Spatial and diurnal distribution of invertebrate and fish fauna of a
*Zostera marina* bed and nearby unvegetated sediments in
Damariscotta River, Maine (USA)

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Abstract

Fish, epibenthos and macroinfauna were collected in a *Zostera marina* bed and nearby unvegetated sediments in the estuary of the Damariscotta River, on the mid-coast of Maine. Samples of epibenthic fauna and fish were collected at low tides both during day and night, and samples of infauna at low tides during the day. The mean density of *Zostera* shoots in the study area was 335 m$^{-2}$. Abundance and species number of fish were greater at night than during the day and greater in eelgrass beds (*Z. marina*) than in unvegetated habitats. Daytime fish collections were dominated by Atlantic silversides (*Medinia medinia*), while juvenile winter flounder (*Pseudopleuronectes americanus*) dominated night collections. Also *Zostera*-associated epifaunal abundances and number of species were significantly higher at night than during the day. *Mysis stenolepis*, *Idotea balthica* and *Littorina obtusata* were dominant species in the epifauna samples. Of the total of 37 invertebrate species encountered, only five occurred both in the infaunal and epifaunal samples. Nineteen different taxa were collected from the benthic core samples. The most abundant invertebrate infaunal taxa were sipunculids, the polychaete *Nereis virens*, and oligochaetes. Infaunal invertebrate abundances and species diversity were significantly higher in eelgrass beds than in unvegetated sediments. The abundance and number of species of benthic invertebrates were also positively correlated to seagrass biomass. Community diversity values ($H'$) were relatively low but fit well in the general pattern of decreasing diversity towards northern latitudes. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

*Zostera marina* L. is the most common seagrass species in temperate coastal areas (Homziak et al., 1982) ranging from Greenland to Spain in the eastern Atlantic and from Arctic Canada to North Carolina in the western Atlantic (Setchell, 1935). *Z. marina* is also common throughout the Pacific Ocean (Setchell, 1935; Kikuchi, 1966, 1980). It is the only seagrass species in the Baltic Sea (Rasmussen, 1973), and it also occurs sporadically in the Mediterranean (Benacchio, 1938).

Eelgrass increases habitat complexity and pro-
vides living space and shelter for a greater variety of animal species and greater abundances of individuals than the adjacent unvegetated habitats (Rasmussen, 1973; Adams, 1976a,b; Orth et al., 1984; Orth, 1992; Boström and Bonsdorff, 1997). Many fish and invertebrate species use eelgrass meadows as feeding and nursery grounds (Petersen, 1918; Heck and Orth, 1980a), including many economically important fish and shellfish. Eelgrass meadows are commonly regarded as among the highly productive near-shore habitats (Thayer et al., 1975; Orth, 1977; Pihl Baden and Pihl, 1990; Mattila, 1995; Boström and Bonsdorff, 1997).

In general, there is a positive correlation between Zostera biomass and faunal abundance, biomass, and diversity as shown for fish (Adams, 1976a), decapods (Heck and Orth, 1980b), and other benthic invertebrates (Lappalainen and Kangas, 1975; Homziak et al., 1982). However, Nelson (1980) did not find any significant amphipod abundance–seagrass biomass correlation, nor did Pihl Baden and Pihl (1984) find any correlation between the biomass of Zostera and the abundance of epifauna.

Diurnal variation in fish densities has been observed in many shallow areas. Usually the catches are bigger by night than by day. This variation is often explained with the daily activity patterns of fish (Adams, 1976a,b; Horn, 1979; Orth and Heck, 1980; Bayer, 1981). Fish may sleep or be more active (e.g. feeding) during the night time, both of which may result in increased susceptibility to capture (Gray and Bell, 1986).

Vertical distribution of Zostera-associated epifauna has been studied only little, but Nagle (1968) found in the Cape Cod area that organisms abundant on Zostera blades occurred in reduced numbers in the sediments surrounding the leaves, while abundant infaunal animals had few representatives as epifauna.

