

Diel Variation in Immigration of Fishes and Decapod Crustaceans to Artificial Seagrass Habitat

SUSAN M. SOGARD¹
KENNETH W. ABLE
Marine Field Station
Institute of Marine and Coastal Sciences
Rutgers University
Great Bay Boulevard
Tuckerton, New Jersey 08087

ABSTRACT: Fish and decapod entry into small (1.5 m²) artificial seagrass habitats positioned on an open sand area in a New Jersey estuary was examined to determine if immigration varied between day and night. To encounter the structured habitats, colonizers had to cross an expanse of bare sand, with its presumably higher predation risk. Contrasts in abundance in the artificial seagrass plots between dawn and dusk indicated higher nighttime immigration for four species, including the fishes *Fundulus heteroclitus* and *Myoxocephalus aeneus*, and the caridean shrimps *Palaemonetes vulgaris* and *Hippolyte pleuracanthus*. Size-frequency distributions of colonizers varied between day and night for two fish species, *Menidia menidia* and *Syngnathus fuscus*, with a greater proportion of smaller individuals immigrating to the artificial seagrass at night. *Callinectes sapidus* also displayed a diel contrast in size distribution but, for this species, proportionately more small individuals colonized the plots during the day. We suggest that diel variability in predation risk and/or diel patterns in motor activity may be responsible for these patterns in immigration.

Introduction

Newly available habitat is rapidly colonized by crustaceans and fishes (Molles 1978; Bell and Devlin 1983; Leber 1985; Shulman 1985; Stoner and Lewis 1985; Virnstein and Curran 1986; Sogard 1989). For a variety of substrate types, there appears to be a large pool of potential colonists ready to exploit new resources. In a previous study, Sogard (1989) compared the development of fish and decapod crustacean communities in different locations in New Jersey estuaries, using artificial seagrass as a colonizing substrate to allow comparison of sites with and without substrates of natural eelgrass (*Zostera marina*). The artificial seagrass plots consistently yielded high densities of fishes and decapods, especially at sites far removed (4+ km) from natural *Zostera marina* meadows. At these sites, colonists had to move across broad expanses of bare sand to reach the small (1.5 m²) plots. Such unvegetated substrates typically entail a greater predation risk than vegetated habitats (Coen et al. 1981; Heck and Thoman 1981; Savino and Stein 1982; Minello and Zimmerman 1983; Leber 1985; Herrnkind and Butler 1986; Wilson et al. 1987; Wilson et al. 1990a).

In the present study we compared colonization of artificial seagrass between day and night to determine if there was a diel pattern in immigration across the predation-risky open sand. The use of an artificial habitat allowed us to manipulate patch size and location. Because artificial seagrass attracts a fauna similar to that of natural seagrass (Bell et al. 1985; Virnstein and Curran 1986; Sogard 1989), we assumed that colonization patterns would be comparable to those occurring in natural patches of vegetated habitat.

Materials and Methods

The study site was a shallow sand flat in a polyhaline cove adjacent to the Rutgers Marine Field Station in Great Bay, New Jersey. Depth was approximately 30 cm at mean low water and 120 cm at mean high water. This site was also used as one of four sites in a previous study of artificial seagrass colonization (Sogard 1989). It was at least 8 km from any natural eelgrass beds; alternative potential sources of immigrating fish and decapods included a marsh creek, patches of sea lettuce (*Ulva lactuca*), a dredged channel, salt marsh banks inside the cove, and a deep natural channel and extensive sand flats outside the cove.

Plots of artificial seagrass were constructed from green plastic ribbon tied to 1.5-m² squares of plas-

¹ Present address: Hatfield Marine Science Center, Oregon State University, Newport, Oregon 97365.

tic mesh, with the blades 300 mm in height and 5 mm wide, attached in a density of 2,952 blades m^{-2} (see Sogard 1989 for additional details). Four plots of artificial seagrass were anchored to sand with reinforcing bar, with a minimum distance between them of 8 m. The plots were placed in position approximately 2 wk prior to the first sampling date to allow time for colonization of the blades by epiphytes. They remained in place throughout the study.

