Diel Variation in Decapod Crustacean and Fish Assemblages in New Jersey Polyhaline Marsh Creeks

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Diel variation in fish and decapod crustacean abundance and species assemblages were examined in two studies to determine patterns of subtidal and intertidal marsh creek habitat use in a southern New Jersey estuary. In the first study, two subtidal marsh creeks were sampled with weirs from April–November 1988 ($n = 42$) and seines from July–November 1988 ($n = 33$), while in the second study two intertidal creeks were sampled with weirs from July–October 1989 ($n = 28$). Fish and decapod species assemblages captured in subtidal weir, subtidal seine and intertidal weir, as measured by both relative abundance and canonical discrimination analyses, were all highly affected by diel period. Total abundance and abundances of 15 species of fish and decapods exhibited significant diel differences, some of which were strongly influenced by season and life history stage (i.e. size cohorts). A detailed examination of the most abundant species, *Menidia menidia*, reveals that adults were more abundant during the day in early summer, suggesting diurnal reproductive movements into the creeks. In contrast, young-of-the-year cohorts were significantly more abundant at night during the late summer and fall, suggesting nocturnal movement into shallow marsh creek habitats. Our observations of strong diel differences in species assemblages point out the need for both day and night sampling in marsh habitats, if the importance of these habitats to fishes and decapods are to be fully understood.

Introduction

Faunal surveys that include only daytime sampling have been shown to underestimate fauna abundance, diversity and biomass (see Stoner, 1991 and citations therein). Although saltmarshes are known to support abundant and diverse communities (see review in Rountree & Able, 1992a), most published studies are based exclusively on daytime surveys (e.g. Nixon & Oviatt, 1973; Subrahmanyam & Drake, 1975; Weinstein, 1979). Therefore, little is known of diel patterns of marsh use by natant fishes and invertebrates.

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To our knowledge no published diel studies have been conducted in any estuarine habitats along the eastern coast of the U.S.A. north of Chesapeake Bay (except McCleave & Fried, 1975). Although we know of no studies that specifically examine diel patterns in subtidal marsh creek habitats anywhere in the world, some limited information on diel patterns can be found in studies of intertidal marsh creek (Shenker & Dean, 1979; Reis & Dean, 1981; Rozas & Hackney, 1984) and tidal freshwater marsh surface (McIvor & Odum, 1986; Rozas & Odum, 1987) habitats in the eastern U.S.A.

Studies in tidal freshwater marsh surface habitats have reported higher total fish abundance at night (McIvor & Odum, 1986; Rozas & Odum, 1987). Higher day abundance of the fish *Leiostomus xanthurus*, and higher night abundance of the shrimp *Palaemonetes pugio* and crab *Callinectes sapidus* have been reported in oligohaline intertidal marsh creek habitats (Rozas & Hackney, 1984). Shenker and Dean (1979) repeatedly sampled a single polyhaline intertidal marsh creek over a 13-day period during the winter (January) and found large diel changes in larval abundance for several fishes. Reis and Dean (1981) later used similar methods during July and August and reported higher day catches of *Anchoa mitchilli*, *Menidia menidia* and *Fundulus heteroclitus*.

A comparison of diel abundance patterns can be used to better understand habitat use patterns. We make a distinction between diel sampling bias that results from a direct avoidance response to the gear, and diel changes in susceptibility to the gear that results from other behavioural changes. Diel changes in abundance resulting from diel changes in a direct avoidance response usually imply increased day avoidance of a sampling gear because of increased visibility. Diel sampling bias, therefore, usually result in inflated night abundances, rather than inflated day abundances. Diel changes in susceptibility to a sampling gear generally involve two major categories of behaviour: (1) diel movement between habitats (e.g. horizontal or vertical migrations that result in movements out of the effective sampling area of a gear), and (2) diel changes in local activity patterns (e.g. foraging activity, reproduction activity, nocturnal burying, etc., or in other words, behaviours that result in increased activity, but do not involve directed movements between habitats). When bias due to direct gear avoidance can be accounted for, it may be possible to determine whether a given diel abundance pattern results from movements or local activity. Either conclusion can provide information useful for understanding patterns of habitat use.

In this study diel patterns in composition and species abundances of fishes and decapod crustaceans that use polyhaline intertidal and subtidal marsh creeks in a southern New Jersey estuary are examined. The primary goals of this study are: (a) to determine if significant diel differences in species assemblages, and/or abundances occur in New Jersey marshes, and (b) to examine these diel patterns in order to gain insight into habitat use by fishes and decapods.

Materials and methods

Study sites

The study was conducted within the Great Bay–Little Egg Harbor estuarine complex in southern New Jersey (Figure 1). Fishes were collected from two subtidal marsh creeks during 1988 and from two intertidal marsh creeks during 1989 with a weir system (Rountree & Able, 1992). All four creeks were polyhaline (22–30‰). The two subtidal creeks, Foxboro and Schooner creeks, are approximately 930 and 1160 m in length, 23 000 and 24 000 m^2 in creek bed area, and are located 2·3 and 1·3 km from Little Egg Harbor
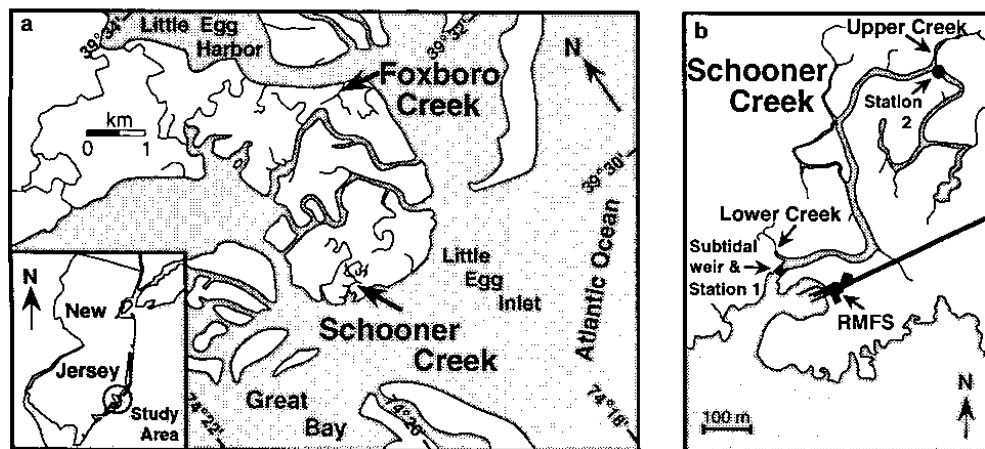
Figure 1. (a) Great Bay–Little Egg Harbor estuarine complex and Schooner and Foxboro creeks located in southern New Jersey. (b) Lower and Upper creeks were both intertidal creeks located approximately 700 m apart within the larger Schooner Creek. Station 1 and 2 designate the sites where environmental data for the intertidal creek samples were obtained. RMFS, Rutgers University Marine Field Station.

Inlet, respectively (Figure 1). Each creek has a single connection with the bay and receives freshwater only through local runoff. A more detailed description of the morphology of the study creeks is presented elsewhere (Rountree, 1992).

The two intertidal creeks are tributaries of Schooner Creek and were designated Lower and Upper creeks (Figure 1). Lower and Upper creeks are, respectively, approximately 110 and 150 m in length, 370 and 1110 m² in creek bed area, 1500 and 3300 m² in total flood area, and are located 73 and 730 m from the mouth of the Schooner Creek.

Sampling gear and methodology

Consecutive day and night tides were sampled from Schooner and Foxboro creeks over 3-day periods approximately fortnightly from July–September 1988 ($n = 28$). Additional samples were taken from Schooner Creek irregularly from April–June ($n = 9$) and October–November ($n = 5$; Rountree & Able, 1992*a*). All statistical analyses exclude the irregular samples with the exception of the *Men. menidia* cohort analysis. Lower and Upper creeks were sampled simultaneously from July–October 1989 during consecutive day and night tides ($n = 26$). Day and night tides were defined as those in which the flood occurred primarily during the day or night, respectively.