Many studies have described the Zostera-associated fauna from the mid-Atlantic coast of North America, particularly in the Chesapeake Bay and North Carolina waters (e.g. Nagle, 1968; Briggs and O’Connor, 1971; Orth, 1973; Marsh, 1973, 1976; Nelson, 1979, 1980; Heck and Orth, 1980b; Orth and Heck, 1980; Homziak et al., 1982; Virnstein et al., 1984; Heck et al., 1989, 1995). By comparison, much less is known about Zostera-associated fauna along the northeast coast of North America above 40°N latitude (but see Lalumière et al., 1994; Heck et al., 1995). What we know about Zostera-associated fauna in the northern temperate zone comes primarily from the Baltic Sea (e.g. Petersen and Boysen Jensen, 1911; Petersen, 1918; Lappalainen, 1973; Rasmussen, 1973; Lappalainen and Kangas, 1975; Lappalainen et al., 1977; Pihl Baden and Pihl, 1984; Pihl Baden, 1990; Mattila, 1995; Boström and Bonsdorff, 1997).

This study describes the diurnal and spatial distribution of the fish and invertebrate fauna of a temperate Zostera marina bed and a nearby mud flat on the northeast coast (43°N latitude) of North America. In particular, we consider how seagrass biomass is related to animal species richness and abundance, describe day–night patterns in faunal abundance and composition, and compare our results with previous studies that have used similar sampling methods.

2. Material and methods

2.1. Study site

Samples were collected in a Zostera marina bed and in a nearby mud flat (at a distance of about 500 m) located in the shore area at Darling Marine Center (43°56′N, 69°35′W) (Fig. 1), Walpole, in the estuary of the Damariscotta River, Maine. The tidal range in this area is approximately 2.5 to 4 m, with two tidal cycles per day. The tidal current is about $0.8 \text{ km h}^{-1}$ during ebb and flood tides. The salinity usually ranges from 28 to 32%, but for shorter periods it can drop to as low as 24% (T. Miller, pers. commun., 1997). The water temperature varied between 16 and 18°C during the sampling period of 7 to 12 September 1996. The depth of the Zostera bed and the mud flat was approximately 0.5 to 1.5 m during low tide. Seagrass density was measured with a 100-cm² quadrat that was haphazardly tossed into the seagrass bed. All shoots inside the frame were then counted ($n = 20$).

2.2. Sampling of fish and decapods

Fish and epibenthic decapods were collected with a 6.35-mm mesh haul seine, 1.6 m high and 8.1 m long. In the grass habitat, a metal chain was added to the bottom of the seine to increase the catch efficiency. This chain was not used in the mud.
habitats. Both sites were sampled daily during both day and night low tides, with two replicate hauls taken each time (Table 1). Each replicate haul was 30 m long; thus an area of about 243 m² was sampled by each replicate. After each haul, the seine was carefully lifted from the water so that organisms remained in the seine bag. The seine was then carried to the shore where the organisms were removed and separated. In the laboratory all fish and decapods were identified, weighed, measured and counted.

2.3. Sampling of infauna

Benthic core samples were taken in the seagrass bed and in the unvegetated area located between the seagrass bed and the shore line. A PVC corer with a 10-cm diameter (bottom area 78.5 cm²) was driven into the sediment to a depth of 10 cm to collect each sample. Sampling sites were chosen ‘semi-randomly’ so that areas with different seagrass densities/biomasses were covered. Samples were taken in an unvegetated area, on the onshore edge of the bed, in the center of the bed, and on the offshore edge of the bed (Table 1). Besides the macrofauna, blades, rhizomes and roots of eelgrass were also collected in the vegetated area.

In the laboratory, samples were rinsed over a 0.5-mm sieve to remove fine sediments. All samples were treated alive. Vegetation was removed by hand, separated into leaves, rhizomes and roots, dried at 60°C for a minimum of 24 h, and then weighed to determine above-ground and below-ground biomass in units of dry weight (DW) (±1 mg accuracy). All organisms were sorted and identified to the lowest possible taxon, and then enumerated.

