to undergo entrainment of synchronous settlement behavior by lunar cues and this factor alone may cause the observed differences in settlement.

The role of fecundity, development, behavior and physiological state in response to environmental factors and the influence of dynamic physical processes in determining the timing and magnitude of settlement are poorly understood and should be examined from a broad evolutionary perspective. Settlement strategies exhibited by *C. sapidus* (an exported estuarine species with a relatively long planktonic life history) and *N. sayi* (a retained estuarine species with shorter planktonic development) suggest that different selective mechanisms may be responsible for the observed patterns. Predation by fish has a dominant influence on selection for noxious spination rather than large body size in zoeae of estuarine brachyura (Morgan, 1989) and may further influence timing of postlarval settlement (i.e., *C. sapidus*) or result in reduction in planktonic larval duration (i.e., *N. sayi*). The present study emphasizes the need to further elucidate mechanisms accounting for the vastly different settlement strategies exhibited by estuarine-dependent brachyura.

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