Subtidal creeks were sampled with a weir that was set to block off the mouth of a creek at high tide and captured fishes leaving the creek with the ebb tide (Rountree & Able, 1992*a*). Two wing nets (15·2 by 3·0 m, with 6·4 mm mesh) were used to block off the mouth of the creek and to lead fishes into the weir (3·0 by 1·2 by 3·0 m high, with 6·4 mm mesh). Deployment of the weir was begun about 30 min before slack high tide and was completed within 1 h. At low tide fish were removed from the weir through a cod-end.

Because the subtidal creek weir is a passive gear that primarily captures animals moving with the ebb tide, seine sampling was also conducted within the creeks to capture less mobile forms and species/individuals that might actively avoid the weir and remain within the creeks. Prior to hauling the weir at low tide, one haul of a bag seine (6·2 by 1·2 m with 3·2 mm mesh) was made after enclosing the approximately 100 m² area between the wings

with a block net. Thus each fortnightly day and night collection consisted of paired weir and seine samples in the subtidal creeks.

The intertidal creeks were sampled with a smaller and more simplified weir (1.8 by 1.2 by 1.2 m high weir, with 4.5 by 1.2 m wings). Due to gear limitations, the weir used at Lower Creek had 6·4 mm mesh, while that used at Upper Creek had 3·2 mm mesh (all wings had 3·2 mm mesh). The intertidal creek weirs were set at high tide in about 15 min and were hauled at low tide when the creek had completely drained except for a small runoff channel. No paired seine samples were taken because the creeks were intertidal.

All samples were put on ice and transported back to the laboratory for sorting and identification. For small samples all species of fishes and decapods were sorted and enumerated. For large samples the entire sample was sorted once to enumerate economically important species, species of special interest, and generally any species present in low abundance that might not be represented in subsamples. After the initial sort, all species were enumerated in a subsample of 10–50% wet weight of the sample.

During subtidal creek sampling, water depth, air and water temperature, salinity, and secchi depth were taken at the weir location at high tide after the weir had been set and at low tide just prior to hauling the gear. Secchi depth was measured under natural light conditions during both day and night. When the secchi disk was visible on the creek bottom, secchi depth was recorded as water depth. Because the intertidal creeks ran dry at low tide, physical data were collected from the center of the subtidal creek directly out from the intertidal creek mouth [sites designated stations 1 and 2, Figure 1(b)]. Therefore, physical data from the Schooner Creek subtidal weir and from the Lower Creek intertidal weir samples were taken at the subtidal weir location [Station 1, Figure 1(b)]. Secchi depth was not recorded during intertidal creek sampling.

Sample analysis

A repeated measures analysis was conducted using a multivariate analysis of variance (MANOVA) model with day and night response variables for each physical factor (e.g. high and low tide water temperatures) and species (Harris, 1985; SAS Institute Inc., 1988). The MANOVA was a nested factorial design with month, week (within month), and creek main effects. Diel main effects (the repeated measure) were tested with profile analysis (Harris, 1985; SAS Institute Inc., 1988). As we have discussed spatial patterns in marsh creek communities elsewhere, based on a subsequent study, we only present the results of the test for the diel main effects here. Environmental data were $\ln(x+15)$ transformed (15 was added to scale all negative values above zero), and species abundances were $\ln(x+0·5)$ transformed for statistical analysis. Univariate analysis of the residuals were performed to check for departures from the assumptions of MANOVA (Sokal & Rohlf, 1981). Separate MANOVAs were performed for subtidal weir and seine species abundances. This was not necessary for environmental data, since weir and seine samples were paired with the same environmental data.

Similar MANOVAs were performed on intertidal weir environmental data and species abundances, except that abundances were first converted to density m^{-2} by dividing each catch by the creek bed area (370 and 1110 m^2, for Lower and Upper creeks, respectively). Density estimates were used because the intertidal creeks drain completely, and Upper Creek was approximately three times the size of Lower Creek. Catches from the subtidal creeks could not be quantified in terms of density, because the creeks did not drain completely, and were very similar in area (23 000 and 24 000 m^2).

Canonical discrimination analysis (CDA) was used to examine interactions between spatial and diel variation in faunal assemblages (Pielou, 1984; Harris, 1985; SAS Institute Inc., 1988). This analysis was performed on arcsine transformed (Sokal & Rohlf, 1981) species relative abundance data. Separate analyses were performed for subtidal weir, seine and intertidal weir samples. The CDA was performed on data grouped by creek (Foxboro and Schooner, or Lower and Upper) and time of day (day or night). Because of the large number of species (i.e. variables), only species that were among the 10 most abundant (relative abundance) species in at least one diel group were entered in the analyses. Pearson correlations of the original transformed variables with the derived canonical variables were calculated to determine species variables which contributed most to the group discrimination (Harris, 1985). Relative abundance for each species was calculated and averaged across all samples separately for each gear.

Menidia menidia *cohort analysis*

Fortnightly length frequency histograms for *Men. menidia*, based on subsamples from each subtidal weir, seine and intertidal weir sample, were examined to identify size cohorts. These size cohorts were visually identified based on the presence of distinct length modes. Each fish length from the subsample was assigned a cohort designation based on its length at date of capture. Abundance of each size cohort within each sample was then estimated based on the cohort's percent frequency in the subsample. Mean cohort abundance within each fortnightly sample week was graphed against the date of the first day of the week to examine temporal change in the diel abundance patterns.

Results

Physical conditions

While environmental variables did not differ significantly between creeks, small but significant diel differences were found in both subtidal and intertidal creeks (Table 1). Low tide water temperature averaged 3 °C warmer during the day than at night for both subtidal and intertidal creeks. No diel differences were observed at high tide. Tidal range in water temperature was significantly greater during the day than during the night, averaging 4 and 3 °C during the day for subtidal and intertidal creeks, respectively. Maximum tidal range in water temperature was 8 °C during the day. At night water temperature dropped as much as 5 °C and rose as much as 7 °C from high to low tide. Tidal range in salinity was significantly greater during the night, averaging 3‰, than day in the intertidal creeks.

Diel differences in species assemblages

Strong diel differences in species assemblages were found for all three sampling gears, based on mean relative abundance (Figure 2). The fish *Men. menidia* dominated night collections for all gears by relative abundance, while day collections were dominated by the fish *L. xanthurus* in the subtidal weir, and by the shrimp *Pal. vulgaris* in both the seine and intertidal weirs. *Palaemonetes vulgaris* was among the dominant species for all gears and diel periods except day subtidal weir samples. The turtle *Malaclemys terrapin*, and fishes *A. hepsetus*, *Caranx hippos* and *Pleuronectes americanus* contributed to the dominant fauna only in day subtidal weir samples. The fishes *Gobiosoma bosc* and *Mugil curema* were among the dominant species only for day seine and intertidal weir samples, respectively.