2.4. Sampling of Zostera-associated epifauna

Epifaunal samples were collected with transparent plastic bags (125 dm³, height ~120 cm). These bags were placed over a couple of individual plants and the shoots were severed just above the sediment surface. The bags were then divided into 20-cm sections by tying cable ties at 20-cm intervals along the shoots and also closing the bags with a cable tie above the shoot tips. A total of 21 samples were collected from the eelgrass bed both during the night and day low tide (Table 1).
In the laboratory, the sample bags were opened section by section and all animals collected were removed, identified and counted. Eelgrass leaves were counted and the length of each leaf was measured.

2.5. Numerical and statistical analyses

Species diversity \( H' \) was estimated using the Shannon–Weaver index (Shannon and Weaver, 1963) according to:

\[
H' = - \sum_{i=1}^{s} p_i \ln p_i
\]

where \( s \) = total number of species, \( p_i = n_i/n \), the proportion of the total number of individuals belonging to the \( i \)th species.

Differences in the spatial distribution (seagrass bed vs. mud flat) and temporal (day vs. night) of the fish and zoobenthos were analysed by \( t \)-test or Mann–Whitney rank comparisons if the populations in the samples were not normally distributed (Sokal and Rohlf, 1995). Also spatial and diurnal differences in mean sizes of fish and decapod species were analysed with \( t \)-tests. Diurnal variation in vertical distribution of Zostera-associated epifauna was analyzed with the \( \chi^2 \)-test. Correlations (Pearson Product Moment Correlation) between the biomass of vegetation and species richness and abundance were also calculated.

3. Results

3.1. Seagrass

The mean density of Zostera was 335 shoots m\(^{-2} \) (±39, s.e., \( n = 20 \)), and the mean leaf number per plant was 3.44 (±0.12, \( n = 223 \)); thus, the average total density was 1152 leaves m\(^{-2} \). Mean leaf length was 52.8 cm (±0.9, \( n = 576 \)) and the range was 7 to 124 cm. The mean above-ground biomass was 56.2 g DW m\(^{-2} \) (±18.4, \( n = 7 \)) and the average below-ground biomass was 198.0 g DW m\(^{-2} \) (±41.5, \( n = 7 \)). The total seagrass biomass varied between 48.9 and 437.8 g DW m\(^{-2} \) (\( \overline{X} \pm \text{s.e.} = 254.2 \pm 54.6 \) g m\(^{-2} \)).
(Urophycis tenuis) (C. Vickery and K.L. Heck Jr., University of South Alabama, unpubl. data), but they were not caught during seining. During the sampling period, striped bass (Morone saxatilis), adult rock crabs Cancer irroratus and green crabs Carcinus maenas were also caught in gillnets during the night (J. Mattila, unpubl. data). These species probably use the seagrass habitat as a feeding ground.

Only 40 fishes belonging to four species were caught on the bare mud flat. Very few individuals were caught during the day (Fig. 2b). All mud species were also found in the seagrass.

A larger number of species and individuals and greater total biomasses were collected at night. The diel differences were most pronounced in the mud (Fig. 2b). Species-specific mean sizes of individuals did not differ for any species that occurred in both habitats. Fish diversity indices ($H'$) were sig-
significantly higher in the seagrass than on the bare mud flat (Table 2). In the mud flat, there was also a statistically significant difference in $H'$-values between the day and night values (Mann–Whitney test, $T = 10.50, p \leq 0.0001$). No such difference ($t$-test, $t = 0.54, p = 0.632$) was noted in the grass bed.

Four decapod species were also caught in the seagrass bed. The most common species was *Crangon vulgaris* (mean length $38.3 \pm 5.4$ mm (s.e.), $n = 749$) followed by *Carcinus maenas* (mean carapace width $37.3 \pm 16.2$ mm, $n = 56$). A few individuals of the crab *Cancer irroratus* ($n = 1$) and caridean shrimp *Eualus* sp. ($n = 4$) were also caught in the grass bed. *Crangon* (mean size $35.4 \pm 5.3$ mm, $n = 480$) and *Carcinus* (mean size $53.0 \pm 12.2, n = 43$) were also the most common decapod species on the bare mud flat. There was no significant difference in the size of *Crangon* between the habitats, but *Carcinus* was significantly larger on the mud flat than in the grass bed ($t$-test, $t = -5.30, p < 0.0001$). *Cancer* (mean size $77.1 \pm 9.0$ mm, $n = 43$) was relatively common on the mud flat but not in the seagrass.