Fishes and decapods were collected from the plots with 1- m^2 throw traps (modified after Kushlan 1981, and identical to those used by Sogard and Able 1991) that were positioned over the artificial seagrass plots and held in place during sampling. Animals were removed with a 1-m wide framed net with 3-mm mesh until three consecutive net passes produced no fish or decapods. After the throw trap was removed, the plots were repeatedly scraped with a push net to remove any animals remaining on the edges (which were not covered by the throw trap). Mud crabs (Xanthidae) and hermit crabs (Paguridae) were excluded from analysis because their tendency to cling to the underside of the mesh bases of the plots and their burrowing behavior prevented this method from being quantitative. Although other species also burrow, we believe our sampling technique effectively removed them; preliminary trials in which the plots were repeatedly netted beyond our sampling criterion continued to collect mud crabs and hermit crabs but not other decapods or fishes.

Sampling took place over five periods: one in June, two in July, and two in August 1989. At dusk on the evening before the first sampling day of each period, all fishes and decapods were removed from the plots and discarded, using the above methods. The plots were subsequently sampled at dawn and dusk for the next 3 d. We assumed that densities at dawn accurately represented the number of organisms moving into the plots during the night, while animals collected at dusk represented daytime colonizers. Since collections were made at the same approximate light level (dawn or dusk), sampling efficiency was probably similar for both time periods. The high densities of organisms colonizing artificial seagrass (Sogard 1989) indicate that animals are likely to remain in the plots once encountered, at least for a period of several hours to several days. Our method did not, however, allow detection of colonizers that might have left the plots prior to our sampling.

Within individual artificial seagrass plots, the three dawn samples were summed and the three dusk samples were summed. With four plots and five sampling periods, this resulted in 20 paired samples of dawn collections (representing night-

time immigrants) and dusk collections (representing daytime immigrants). To compare immigration rates between dawn and dusk, we conducted Wilcoxon signed ranks tests on the 20 pairs. Paired comparisons (dawn and dusk collections from a single seagrass plot) were appropriate for this study because individual plots potentially varied in their attractiveness to immigrants, and the availability of recruits varied over the course of the study. Blue crabs (*Callinectes sapidus*) included a wide size range, from early juveniles to adults; for statistical analysis they were divided into two size classes, <50 mm or ≥ 50 mm carapace width.

To determine if there were size-related differences in patterns of immigration to the artificial seagrass plots, we examined the size distribution of colonizing individuals, using Kolmogorov-Smirnov two-sample tests to compare dawn and dusk. Frequency distributions of total lengths for winter flounder (*Pleuronectes americanus*), northern pipefish (*Syngnathus fuscus*), and Atlantic silverside (*Menidia menidia*), and carapace widths for *Callinectes sapidus* were compared. Because other decapods were not measured during processing we could not compare size distributions of the shrimp species. The size frequency distribution of *M. menidia* was estimated from a measured subsample ($n = 30$) in cases where >30 individuals were collected from a plot.

Throw traps were also used to sample the fish and decapod community on the sand substrate surrounding the artificial seagrass plots. Two throw trap samples on sand were collected at a distance of 2 m or 3 m from a plot with each dawn and dusk sampling effort, providing a total of 58 sand samples. Sand samples were collected from undisturbed areas, in contrast to the artificial seagrass plots, which had been cleared of all fishes and decapods either 9 h prior to sampling at dawn (nighttime colonization) or 15 h prior to sampling at dusk (daytime colonization).

Results

COLONIZING COMMUNITY

Colonists of the artificial seagrass plots were dominated by a relatively small number of species, the fishes *Menidia menidia*, *Syngnathus fuscus*, *Pleuronectes americanus*, *Myoxocephalus aeneus* (grubby), and *Fundulus heteroclitus* (mummichog), and the decapod crustaceans *Palaemonetes vulgaris* (marsh grass shrimp), *Crangon septemspinosa* (seven-spined bay shrimp), *Hippolyte pleuracanthus* (false *Zostera* shrimp), and *Callinectes sapidus* (Table 1). Densities of organisms on the adjacent sand substrate were low for most species, with the exception of the small schooling fishes *M. menidia* and *Anchoa mitch-*

TABLE 1. Number of individuals of fishes and decapod crustaceans collected at dawn and dusk in artificial seagrass plots and adjacent unvegetated sand substrates in Great Bay, New Jersey. Sampling effort included 120 1-m² samples from artificial seagrass collected after 9 h (dawn) or 15 h (dusk) of colonization time and 58 1-m² samples from undisturbed bare sand. Species are listed in order of the total number collected.