TABLE 1. Comparison of mean (minimum, maximum) physical conditions between high and low tide stages, and between day and night for two subtidal creeks (July–September 1988) and two intertidal creeks (July–October 1989) in a southern New Jersey estuarine complex

Variable	Subtidal creeks		Intertidal creeks	
	Day	Night	Day	Night
High tide				
Air temperature (°C)	24 (17, 32)**	19 (11, 27)	21 (12, 23)	19 (6, 23)
Water temperature (°C)	20 (17, 25)	20 (16, 26)	21 (13, 24)	21 (11, 24)
Salinity (‰)	32 (30, 32)*	31 (30, 32)	27 (24, 30)	28 (22, 30)
Secchi depth (m)	0·9 (0·4, 1·4)*	0·7 (0·4, 0·9)	no data	no data
Depth (m)	1·5 (0·8, 2·0)*	1·3 (0·8, 1·7)	1·7 (1·4, 2·1)	1·9 (1·2, 2·3)
Low tide				
Air temperature (°C)	22 (15, 28)***	20 (9, 31)	22 (9, 28)	19 (9, 23)
Water temperature (°C)	24 (19, 28)***	21 (13, 26)	24 (12, 29)*	21 (10, 24)
Salinity (‰)	31 (25, 33)	31 (30, 33)	26 (21, 29)	25 (20, 28)
Secchi depth (m)	0·4 (0·2, 0·6)	0·4 (0·3, 0·8)	no data	no data
Depth (m)	0·7 (0·3, 1.0)*	0·6 (0·3, 0·9)	0·7 (0·5, 1·0)	0·8 (0·5, 1·0)
Tidal range (high–low)				
Air temperature (°C)	3 (2, 4)	−1 (−13, 8)	−2 (−5, 3)	0 (−6, 4)
Water temperature (°C)	−4 (−8, −1)**	−1 (−7, 5)	−3 (−5, 1)**	0 (−4, 3)
Salinity (‰)	1 (−1, 7)	−1 (−1, 0)	1 (−1, 4)	3 (0, 7)*
Secchi depth (m)	0·5 (0·1, 0·8)	0·2 (−0·1, 0·5)	no data	no data
Depth (m)	0·8 (0·5, 1·1)	0·8 (0·5, 1·0)	1·0 (0·6, 1·4)	1·1 (0·4, 1·4)
Sample size	12	15	11	12

Differences between day and night were tested separately for subtidal and intertidal creeks with a multivariate analysis of variance (MANOVA) with day and night response variables and month, week (within month) and creek main effects (see text). Significant differences between day and night are indicated ($*P<0·05$, $**P<0·01$, $***P<0·001$).

Significant differences in species assemblages among treatment groups (diel and creek combinations) were found in the CDA analyses for all gears (Tables 2 and 3, Figures 3 and 4). For subtidal weir samples day and night samples clustered separately only for Foxboro Creek, while for seine samples day and night groups clustered separately for both creeks. Night intertidal weir samples from both Lower and Upper creeks clustered together, while day samples clustered separately from night samples and from each other (Figure 4). Although neither canonical variable should be viewed as solely representing diel or spatial effects, the first canonical variable (Can1) tends to separate spatial groups (creeks), while the second canonical variable (Can2) tends to separate diel groups. Note, however, that day and night samples would cluster separately based on Can1 alone.

Correlations of species relative abundances with the derived canonical variables suggest some of the dominant contributors to diel and spatial discrimination among collections. The fish *Strongylura marina* was positively correlated with Foxboro Creek day weir samples. The fishes *F. heteroclitus*, *G. bosc* and decapods *Cal. sapidus*, and *Pal. vulgaris* were positively correlated, while *Men. menidia* was negatively correlated, with Foxboro Creek day seine samples (Table 2). In the intertidal weir collections the crab *Cal. sapidus*, and fishes *F. majalis*, *F. heteroclitus* and *Sphyraena borealis* were positively correlated with Lower Creek day samples, while the shrimp *Pal. vulgaris* and fish *Men. beryllina* were positively correlated with Upper Creek day samples. Although the Can2 has a low significance level ($a = 0·1$, Table 3), species positively correlated with Can2 tend to be strongly

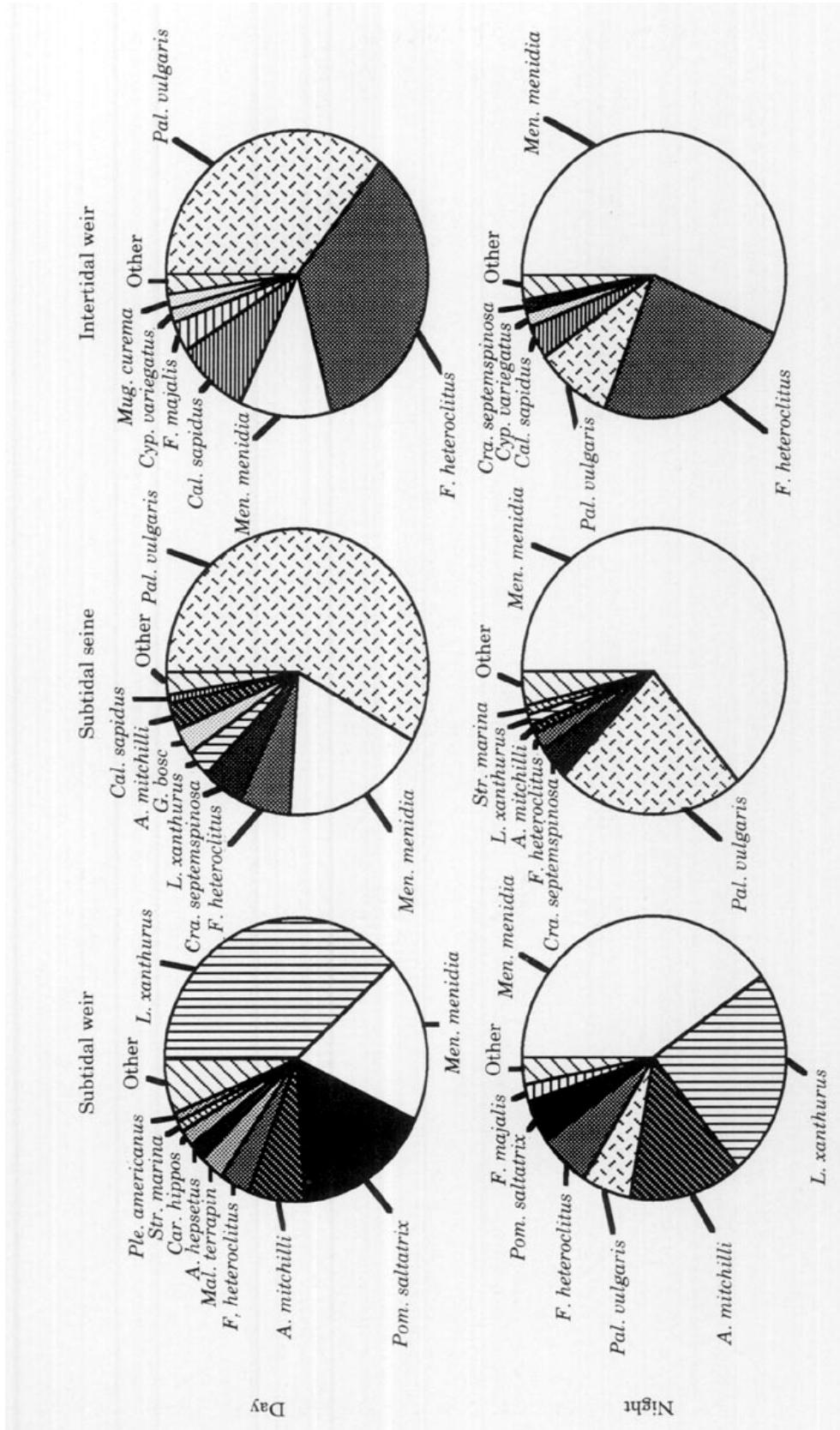Figure 2. Mean percent relative abundance of all species ≥ 1% by diel period and sampling gear. Subtidal weir (*n* = 21) and seine samples (*n* = 22) were taken fortnightly from two creeks during July–September 1988. Intertidal weir samples (*n* = 26) were taken fortnightly from two creeks during July–October 1989.