### 3.3. Infauna

Nineteen different taxa were collected from the benthic cores (Fig. 3). The mean total abundance in the seagrass bed was $2693 \text{ ind m}^{-2} (\pm 902, \text{s.e.})$ and outside the bed $1486 \text{ ind m}^{-2} (\pm 740)$ (Table 2). One sample taken in the unvegetated area also contained a large abundance (12 484 ind m$^{-2}$) of sipunculids. The sample was considered to contain an atypical aggregation of worms for the unvegetated habitat, and it was omitted from all statistical analyses. The three most abundant taxa in the eelgrass bed were sipunculids, the polychaete *Nereis virens* and oligochaetes.

Invertebrate abundance showed a significant correlation with *Zostera*-biomass (Fig. 4a), although the total species number did not (Fig. 4b). The total above- and below-ground biomass of *Zostera* varied between 2.6 and 438.0 g DW m$^{-2}$ ($\pm$ s.e. $= 188.8 \pm 50.6$ g DW m$^{-2}$, $n = 10$). On average, 22% of the total biomass was above-ground biomass. The $H'$ value of the invertebrates in the seagrass bed was on average $1.07 \pm 0.17$ and outside the bed $0.69 \pm 0.57$ (Table 2).

### 3.4. Zostera-associated epifauna

A total of nineteen species was recorded from the epifauna samples. The most abundant species were *Mysis stenolepis*, *Littorina obtusata* and *Idotea balthica* (Fig. 5). As with the fishes, species number (Mann–Whitney test $T$-value $3.73, p < 0.001$) and total abundance ($t$-test, $t = 3.73, p = 0.001$) were significantly higher during the night low tide.
Fig. 3. Abundance of infaunal species (mean number per m$^2 \pm$ s.e.) in the seagrass and mud-flat sites. Solid bars = mud flat, stippled bars = seagrass. Note the logarithmic scale.

than during the day low tide. These differences were mainly due to higher night time densities of $M$. stenolepis ($t$-value = $-2.91$, $p = 0.006$), $L$. obtusata ($t$-value = $-2.67$, $p = 0.011$), $L$. balthica ($t$-value = $2.26$, $p = 0.030$), and $L$. rudis ($t$-value = $3.96$, $p < 0.001$). About 50% of the animals were found in the leaf segments between 20 and 60 cm above the bottom (20–40 cm: 25% and 27%; 40–60 cm: 25% and 23%; day and night, respectively) when the animal occurrence was related to available leaf surface (Fig. 6). During the day, leaf tips were occupied proportionately less than during the night. However, there was no statistically significant difference in the vertical distribution between the day and night samples ($\chi^2$-test, $\chi^2 = 20.0$, d.f. = 16, $p = 0.220$).

The diversity values were significantly higher in the night samples ($\bar{T} = 1.530 \pm 0.090$) than in the day samples ($\bar{T} = 1.160 \pm 0.132$) (Mann–Whitney test, $T = 364.5$, $p = 0.030$). The average species number was also highest in the lower part of the leaves and decreased with increasing height. The highest species number was recorded in the 20 to 40 cm segment ($1.9 \pm 0.4$ species per sample during the day and $3.8 \pm 0.4$ species per sample during the night), and the lowest species number was recorded in the 60 to 80 cm section during the day ($0.6 \pm 0.3$ species per sample) and in the 80 to 100 cm section during the night ($0.7 \pm 0.4$ species per sample). Only gastropods ($L$. spp.), bivalves ($M$. edulis), amphipods ($A$. longicornis and $C$. linearis), and isopods ($I$. sp.) were found in the topmost 20 cm of the leaves.