Species	Artificial Seagrass		Sand	
	Dawn	Dusk	Dawn	Dusk
Fishes				
<i>Menidia menidia</i>	1,256	792	484	157
<i>Anchoa mitchilli</i>	0	14	1	71
<i>Syngnathus fuscus</i>	39	37	2	3
<i>Pleuronectes americanus</i>	18	14	18	14
<i>Myoxocephalus aeneus</i>	13	3	0	0
<i>Fundulus heteroclitus</i>	12	2	1	0
<i>Tautoglabrus adspersus</i>	2	5	0	0
<i>Tautoga onitis</i>	2	4	0	0
<i>Gobiosoma bosc</i>	5	1	0	0
<i>Anguilla rostrata</i>	4	0	0	0
<i>Monacanthus hispidus</i>	2	1	0	0
<i>Opsanus tau</i>	1	1	0	0
<i>Scorpaena</i> sp.	1	1	0	0
<i>Caranx</i> sp.	0	1	0	1
<i>Hippocampus erectus</i>	1	0	0	0
<i>Chaetodon ocellatus</i>	1	0	0	0
<i>Fistularia tabacaria</i>	0	1	0	0
<i>Etropus microstomus</i>	0	0	1	0
Decapods				
<i>Crangon septemspinosa</i>	412	519	2,150	2,003
<i>Palaemonetes vulgaris</i>	2,979	611	14	22
<i>Hippolyte pleuracanthus</i>	389	87	3	1
<i>Callinectes sapidus</i>	70	80	18	21
<i>Carcinus maenas</i>	3	5	0	0
<i>Callinectes similis</i>	2	2	3	0
<i>Ovalipes ocellatus</i>	1	0	1	2

illi (bay anchovy), *P. americanus*, and *C. septemspinosa*. Because capture efficiencies of enclosure traps are very high on both vegetated and unvegetated substrates (70% to nearly 100%, Kushlan 1981; Pihl and Rosenberg 1982), the contrast between sand and artificial seagrass substrates was not likely due to differing capture rates.

Over the 3 d of sampling, densities of fish and decapods on an individual seagrass plot were variable and did not exhibit any consistent trends. Thus, there was no indication that repeated sampling depleted the supply of available colonists.

DAWN-DUSK COMPARISONS

Results of Wilcoxon's tests indicated statistically significant differences between dawn and dusk abundances in the artificial seagrass plots for *Myoxocephalus aeneus* ($p = 0.047$), *Fundulus heteroclitus* ($p = 0.016$), *Palaemonetes vulgaris* ($p < 0.001$), and *Hippolyte pleuracanthus* ($p < 0.001$). Colonization levels were higher at night for each of these groups (Figs. 1 and 2). The total numbers of grubby (*M. aeneus*, $n = 16$) and mummichog (*F. het-*

eroclitus, $n = 14$) collected were low, however. All other tested species did not differ ($p > 0.05$) in abundance between dawn and dusk.

For the decapods, dawn-dusk differences were particularly striking for the two shrimp species. For the most abundant species in the artificial seagrass, *P. vulgaris*, 83% of the immigration to the plots occurred at night. Similarly, 82% of the *H. pleuracanthus* colonized the plots at night.

Size comparisons revealed significantly different size-frequency distributions at dawn and dusk for *Menidia menidia* (Kolmogorov-Smirnov tests, $p < 0.001$), *Syngnathus fuscus* ($p = 0.017$), and *Callinectes sapidus* ($p = 0.003$). During the night, proportionately more small Atlantic silversides colonized the plots, with larger individuals more likely to enter the plots during the day (Fig. 3). Small-sized (<70 mm TL) northern pipefish colonized the artificial seagrass plots only during the night (Fig. 4). These two species did not differ in total density between dawn and dusk collections (Table 1), but apparently the smaller fish were more likely to move into the artificial seagrass plots at night. In contrast, proportionately more small blue crabs moved into the plots during the day, while larger crabs were more likely to colonize at night (Fig. 5).

Discussion

Immigration to the artificial seagrass plots was higher at night for two fish species (although abundances of both were low) and two decapod species. Two additional fish species exhibited apparent ontogenetic differences, with proportionately more small individuals colonizing the plots at night. Due to the long summer day lengths, more time was available for colonization during the day (about 15 h) than during the night (about 9 h). Thus, if most colonizers remain in the plots once they encounter them, our inference of higher nighttime colonization for these groups is conservative.