TABLE 2. Canonical discrimination analyses of species relative abundance variables (arcsine square-root transformed) for data grouped by subtidal creek (Schooner and Foxboro), and diel period (day and night) for weir ($n = 21$) and seine ($n = 22$) samples taken from July–September 1988 (see plot of canonicals in Figure 3)

Subtidal weir				Subtidal seine		
	Pearson correlation				Pearson correlation	
Species	Can1	Can2	Species		Can1	Can2
Strongylura marina	0·59**	0·26	Fundulus heteroclitus		0·58**	−0·18
Fundulus heteroclitus	0·26	0·33	Callinectes sapidus		0·57**	−0·04
Pomatomus saltatrix	0·17	−0·21	Gobiosoma bosc		0·49*	0·41
Anchoa mitchilli	0·11	0·10	Palaemonetes vulgaris		0·48*	0·56**
Leiostomus xanthurus	0·05	−0·21	Anchoa mitchilli		0·06	0·01
Callinectes sapidus	−0·03	−0·17	Sphyraena borealis		−0·07	0·54**
Anchoa hepsetus	−0·13	−0·17	Leiostomus xanthurus		−0·10	0·34
Menidia menidia	−0·14	0·13	Syngnathus fuscus		−0·25	0·76***
Sphyraena borealis	−0·31	−0·48*	Crangon septemspinosa		−0·25	0·62***
Palaemonetes vulgaris	−0·34	0·78***	Menidia menidia		−0·58**	−0·58***
Squared canonical correlation	0·95**	0·64	Squared canonical correlation		0·95***	0·73
Multivariate F (difference among groups)	2·79**		Multivariate F (difference among groups)		3·6***	

Pearson correlations of the transformed species variables on the derived canonical variables (Can1 and Can2) are given.
*$P < 0·05$, **$P < 0·01$, ***$P < 0·001$

TABLE 3. Canonical discrimination analysis among intertidal creek and diel collection groups for species relative abundance data (see plot of canonicals in Figure 4)

Species	Pearson correlation	
	Can1	Can2
Callinectes sapidus	0·61***	−0·43
Fundulus majalis	0·50**	−0·32
Fundulus heteroclitus	0·43*	−0·26
Sphyraena borealis	0·41*	−0·23
Crangon septemspinosa	0·20	0·15
Pomatomus saltatrix	0·17	−0·09
Cyprinodon variegatus	0·10	−0·16
Mugil curema	0·04	−0·08
Menidia menidia	−0·06	−0·65***
Menidia beryllina	−0·49*	−0·24
Palaemonetes vulgaris	−0·78*	−0·51**
Squared canonical correlation	0·96***	0·80^a
Multivariate *F* (difference among groups)	4·9***	
Sample size	26	

Pearson correlations of the original tranformed (arcsine square-root) species variables on the derived canonical variables (Can1 and Can2) are given.
*P < 0·05, **P < 0·01, ***P < 0·001, ^{a}P = 0·06.

correlated with night samples (*Men. menidia*), while negatively correlated species (*Pal. vulgaris* and *Cal. sapidus*) tend to be strongly correlated with day samples.

Canonical discrimination analyses indicate a strong diel and spatial interaction on creek communities. Differences between the two subtidal creeks (Table 2, Figure 3) and between the two intertidal creeks (Table 3, Figure 4) were much greater during the day than night. Additionally, subtidal seine samples exhibited stronger diel differences in the smaller, and much shallower (Table 1) Foxboro Creek compared to Schooner Creek (Table 2, Figure 3).

Diel differences in species abundances

The abundances of 10 species, total number of fish, and total fauna (fishes and decapods) exhibited significant diel differences in subtidal weir samples, while abundances of four species, total fish, and total fauna exhibited significant diel differences in seine samples (Table 4). Diel differences in total fish and total fauna were largely due to *Men. menidia* (Table 4). Six fishes, *Men. menidia*, *Mug. curema*, *Mustelus canis*, *Opsanus tau*, *Alosa pseudoharengus* and *Cynoscion regalis*, were more abundant at night, while six other fishes, *G. bosc*, *Pomatomus saltatrix*, *Ple. americanus*, *Tautoga onitis*, and the hermit crab *Pagurus longicarpus*, were more abundant during the day. *Menidia menidia*, the shrimp *Crangon septemspinosa*, *Pom. saltatrix*, and total number of fish were significantly more abundant in intertidal weirs at night, while *Mug. curema* and *Men. beryllina* were more abundant during the day (Table 5). Total fish abundances were much greater at night for both subtidal and intertidal creeks (Tables 4 and 5).

The direction and/or magnitude of diel abundance differences were strongly influenced by season for some species (e.g. *Men. menidia*, *F. heteroclitus*, *Str. marina*, *Pal. vulgaris*). This pattern is best illustrated by the most abundant species *Men. menidia* (Figure 5). Major peaks in the night abundance of *Men. menidia* in all three gears during late July and
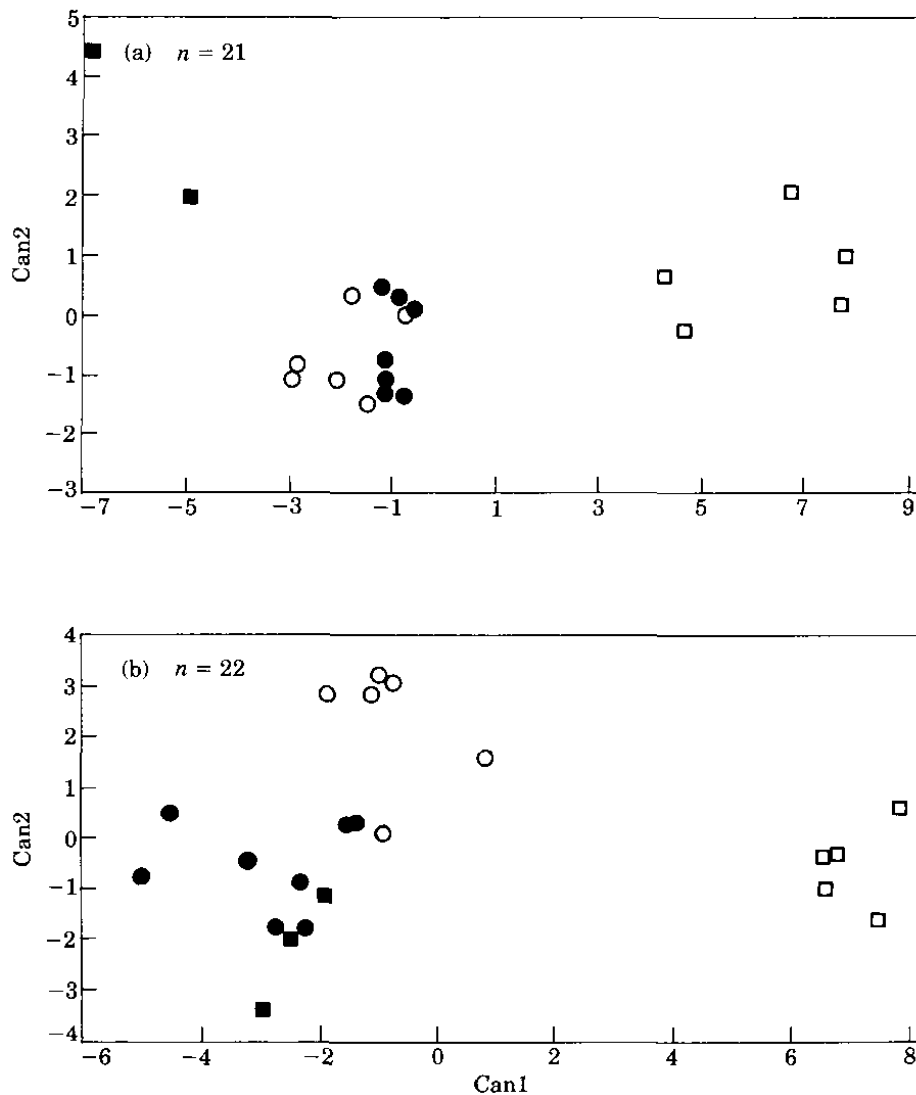
Figure 3. Canonical discrimination analyses of subtidal creek (a) weir and (b) seine species arcsine transformed relative abundance data grouped by creek and diel period. Statistics are given in Table 2. Schooner Creek day (○) and night (●), Foxboro Creek day (□) and night (■).