4. Discussion

A total of 35 invertebrate species and thirteen fish species were found in samples from the eelgrass habitat. In the bare mud habitat, a total of thirteen invertebrate species and four fish species were found. The average density of benthic invertebrates in the core samples in the $Z$. meadows was 2693 ind m$^{-2}$. These densities are similar to those observed in other temperate $Z$. meadows of higher latitudes (Lappalainen, 1973; Bostrom and Bonsdorff, 1997). In the mid-Atlantic region, lower invertebrate densities in $Z$. meadows have often been observed both on the European west coast (Roscoff, France: 990 to 1310 ind m$^{-2}$; Jacobs, 1980) and the American east coast (Beaufort–Morehead City, North Carolina: 700 to 1000 ind m$^{-2}$; Thayer et al., 1975). However, in Chesapeake Bay, Orth (1973) found high summer densities of benthic invertebrates (2350 to 14 725 ind m$^{-2}$).
The positive correlation between benthic invertebrate abundance and seagrass is also consistent with the findings of most earlier studies (Lappalainen and Kangas, 1975; Adams, 1976a; Heck and Orth, 1980b). In our study, the differences observed between the seagrass site and the bare mud-flat site could theoretically also have been caused by the difference in location instead of presence/absence of seagrass only. This, however, is unlikely, and since the results accord well with earlier results from other areas, we are convinced that the biomass of seagrass is the main factor explaining differences in faunal abundances.

Only five invertebrate species were common to the samples taken with the benthic corer and the epifauna bags. This is consistent with earlier results on vertical distribution of invertebrates in Zostera meadows (Nagle, 1968). The species number and abundances of epifaunal species associated with Zostera leaves were higher during the night than during the day. We believe that this pattern is mainly caused by the diel activity patterns of crustaceans such as Crangon vulgaris and Mysis spp., which may bury themselves in the sediment during the day, becoming more active and motile during the night. In seagrass beds, physical conditions such as oxygen saturation may vary drastically within short time intervals. Oxygen saturation may drop to near zero for several hours during night low tides (Broekhuysen, 1935). Low oxygen content during the night may markedly affect activity patterns of both invertebrates and fish, and force mobile species that are normally bottom dwellers higher up the water column, which could partly explain the increased animal abundances observed in the night samples.

Fish species collected in the Zostera meadow in the Damariscotta River are primarily cold-water species whose ranges extend from the Arctic to the mid-Atlantic coast of the United States (Bigelow and Schroeder, 1953). Eight of the species collected in the Zostera meadow (Anguilla rostrata, Apeltes quadracus, Gasterosteus aculeatus, Menidia menidia, Microgadus tomcod, Myoxocephalus aenaus, Pseudopleuronectes americanus and Syngnathus fuscus) are also commonly found in seagrass meadows in Cape Cod, Massachusetts (Heck et al., 1989). More fish were caught during the night than during the day, although the day–night difference in the grass bed was not as marked as in some other seagrass habitats (Adams, 1976a; Horn, 1979; Orth and Heck, 1980; Bayer, 1981). Several factors may cause the number of fish to increase in night catches. The higher abundances at night may be due to fish from deeper areas that visit seagrass meadows in greater numbers during darkness. Such a nocturnal activity pattern may be a means of avoiding daytime predators. In our study, the American eel was found in the Zostera meadow only during the night. On the other hand, some bigger predators, such as striped bass and adult decapods (Cancer irroratus and Cancer maenas), were also caught with gillnets in the eelgrass bed during the night. These species most likely use the meadows as feeding areas, as eelgrass meadows are known to be important feeding
areas for many fish species. For example, Adams (1976b) found that 56% of the food consumed by eelgrass-associated fish species is also produced in the grassbeds.

Seagrass beds are commonly considered to be refuges for juveniles and small individuals. We found that the average size of *Carcinus maenas* was smaller in the seagrass than in the mud flat. Since the mud flat is a simple habitat where predation risk is likely to be higher than in the complex seagrass habitat, it is likely that the smaller *Carcinus maenas* used the seagrass as a refuge and nursery area (Heck and Orth, 1980a,b). Lalumière et al. (1994) have analogously shown that smaller fourhorn sculpins inhabit *Zostera* beds to a greater extent than adjacent unvegetated areas. In our study area, individuals of winter flounder caught in the daytime sampling were smaller than individuals caught in the night sampling. However, the small individuals were present during both periods (2.3–6.7 cm by day and 2.5–9.6 cm by night; one larger individual (29 cm) was also caught during the day low tide). It is possible that more large individuals come in during the night to feed and that the smaller ones stay within the seagrass bed throughout the day for better protection.