One potential explanation for higher colonization at night is that the predation risk associated with movement over bare sand substrates is reduced. During the day, structure-dependent fishes and decapods presumably reside in potential refuge habitats (salt marsh banks, peat reefs, algae patches, tidal creeks, etc.) and avoid sand substrates; this pattern is supported by abundance data from daytime collections (Sogard and Able 1991). If the efficiency of visual predators is reduced at night, the diminished risk of movement across expanses of bare sand could provide these small epibenthic species an opportunity to disperse. The dense structure provided by an artificial seagrass plot apparently induces organisms to remain once a plot is encountered. Contrasts in the size-frequency distribution of colonists between

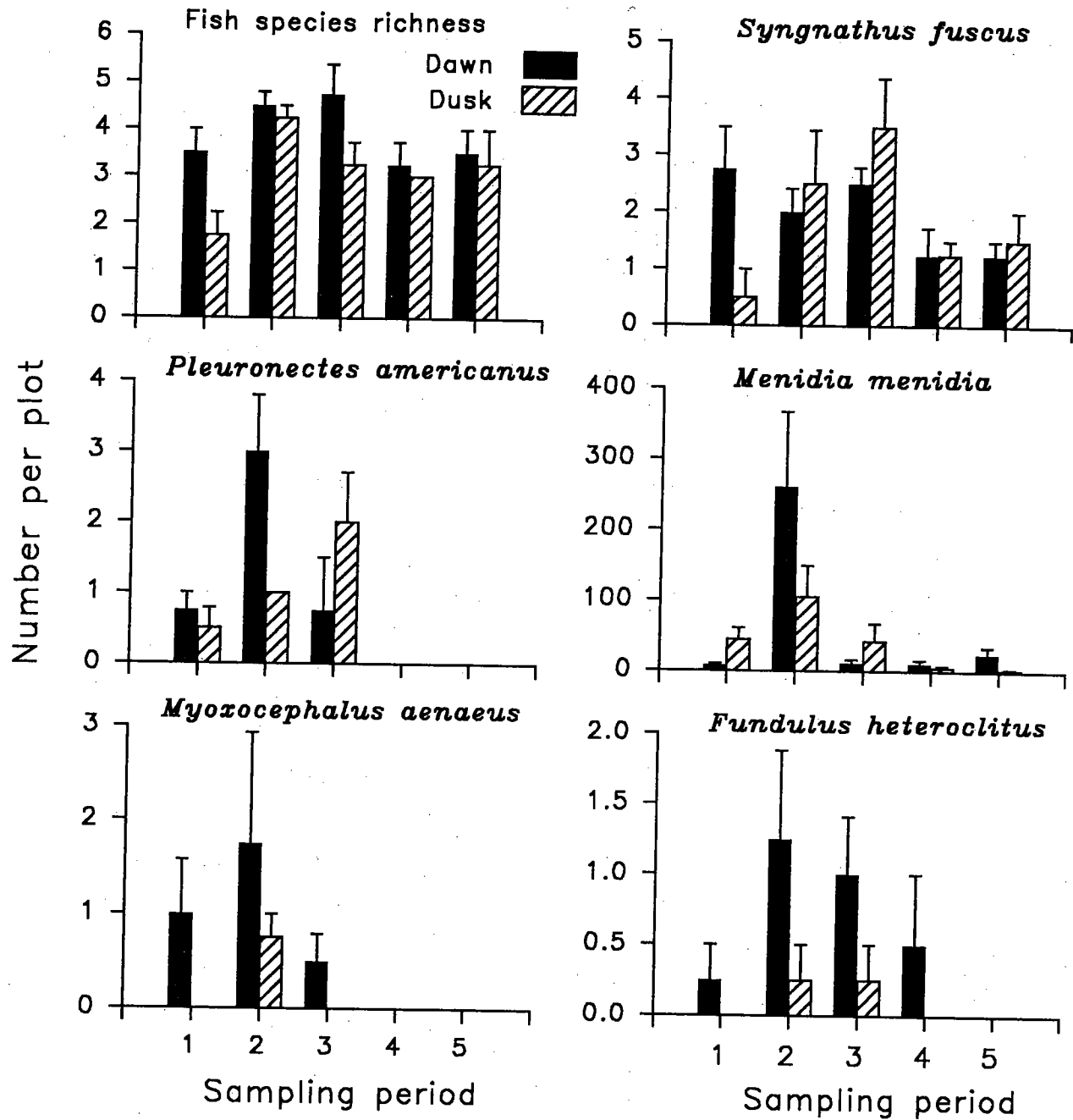


Fig. 1. The mean number (and SE) of fish species and individuals of the common species collected from artificial seagrass plots at dawn (representing nighttime colonization) and dusk (representing daytime colonization) across five sampling blocks in 1989 (June through September). Bar values are the means from four plots, with collections over 3 d of sampling summed for each plot.

day and night could be related to size-dependent differences in susceptibility to predators (e.g., Parker 1971), with smaller individuals more likely to avoid sand substrates during the day.

Alternatively, higher immigration at night could be a result of higher activity levels. Activity patterns have been described for only a few of the species

in this study, although some congeners have been examined. Using push-net sampling in tropical seagrass habitats, Bauer (1985) found significantly higher night abundances of all the caridean shrimp abundant enough to test (nine species), presumably due to higher activity and thus greater susceptibility to the net. Hagerman (1970) found