August resulted in the significant diel effect in the MANOVA (as reported above). Secondary peaks in night abundances during October in the subtidal weir and seine samples also suggests that a second period of high diel differences occurred in the fall.

Diel differences for Menidia menidia *cohorts*

Mean length of *Men. menidia*, for all cohorts combined, captured in day samples in the intertidal weir samples was much smaller than during the night from July–September (Figure 5). Similarly, mean length of *Men. menidia* in night subtidal seine samples averaged 10–20 mm total length (TL) larger than during the day. Diel differences in *Men. menidia* length were not apparent from subtidal weir samples.
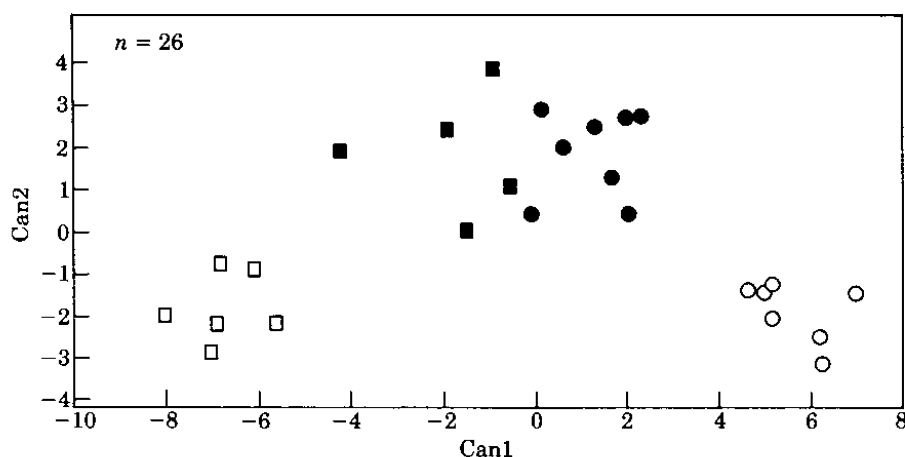
Figure 4. Canonical discrimination analysis of intertidal weir species arcsine transformed relative abundance data grouped by creek and diel period. Statistics are given in Table 3. Lower Creek day (○) and night (●), Upper Creek day (□) and night (■).

TABLE 4. Diel comparison of mean (SE) species abundances for subtidal weir and seine samples collected from Foxboro and Schooner creeks (July–September 1988)

Species	Weir		Seine	
	Day	Night	Day	Night
Menidia menidia	119 (48)	5126 (3062)**	536 (249)	3087 (1146)**
Palaemonetes vulgaris	15 (9)	544 (376)	1208 (238)	883 (258)
Leiostomus xanthurus	361 (143)	433 (137)	52 (21)	30 (12)
Anchoa mitchilli	48 (34)	420 (223)	58 (36)	20 (8)
Fundulus heteroclitus	36 (33)	291 (204)	100 (49)	54 (17)
Crangon septemspinosa	0	17 (14)	99 (36)	158 (87)
Gobiosoma bosc	0	0	53 (15)*	28 (8)
Anchoa hepsetus	56 (56)	4 (4)	0·1 (0·1)	0
Pomatomus saltatrix	39 (8)**	17 (4)	2 (1)	5 (2)
Sphyraena borealis	9 (8)	1 (1)	26 (24)	0
Mugil curema	0·2 (0·2)	11 (7)*	1 (0·9)	1·7 (1)
Pleuronectes americanus	2·5 (1)**	0·8 (0·4)	3·6 (1)	1·8 (1)
Mustelus canis	0	4·4 (2·4)**	0	0·9 (0·8)
Lucania parva	0	0	5·3 (2·9)***	0·1 (0·1)
Opsanus tau	0	0·5 (0·2)*	0·6 (0·2)	1·3 (0·6)
Tautoga onitis	0·5 (0·2)**	0·1 (0·1)	1·4 (1)	0·6 (0·3)
Pagurus longicarpus	0·6 (0·4)*	0	2 (1)	0
Cyprinodon variegatus	0	2·2 (1·9)	3·2 (2·1)*	0·2 (1·1)
Alosa pseudoharengus	0·2 (0·1)	1·1 (0·7)**	0	0
Cynoscion regalis	0	0·9 (0·5)**	0	0
Total invertebrates	18 (10)	672 (458)	1327 (266)	1061 (332)
Total fish	758 (272)	6413 (3114)*	878 (292)	3626 (1159)**
Total	781 (272)	7769 (3773)*	2205 (489)	4324 (1214)*
Sample size	11–13	12–15	11–12	11–13

Abundances of 11 dominant species, plus additional species exhibiting significant diel differences are given. Differences between day and night were tested separately for subtidal weir and seine data with a multivariate analysis of variance (MANOVA) with day and night response variables and month, week (within month) and creek main effects (see text). Significant differences between day and night within gears are indicated. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

TABLE 5. Mean (SE) density per 100 m² of the dominant intertidal creek species

Species	Day	Night
Menidia menidia	25·4 (13)	608 (392)*
Palaemonetes vulgaris	115 (43)	36 (13)
Fundulus heteroclitus	48·8 (12)	78 (39)
Callinectes sapidus	6·1 (1)	3·4 (0·9)
Mugil curema	2·8 (1·8)*	1·2 (0·6)
Fundulus majalis	1·8 (0·6)	1·4 (0·6)
Cyprinodon variegatus	1·6 (0·7)	1·4 (0·8)
Menidia beryllina	1·6 (1·0)*	0.3 (0·2)
Crangon septemspinosa	0.4 (0.3)	0·8 (0·5)**
Fundulus luciae	0·3 (0·1)	0·7 (0·5)
Total invertebrates	121 (43)	41 (13)
Total fishes	83 (22)	693 (389)*
Total	204 (58)	734 (392)
Sample size	13	13

Diel differences were tested with a multivariate analysis of variance (MANOVA) with day and night response variables and month, week (within month), and creek main effects (see text). Significant differences are indicated as $*P<0·05$, $**P<0·01$, $***P<0·001$.

Diel abundance and length patterns of *Men. menidia* were strongly influenced by cohort and sampling gear (Figures 6 and 7). A single adult and two major young-of-the-year (YOY) cohorts of *Men. menidia* occurred in both subtidal (1988) and intertidal (1989) creek data (Figure 6). During each year the first and second YOY cohorts were tracked through early August (Figure 6) when a major peak in the abundance of the first cohort occurred (Figure 7). After early August it became difficult to distinguish the size limits of the cohorts, and all subsequent individuals were assigned to an ' unknown ' cohort. This cohort was most likely comprised mainly of the second YOY cohort, but also included small numbers of adult and first YOY cohort individuals, as well as a small number of new recruits that continued to enter the catches through early September (especially in the intertidal creek samples, Figures 6 and 7).