Quantitative fish abundances are hard to estimate from seine catches, since catch efficiency may vary considerably according to species and the time of the day (Gray and Bell, 1986). However, an attempt was made to roughly estimate the number of fish per square metre at the study sites. For this purpose, the seining efficiency was assumed to be 50% for all species in both habitats (compare Kjelson, 1977). The approximate daytime abundances were then calculated to be 1.12 ind m\(^{-2}\) in the *Zostera* meadow and 0.01 ind m\(^{-2}\) in the mud flat. The corresponding densities during the night low tide were 1.23 ind m\(^{-2}\) and 0.07 ind m\(^{-2}\). Sogard and Able (1991) estimated fish densities in New Jersey estuaries (*Zostera* and *Ulva lactuca* habitats) during September to range between 7.3 and 9.7 m\(^{-2}\). Atlantic silversides dom-
inated their catches (2.5 to 4.2 ind m$^{-2}$). Adams (1976a) estimated the fish populations in Zostera meadows in Beaufort, North Carolina, to be about 0.8 to 2.0 ind m$^{-2}$ in September. Our density estimations were relatively low compared to the mid-Atlantic fish densities. Since seining is a relatively unreliable method of quantitative sampling, we may have overestimated the catch efficiency of our samples. Adams (1976a) used both seine and trawl to collect his samples. The efficiency of these gear was most likely close to ours, and so were also the abundance estimates. Sogard and Able (1991) collected their samples with a throw trap which is a relatively good quantitative sampling method (Pihl and Rosenberg, 1982), and consequently the abundance estimates in Sogard and Able’s study were also clearly higher than ours. Any underestimate of true densities by seine catches is likely to be greater in seagrass beds than in bare sediments. This means that in our study the differences between seagrass bed and mud flat are likely to be greater than actually reported.

Species richness and diversity values in the Damariscotta River study area were relatively low compared to eelgrass areas in the mid-Atlantic region of North America (Nagle, 1968; Briggs and O’Connor, 1971; Adams, 1976a; ; Nelson, 1980; Orth and Heck, 1980; Thayer et al., 1984; Fonseca et al., 1990; Heck et al., 1995), but both fish and infaunal diversity in the eelgrass bed were higher than in the non-vegetated area nearby. Lalumière et al. (1994) did not find any support for high species diversity in a Zostera bed in the James Bay. Their study did not, however, contain any comparisons with adjacent non-vegetated habitats. Lalumière et al. (1994) propose the shortness of the growing season and harsh climate as reasons for low diversity in the James Bay. The diversity values calculated for fauna in the Damariscotta River Zostera meadow fit well in general latitudinal diversity patterns for Zostera in temperate areas (i.e. decreasing diversity with increasing latitude; e.g. Setchell, 1935; Virmstein et al., 1984). Although the diversity of the Zostera-associated fauna tends to decrease towards the northern latitudes, it usually remains significantly higher than the diversity in adjacent non-vegetated areas (Rasmussen, 1973; Pihl, 1986; Mattila, 1995; Boström and Bonsdorff, 1997).

5. Conclusions

The Zostera bed studied in the Damariscotta River supported significantly higher numbers of species and individuals of both invertebrates and fish than the nearby bare mud flat. Densities were higher at night than during the day. The invertebrate densities were similar or even higher than densities found in most other Zostera areas. Totally, 35 invertebrate species were found in the Zostera bed. In contrast, fish densities were low compared to reports of mid-Atlantic fish densities. A clear distinction was found in the vertical distribution of invertebrate species; fourteen taxa were found only in the epifaunal Zostera samples. The fish fauna consisted of primarily cold-water species that are typical also in the mid-Atlantic region of the North American coast.

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