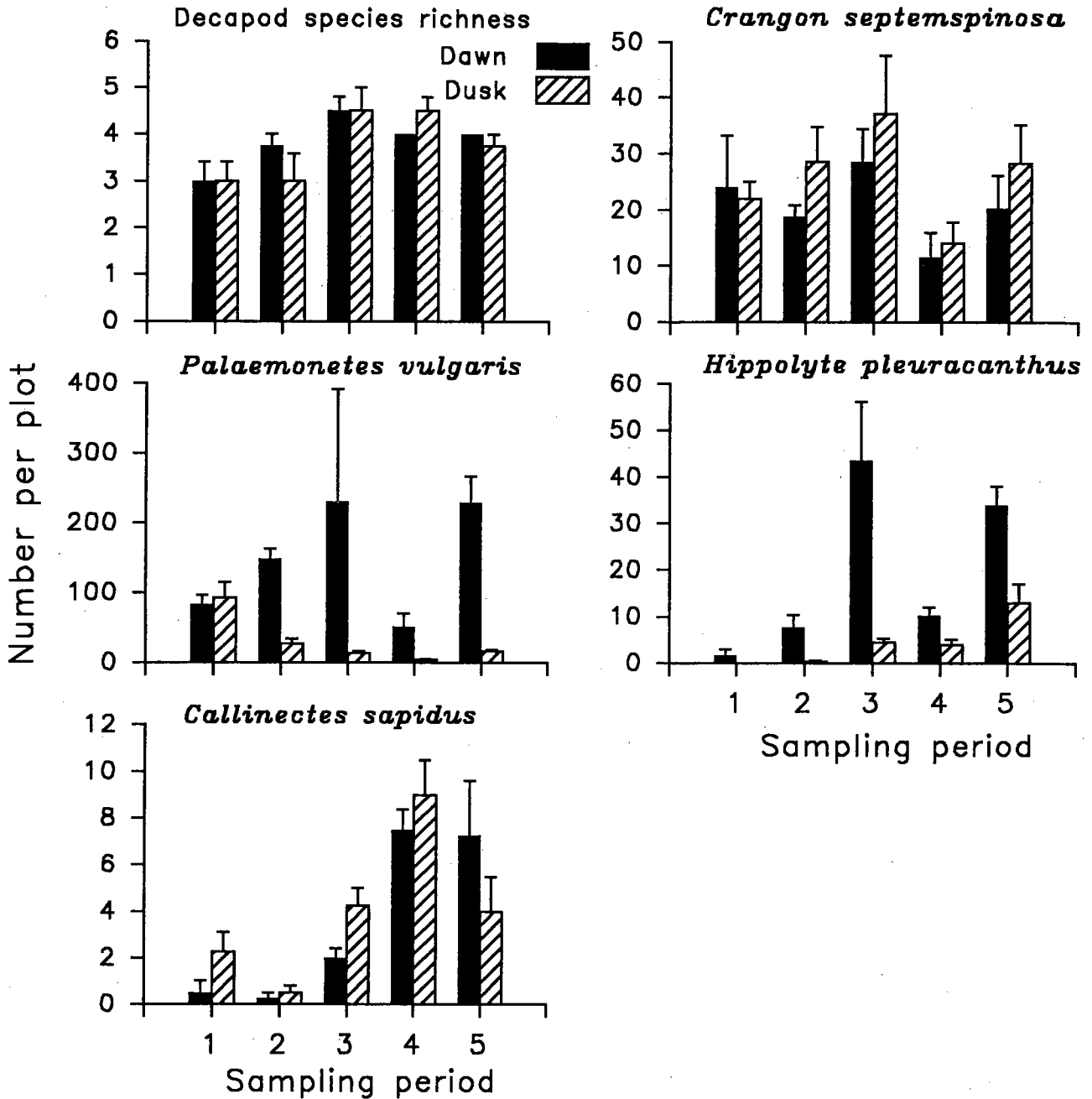


Fig. 2. The mean number (and SE) of decapod crustacean species and individuals of the common species collected from artificial seagrass plots at dawn (representing nighttime colonization) and dusk (representing daytime colonization) across five sampling blocks in 1989 (June through September). Bar values are the means from four plots, with collections over 3 d of sampling summed for each plot.

that the caridean *Crangon vulgaris* was more active at night. In this study, *Crangon septemspinosus* had a nearly significant tendency ($p = 0.057$) toward daytime colonization of the plots, but *Palaemonetes vulgaris* and *Hippolyte pleuracanthus* had significantly higher immigration levels at night. American eels

(*Anguilla rostrata*) are also more active at night (Helfman et al. 1983); four individuals of this species were collected in this study, all from dawn samples in the artificial seagrass plots. Adult male blue crabs are active by both day and night, but move at faster rates of speed at night (Wolcott and Hines

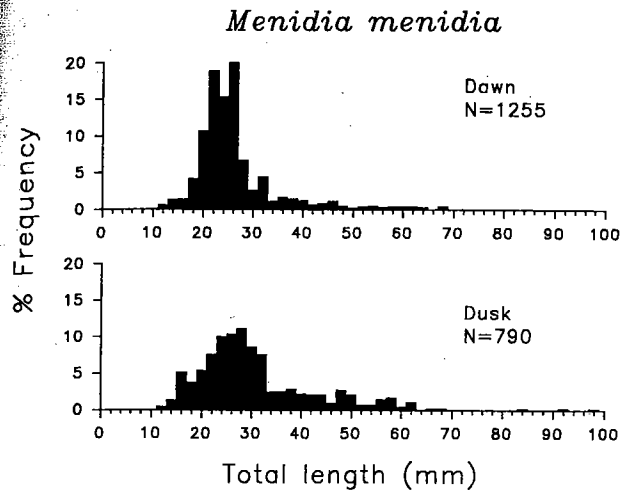


Fig. 3. Relative size-frequency distributions of Atlantic silver-side (*Menidia menidia*) collected at dawn and dusk in artificial seagrass plots. For samples with >30 fish collected, the size distribution was estimated from a subsample of 30 individuals.

1990); we found no difference in dawn and dusk abundances of blue crabs, although there was a greater proportion of large crabs in the dawn samples. *Pleuronectes americanus* of a slightly larger size range than encountered in this study were found to be nocturnally active by Casterlin and Reynolds (1982). This species showed no difference in immigration to artificial seagrass between night and day. In contrast to the above, *Fundulus heteroclitus* has higher activity levels during the day (Kavaliers 1980), yet was more likely to immigrate to artificial seagrass plots at night.

The development of a diel pattern in activity could ultimately be linked to variability in predation risk. Bauer (1985), for example, suggested that reduced predation risk from visual hunters at night allowed caridean shrimp to move up into the water column above the seagrass canopy. Similarly, Vance (1992) proposed that a pattern of higher nighttime activity in three species of penaeids resident in seagrass and mangrove habitats was related to decreased fish and bird predation at night.