It is apparent from the cohort abundance data that the multiple peaks in *Men. menidia* night abundance (Figure 5) resulted largely from peaks in the abundance of different cohorts (Figure 7). For example, the major peaks in August and October resulted primarily from peaks in the abundance of the first and unknown YOY cohorts, respectively. It is also clear from the cohort length and abundance data (Figures 6 and 7), that the diel patterns in *Men. menidia* length (Figure 5) resulted from cohort effects. The small mean length of *Men. menidia* in the day intertidal weir samples resulted from the complete lack of adults, and low abundance of the first YOY cohort. At night, however, large numbers of larger individuals (60–80 mm TL) from all three YOY cohorts, as well as adults were collected in intertidal weir samples (Figures 6 and 7). The diel length differences were not as strong in the seine samples, because some adults were present, and the first YOY cohort was more abundant during the day. Contrastingly, all cohorts were present in both day and night subtidal weir samples, accounting for the lack of diel length differences (Figure 7). However, subtidal weir samples were clearly biased against small size classes (Figure 6). The adult cohort was the only cohort to exhibit greater day abundance, but only in the early summer subtidal weir samples.
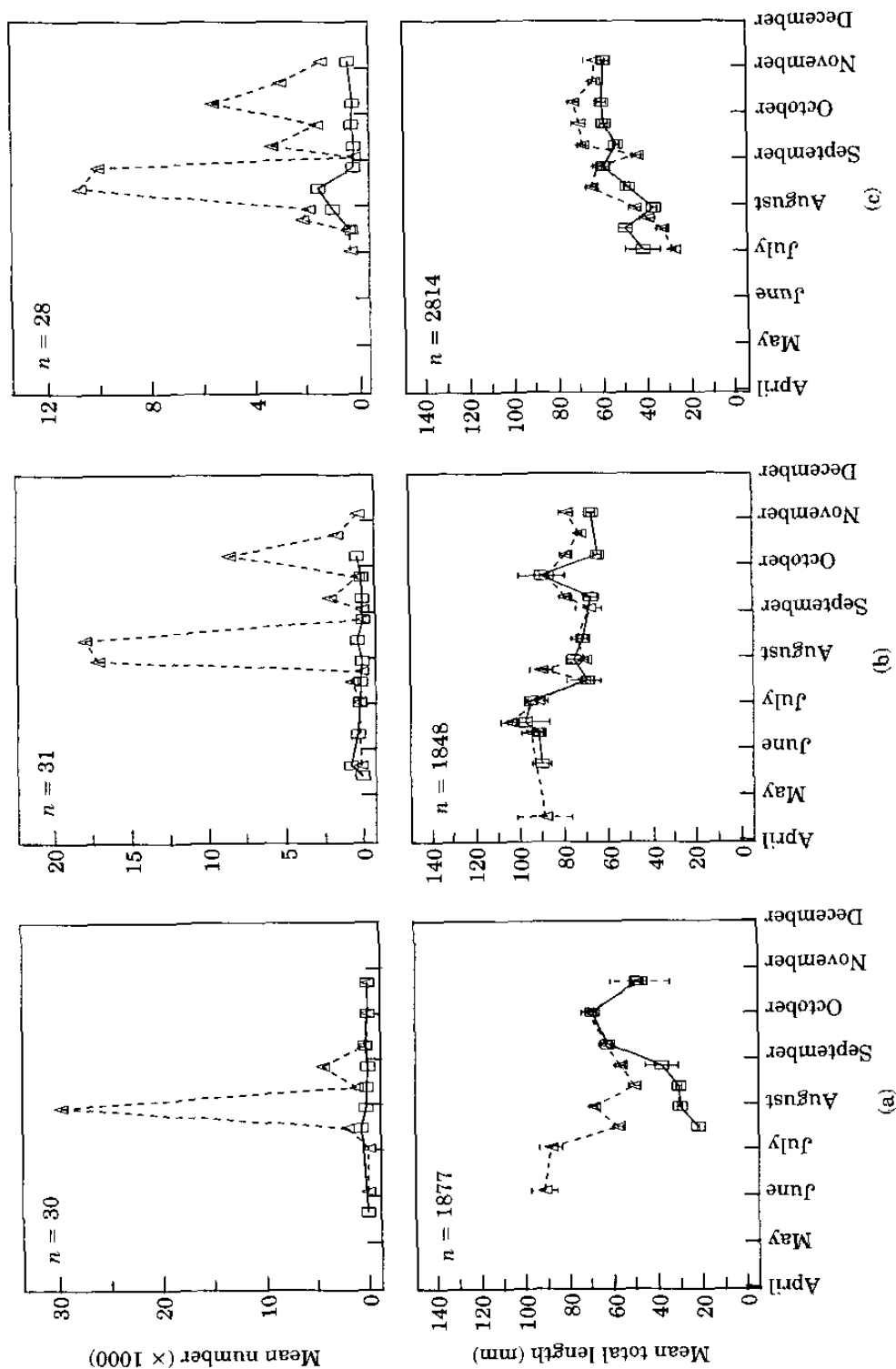
Figure 5. Diel (day, □ and night, △) comparison of total *Menidia menidia* abundance and mean total length for (a) intertidal weir, (b) subtidal weir, and (c) subtidal seine samples. Vertical bars represent 2 SE about the length means. Sample sizes indicated in the graphs represent the number of collections and number of fish measured for abundance and length plots, respectively.
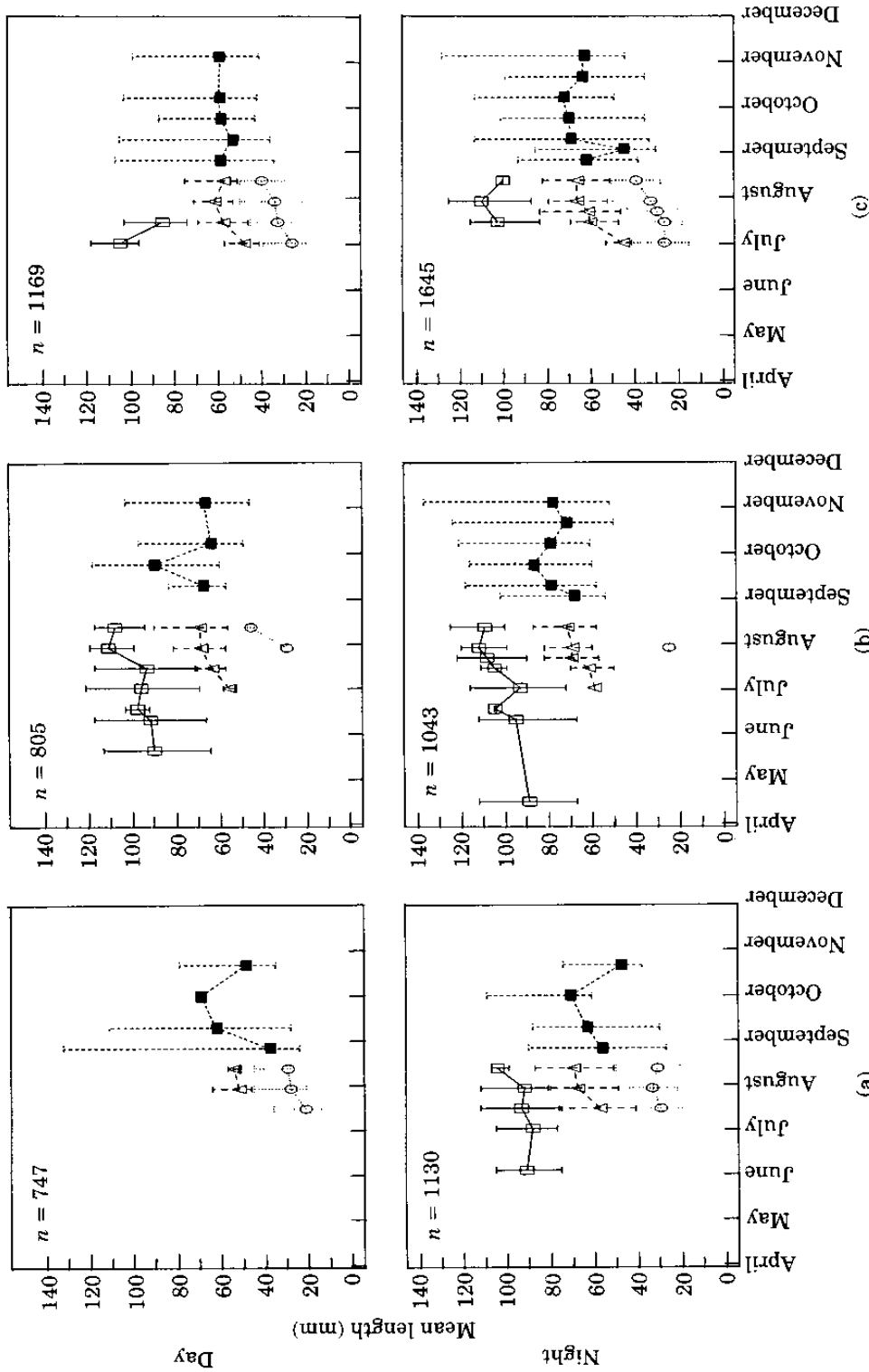
Figure 6. Comparison of day and night seasonal patterns in *Menidia menidia* mean total length by size cohort (adult, □; first YOY cohort, △; second YOY cohort, ○; and unknown cohort, ■) from (a) intertidal weir samples during June–October 1989, (b) subtidal weir samples during April–November 1988, and (c) subtidal seine samples during July–November 1988. Sample sizes indicated in the graphs represent the number of fish measured. Vertical bars are ranges.
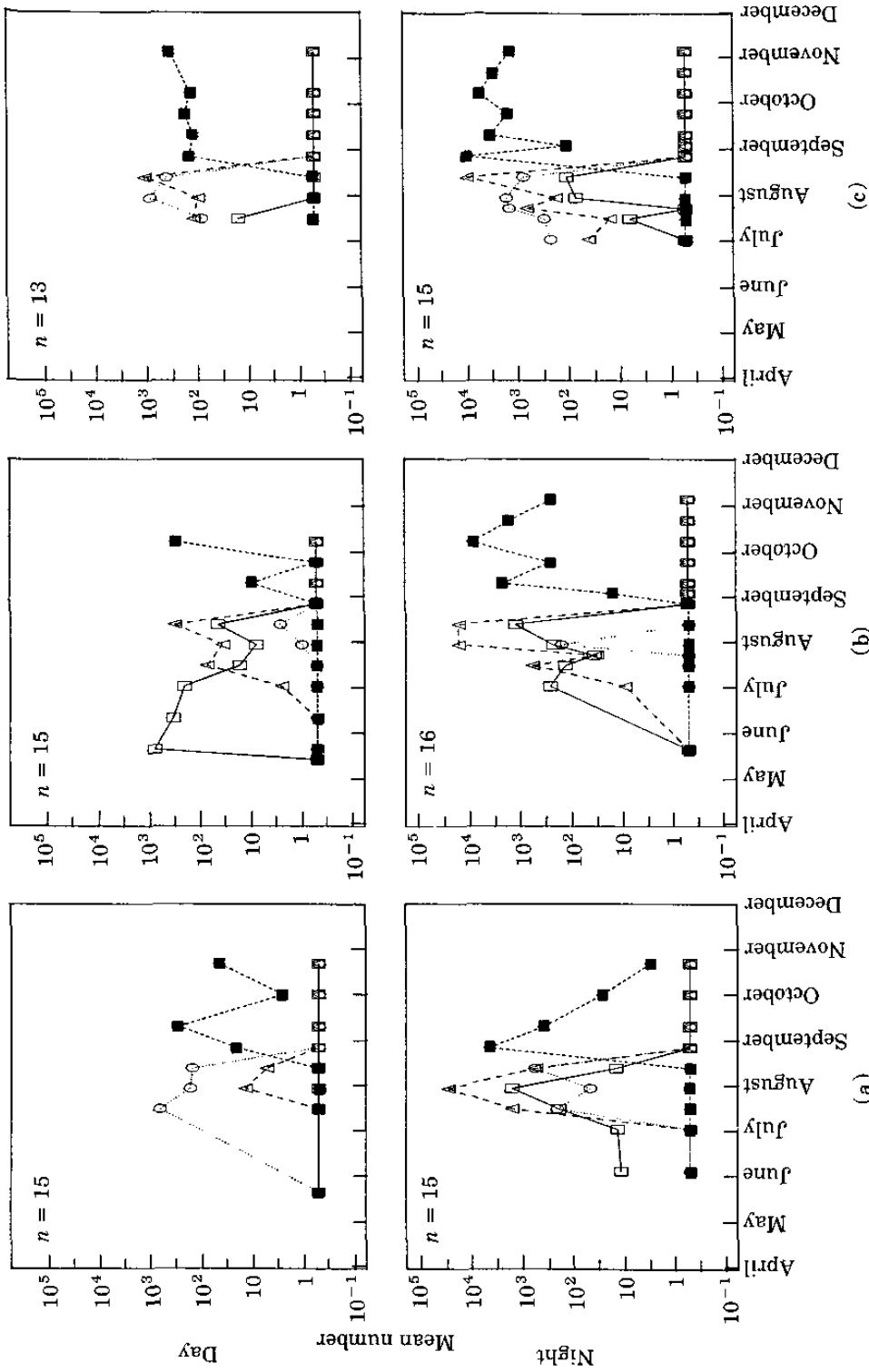
Figure 7. Seasonal abundance of *Menidia menidia* cohorts (adult, □; YOY cohort, ■; second YOY cohort, △; and unknown cohort, ■) by gear and diel period for (a) intertidal weir, (b) subtidal weir, and (c) subtidal seine samples. Sample sizes indicated in the graphs represent the number of collections made for each gear and diel period.

Discussion

Diel differences in assemblages

Marsh creek species assemblages exhibited strong diel differences, based on dominant species relative abundances (Figure 2) and CDA (Figures 3 and 4), regardless of the gear considered (subtidal weir or seine, or intertidal weir). It is clear from these patterns, that sampling exclusively during day or night could lead to very different pictures of marsh creek community structure, just as Stoner (1991) found for open bay habitat in tropical estuaries. A sampling program using only day collections would have incorrectly concluded that *L. xanthurus* and *Pal. vulgaris* were the dominant species in subtidal creeks, and *Pal. vulgaris* and *F. heteroclitus* were dominant in intertidal creeks in New Jersey marshes (Figure 2). The relative abundance of *Men. menidia* would have been greatly underestimated. Clearly, in order to properly determine the importance of marsh habitat to decapods and fishes, and to fully understand how marsh habitats are used, future studies must include both day and night sampling.

Diel and spatial interactions

The strong diel and spatial interaction on subtidal and intertidal marsh creek species assemblages indicated by the CDA may have resulted from spatial differences in diel variation in environmental conditions. In a related study we discuss the influence of creek morphology on environmental conditions within the creeks. Similarly, Hackney *et al.* (1976) found that diel changes in physical conditions in oligohaline tidal marsh creeks were a function of location in the creek, and that they had a strong influence on community structure. Both tidal and diel variation in physical conditions tends to increase with decreasing water depth (Hackney *et al.*, 1976; Rountree, 1992), and consequently with increasing creek size. Hence, the increased discrimination between Upper and Lower intertidal creek communities during the day may result from changes in environmental conditions along a mouth-to-headwater creek gradient within the larger subtidal creek system. Similarly the increased discrimination between day and night communities at Foxboro Creek relative to Schooner Creek may have resulted from greater diel variation in conditions at the shallower Foxboro Creek.

Diel differences in abundances

We believe that the strong diel difference in species abundances (Tables 4 and 5), and consequently in species assemblages (Figures 2–4), are due primarily to diel movements and to diel changes in activity. We see little indication that day gear avoidance significantly biases our inference of diel behaviour patterns for most species, although estimates of the magnitude of diel abundance differences may have been biased. For example, extremely high night abundances of *Men. menidia* in the intertidal creeks clearly reflect nocturnal movements into the intertidal marsh, since *Men. menidia* must leave the intertidal creeks with the ebb tide. Similar diel differences in the subtidal weir and seine samples also suggest diel movements in the subtidal creeks. Our visual observations support this conclusion. Very large concentrations of *Men. menidia* typically filled the subtidal creeks near the mouth at low tide following night flood tides (night samples). Such large concentrations were never observed at low tide following day flood tides (day samples). It was obvious from these observations that large concentrations of *Men. menidia* move into subtidal marsh creeks during night flood tides and become trapped in the creek above the weir as the tide falls.