There is currently little evidence, however, to support the hypothesis of reduced predation risk on exposed sand substrates at night. In fact, although postlarval spiny lobsters (*Panulirus argus*) were nocturnally active and more likely to leave habitat patches and move across open sand at night, predation rates on tethered individuals did not vary between day and night (Herrnkind and Butler 1986). Minello et al. (1987) manipulated light levels by varying turbidity in experimental tests of predation on brown shrimp (*Penaeus aztecus*), and found that lower light levels reduced pre-

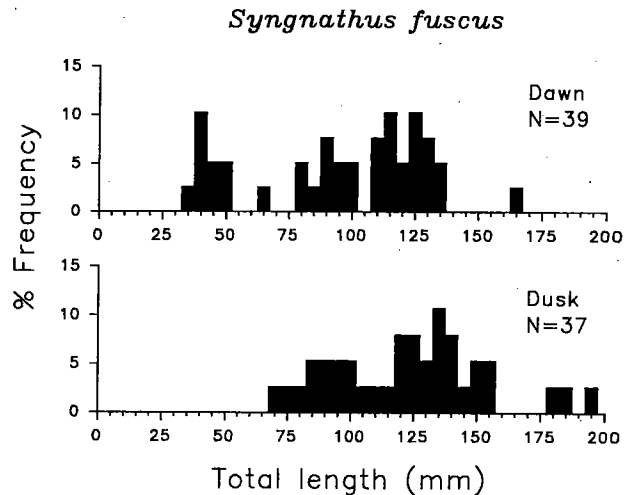


Fig. 4. Relative size-frequency distributions of northern pipefish (*Syngnathus fuscus*) collected at dawn and dusk in artificial seagrass plots.

ation by two fish predators, but increased predation by another. High turbidity may not adequately represent nighttime conditions, however, due to the concentration of suspended particles, which could potentially interfere with sensory systems.

Increased movement across sand substrates at night (and thus increased encounters with the artificial seagrass plots) should be reflected in higher abundances of fishes and decapods on sand at night. Our collections on sand substrates in this study were not applicable to such a comparison because light levels were similar at dawn and dusk. Presumably, animals that reside in sheltered habitats during the day would avoid open sand at dawn

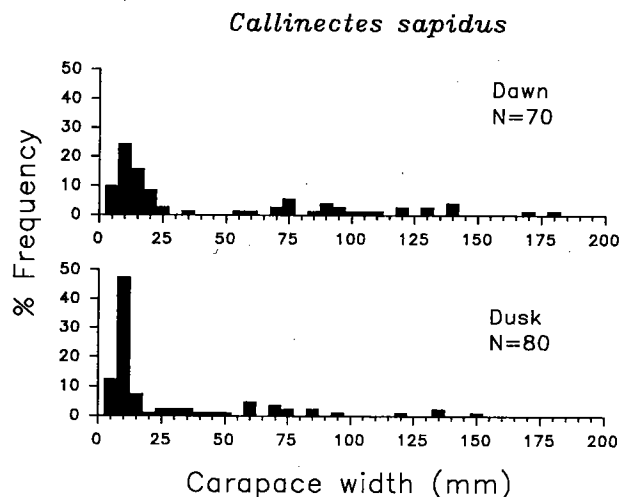


Fig. 5. Relative size-frequency distributions of blue crab (*Callinectes sapidus*) collected at dawn and dusk in artificial seagrass plots.

or dusk light levels. Wilson et al. (unpublished data) conducted quantitative diel sampling on vegetated and unvegetated substrates of New Jersey estuaries. They collected greater numbers of *Palaeomonetes vulgaris* on sand substrates at night; at a site near an eelgrass bed, 0 shrimp were collected during the day and 26 were caught at night, and at the same site used in our study, 33 shrimp were caught on sand by day and 70 by night. Abundances of other species on sand substrates in the Wilson et al. (unpublished data) study either did not differ between day and night (*M. menidia*, *S. fuscus*, *G. bosc*, *C. septemspinosa*) or were too low in abundance on sand to allow diel comparisons.

The species composition of the fish and decapod community colonizing the artificial seagrass plots was similar to that found in natural vegetated habitats in New Jersey estuaries. All of the species common in either *Ulva lactuca* or *Zostera marina* habitats (Sogard and Able 1991) were collected in artificial seagrass in this study, with the exception of the fishes *Apeltes quadracus* and *Lucania parva*. Among the natural habitats examined by Sogard and Able (1991), the latter two species were collected only from eelgrass beds, which are not present near the collection site in this study. Apparently, these two species rarely occur in the alternative structured habitats, such as macroalgae patches and saltmarsh banks, available in southern New Jersey estuaries. In contrast, both species readily colonized artificial seagrass that was adjacent to natural eelgrass (Sogard 1989).