Menidia menidia *ontogenetic patterns*

Ontogenetic differences in habitat use by *Men. menidia* are suggested from the diel patterns in cohort abundance and size. Clearly, *Men. menidia* makes only limited use of intertidal habitat in the day during July–September, with only small numbers of the smallest size classes occurring in this habitat. Similar, less extreme, patterns were evident in the subtidal creeks, although larger sizes were more frequent during the day. However, larger size classes of YOY, together with adults, make extensive use of both intertidal and subtidal creek habitats at night. These patterns suggest that larger size classes of *Men. menidia* tend to avoid the shallow subtidal and intertidal marsh creeks during the day. These patterns also imply that larger size classes of *Men. menidia* are more mobile than smaller size classes, a suggestion also made by Barkman *et al.* (1981). Briggs and O'Conner (1971) similarly suggested ontogenetic differences in habitat use by *Men. menidia*. They found that *Men. menidia* was generally more abundant over shallow sand bottom in Great South Bay, New York, but that smaller individuals appeared to prefer adjacent eelgrass habitat. These patterns suggest a tendency for small size classes of *Men. menidia* to prefer more sheltered habitats, such as eelgrass, intertidal creeks and shallow subtidal creek habitats.

Diel movements of YOY *Men. menidia* may be related to seasonal migrations. Since peak diel differences in cohort abundances corresponds to the timing of each cohort's peak emigration from the subtidal creek habitat (as indicated above), it may be hypothesized that YOY *Men. menidia* go through a period of diel movements in the marsh prior to their final emigration from the creek nursery habitats.

Most previous estuarine studies have reported higher night catches of *Men. menidia* (McCleave & Fried, 1975; Shenker & Dean, 1979; Middleton, 1986) and *A. mitchilli* (Livingston, 1976; Shenker & Dean, 1979; Middleton, 1986), in good agreement with our study. Contrastingly, Reis and Dean (1981) reported higher day catches of *Men. menidia* and *A. mitchilli* in South Carolina intertidal creeks, but their samples were dominated by small size classes (38 and 22 mm TL, mean length for *Men. menidia* and *A. mitchilli*, respectively; Reis, 1977), while both our subtidal and intertidal creek samples were dominated by larger size classes of both species (i.e. > 50 mm TL). The contradiction between Reis and Dean (1981) and other studies, including ours, may result from size related differences in habitat use, or from gear differences in size selection.

Causes of diel movements

Diel movements into intertidal and subtidal marsh creek habitats may result from several causes, including foraging movements, predator avoidance behaviour, reproductive behaviour and responses to diel changes in physical conditions. The most abundant species, *Men. menidia*, is known to be a diurnal (Moore, 1968; Morgan, 1990) zooplanktivore (Moore, 1968; Gilmurray & Daborn, 1981; Werme, 1981; Grover, 1983; Cadigan & Fell, 1985; DeLancey, 1989; Morgan, 1990), therefore, its nocturnal movement into the creeks is not likely to result from foraging movements. Nocturnal movement into the creeks for this species is also not likely to result from reproductive movements, since these nocturnal movements were expressed primarily by YOY cohorts, or by adult cohorts after the reproductive season had passed. Further, *Men. menidia* is known to spawn exclusively on day high tides in the intertidal marsh (Middaugh & Lempesis, 1976; Middaugh, 1981; Middaugh *et al.*, 1981; Middaugh & Takita, 1983; Conover & Kynard, 1984). However, the high day abundance of *Men. menidia* in the subtidal weir samples during early summer may have resulted from spawning movements of adults (Figure 7), since some spawning activity may still occur during this period.

We suspect that predation pressures cause *Men. menidia*'s nocturnal movements into the creeks, since other possible causes appear unlikely (as discussed above). Interestingly, major diel differences in *Men. menidia* abundance first occur during July, corresponding with the appearance, or peak abundance, of several predators (Rountree & Able, 1992*a*) known to be piscivorous, including: adult crab *Cal. sapidus* (Fitz & Wiegert, 1991), and fishes *Paralichthys dentatus* (Rountree & Able, 1992*b*), *Str. marina* (Tracy, 1910; Carr & Adams, 1973; Subrahmanyam & Drake, 1975), *Pom. saltatrix* (Friedland *et al.*, 1988), *Sph. borealis* and *Cyn. regalis* (pers. obs.).

Causes of the diurnal movements of *Men. menidia* out of the creeks are less certain, but most likely include foraging activity (see our comments above), and responses to diel changes in physical conditions within the creeks. Low day catches of *Men. menidia* during the summer may have resulted from high summer water temperatures (Table 1), or from extreme diel and tidal variation in other physical conditions such as dissolved oxygen concentration (pers. obs.). Hoff and Westman (1966) reported that 80–90 mm TL *Men. menidia* (probably adults) acclimated to 21 °C water temperatures, had an estimated upper median tolerance limit of 30·4 °C. We have observed temperatures in excess of 30 °C in the upper reaches of the subtidal creeks during July and August (unpubl. data). However, avian predation on spawning adults of *Men. menidia* in intertidal habitats has been noted (Takita *et al.*, 1984), and the potential importance of diurnal predation pressures in the creeks can not be discounted.

Although less information is available for most of the other species that exhibited significant diel abundance differences, similar arguments to those made above can be made for many species. Reproductive behaviour can be ruled out for six (*Pom. saltatrix, Mug. curema, Ple. americanus, Mus. canis, T. onitis,* and *Alo. pseudoharengus*) of the 15 species that exhibited significant diel abundance differences because these species occurred only as YOY in the creeks (Rountree & Able, 1992*a*). Diel reproductive behaviour can not be ruled out as the cause of the observed abundance patterns for the remaining species, since adults were present, but is considered unlikely.

Three species with significantly higher day abundances in the subtidal weirs are known to be weakly (*Pom. saltatrix*) to strongly diurnal (*T. onitis* and *Ple. americanus*; Olla *et al.*, 1969; Olla & Studholme, 1978) and may either use the creeks during diurnal foraging, or simply be more susceptible to the gear during the period of increased diurnal activity. Since *Ple. americanus* has previously been shown to undergo tidal foraging movements into shallow marsh habitats (Olla *et al.*, 1969; Tyler, 1971; Wells *et al.*, 1973), its diel abundance patterns in the marsh creeks are likely to be related to foraging movements. Alternatively, the high water temperatures recorded in the creeks (28–29 °C, Table 1) during some low tides are near the lethal temperatures for *Ple. americanus* (Hoff & Westman, 1966; Pearce, 1969), suggesting that diurnal movements out of the creeks might occur in response to physical conditions.

The rapid change over the diel and tidal cycle of physical conditions observed within the creeks (Table 1) may pose an additional stress to some species, and may be more important than absolute physical conditions at any given time. Even small, non-lethal, changes in conditions on the scale observed during this study (e.g. 3–4 °C over ebb tide, Table 1) may promote movements, such as behavioural thermoregulatory movements, due to energetic effects (Miller & Dunn, 1980; Rountree & Able 1992*a*). Important factors that are affected by time of day in marsh creeks are temperature, salinity, and dissolved oxygen concentration (Hackney *et al.*, 1976; Table 1). Despite indications from numerous studies of strong diel changes in environmental conditions in shallow estuarine habitats (Nicol,

1936; Hoese & Jones, 1963; Cameron, 1969; Nixon & Oviatt, 1973; Müller, 1978; Vetter & Hodson, 1982; Tewksbury & Conover, 1987; Breitburg, 1988; Portnoy, 1991) the influence of diel environmental variability on estuarine communities has received little attention (however, see Nixon & Oviatt, 1973; Hackney *et al.*, 1976; Müller, 1978).

Acknowledgements

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