The lack of a day-night difference for *P. americanus* and the tendency of *C. septemspinosa* toward greater daytime colonization was not surprising since both species were relatively common on unvegetated sand substrates in both this study (Table 1) and that of Sogard and Able (1991). These species were presumably not dependent on vegetation as a predator refuge, since they are cryptic on sand and able to burrow. Thus, their susceptibility to visual predators may not vary between day and night.

Although *S. fuscus* tend to be closely associated with vegetated habitats (Briggs and O'Connor 1971; Sogard and Able 1991), they did not differ in overall immigration levels to the artificial seagrass plots between day and night. Similarly, in a laboratory study, Roelke and Sogard (1993) found no significant diel difference in the occupation of bare sand substrates by pipefish. Their experiments determined habitat preferences of pipefish for artificial seagrass or sand substrates under day and night light regimes, in the presence and absence of a potential predator. Although there was a tendency for movement on to bare sand substrates to be greater at night, this difference was

not statistically significant. Their experiments were conducted with adults; juveniles may be more likely to avoid bare sand substrates during the day. In this study, pipefish <70 mm TL moved into the artificial seagrass plots only at night.

M. menidia also displayed proportionately higher nighttime immigration by small individuals; 80% of the silversides collected at dawn were <30 mm TL, in contrast to 55% of those collected at dusk. Rountree and Able (1993) examined diel contrasts in fish abundance in marsh creeks near our study site. Consistent with our results, they concluded that young-of-the-year silversides were more abundant in shallow creek habitats at night. Adults, in contrast, were often more abundant during the day. Briggs and O'Connor (1971) found that overall abundances of *M. menidia* were greater on sand substrates, but the size distribution in eelgrass was skewed toward smaller individuals. Rountree and Able (1993) also concluded that smaller silversides prefer sheltered habitats. If the ontogenetic contrast is related to predation risk, small silversides may be more likely to avoid open sand habitat during the day, and thus would not encounter the artificial seagrass plots.

The behavior of *C. sapidus* did not support a hypothesis of reduced predation risk at night. Small individuals did not differ in their timing of immigration to the artificial seagrass plots, and comparison of size distributions suggests that the smallest crabs were actually more likely to move across the bare sand substrate and into the plots during the day. The greater predation risk of unvegetated substrates for small blue crabs has been clearly documented (Wilson et al. 1987; Barshaw and Able 1990; Wilson et al. 1990a), although they are distributed across a variety of habitat types in New Jersey estuaries (Wilson et al. 1990b; Sogard and Able 1991). Based on size-frequency comparisons, larger crabs were slightly more likely to move into the plots at night. Because much of the predation on small blue crabs may be attributable to cannibalism by larger blue crabs, smaller individuals may reduce their predation risk by movement during the day rather than at night.

For a particular system, such as the shallow estuarine bay used in this study, the degree to which predation risk varies temporally needs to be assessed experimentally for different prey species before diel patterns in activity or habitat usage can be attributed to predator avoidance. Diel variability in predation risk will undoubtedly vary for different prey species, depending on the species composition and abundance of potential predators and alternative prey.

A major question regarding the immigration process is the source of artificial seagrass colonists.

Based on size distributions, only a small portion could be settling recruits from the plankton. *Syngnathus fuscus* <50 mm, for example, are largely planktonic (Campbell and Able unpublished data), suggesting that the smaller pipefish in dawn samples were settling individuals. Most colonists, however, presumably arrive from other habitats. They could potentially emigrate from other structured habitats, such as *Ulva* patches. The motivating factors resulting in individuals leaving protective habitats remain unexplained. Virnstein and Curran (1986) list several potential reasons, including temporary predator escape, avoiding competitors, searching for food after local depletion, and finding mates. These situations would have to occur commonly to support the levels of movement over bare sand demonstrated by this study and that by Sogard (1989).

An alternative source of colonists is the unvegetated substrate itself. Most of the colonizing species are rare but present on unvegetated substrates, which cover a large area in southern New Jersey estuaries. If these individuals tend to remain in artificial seagrass once it is encountered, they could account for the observed pattern, with the high densities of colonists representing concentration of a sparsely distributed population. Conclusions regarding the source of colonists and the degree of movement among different habitats will be possible only with detailed observation of the activity patterns of individuals and the turnover rate of individuals within particular habitats.

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