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Secondary Production of Macrobenthic Communities in Seagrass (*Zostera marina*, Eelgrass) Beds and Bare Soft Sediments Across Differing Environmental Conditions in Atlantic Canada

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Abstract In nearshore ecosystems, habitats with emergent structure are often assumed to have higher ecosystem functioning than habitats lacking structure. However, such habitat-specific differences may depend on the surrounding environment. In this study, I examine the robustness of habitat-specific differences in ecosystem functioning for seagrass (*Zostera marina*) and adjacent bare soft sediments across varying environmental conditions on the Atlantic Coast of Nova Scotia, Canada, using secondary production as a metric. I also examine relationships of community secondary production and faunal structure with measured environmental variables (water depth, temperature, exposure, sediment, and plant properties). Benthic secondary production (invertebrates ≥500 μm) was higher in seagrass compared to bare sediments only at exposed sites with sandy sediments low in organic content, deep and cool water, and high belowground plant biomass. A regression relating community secondary production to the environmental variables explained 56% of the variance, while a constrained ordination explained 16% of the community structure. Important environmental determinants of community production were shoot density, temperature, depth, exposure, sediment organic content, and belowground plant biomass. Community structure was influenced by these variables plus sediment sand content and canopy height. This study shows that habitat-specific differences in secondary production may not be consistent across varying environmental conditions. Furthermore, seagrass beds are not always associated with higher ecosystem functioning than adjacent bare sediment. Both the surrounding environmental conditions and the presence of habitat structure should be considered for optimal management of nearshore ecosystems.

Keywords Benthic invertebrates · Canonical correspondence analysis · Ecosystem functioning · Nova Scotia

Introduction

Secondary production is the incorporation of organic matter or energy by heterotrophic organisms and represents a major pathway for energy flow through ecosystems (Winberg 1971). As an emergent property of ecosystems, secondary production incorporates various population and individual processes (e.g. reproduction, survivorship), biotic interactions (e.g. competition, predation), and environmental conditions (e.g. temperature, water depth) that all influence energy transfer (Hooper et al. 2005; Dolbeth et al. 2012). Secondary production can thus be considered a metric of ecosystem functioning and is a useful tool to evaluate various aspects of ecosystem dynamics, the impacts of environmental change, and function-diversity relationships (Hooper et al. 2005; Benke and Huryn 2010; Dolbeth et al. 2012).

In nearshore marine ecosystems, secondary production is dominated by benthic invertebrates that are important intermediaries in the energy flow from primary producers to higher trophic levels (Crisp 1984). Studies of secondary production in these ecosystems have typically focussed on identifying differences among habitat types, often finding higher secondary production in habitats with emergent structure relative to

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habitats lacking such structure (e.g. Heck et al. 1995; Bologna 2006; Cowles et al. 2009; Wong et al. 2011). These habitat-specific differences are often assumed to be robust across all environmental conditions where the habitats occur. However, such differences can depend on the species community composition, habitat attributes, and the surrounding environmental conditions (e.g. Asmus and Asmus 1985; Sprung 1994; Edgar et al. 1994; Cowles et al. 2009). Examination of habitat-specific differences in secondary production across varying environmental conditions would provide insight into the robustness of these relationships. Also, the environmental determinants of secondary production could be identified, providing not only predictive capacity but also insight into the mechanisms underlying any observed patterns in secondary production. In this study, I examine these aspects of benthic secondary production for two common nearshore habitat types, seagrass beds, and bare soft-sediment bottom, located across environmental conditions varying in water temperature, depth, sediment properties, and seagrass bed characteristics.

In Atlantic Canada, seagrass (eelgrass; *Zostera marina*) beds are found across a range of environmental conditions, including protected sites with shallow, warm water and silty sediments to more exposed sites with deep, cool water and sandy sediments. Benthic secondary production would likely differ across these conditions, and habitat-specific differences in secondary production may not be consistently observed. This would have important implications for habitat restoration practices that often preferentially restore habitats with emergent structure, assuming they provide higher ecosystem functioning than habitats without emergent structure. Thus, the objectives of this study were to (1) estimate benthic community secondary production and its underlying faunal structure in seagrass and adjacent bare soft-sediment habitats, located across varying environmental conditions on the Atlantic Coast of Nova Scotia, Canada; (2) determine if habitat-specific differences in community secondary production and structure are evident and persist across the range of environmental conditions examined; and (3) examine relationships of community secondary production and structure with measured environmental variables (i.e. water, plant, and sediment properties), in an effort to understand any patterns in habitat-specific differences that are observed.

Materials and Methods

Study Sites and Sampling Design

Macrobenthic invertebrate communities (infauna and epifauna ≥500 μm, excluding shrimps and crabs) were sampled in seagrass (*Z. marina*) beds and adjacent bare soft-sediment bottom on the Atlantic Coast of Nova Scotia, Canada (Fig. 1). Ten field sites that spanned a range of environmental conditions were sampled (Table 1, Fig. 1). At all sites, the seagrass beds were

monotypic and usually continuous with little fragmentation. The bare-sediment habitats were located adjacent to the seagrass beds. Sampling at seven sites was conducted in mid-July to mid-August 2013, while three sites were sampled in mid-August 2009 (cores) and mid-end of July 2012 (pop-up nets). I acknowledge that inter-annual variability in benthic invertebrate recruitment may have resulted in differences among sites sampled in different years; however, multi-year data available suggests that such differences are small (Wong, unpublished data). Data from all sites are included here to ensure adequate representation of the full range of environmental conditions inhabited by *Z. marina* in Nova Scotia, while acknowledging the assumption of low inter-annual variability.

Sampling stations were haphazardly distributed within each habitat and situated at least 10–20 m apart. Stations were approximately the same depth within each habitat and site combination. Within the seagrass beds, sampling was conducted at least 2 m from any seagrass-bare interface (Wong and Dowd 2015). Sampling was conducted at low to mid tide by snorkelling or scuba diving depending on the water depth (Table 1).

Field Sampling of Benthic Invertebrate Communities

Benthic invertebrates were sampled using a hand corer and pop-up net. The hand corer was used in both seagrass and bare sediments, captured fauna living in the sediments, on the sediment surface, and (when sampling in seagrass beds) among and on seagrass plants. At each sampling station ($n = 10$), the 10-cm-diameter hand corer was inserted 12 cm into the sediment and extracted. Care was taken to ensure seagrass leaves and stems were fully captured within the corer. In a few cases where this was not possible (i.e. when leaves were very long), shoots were cut at the sediment surface and collected separately. Cores obtained by divers were capped on both ends prior to transport to the water surface. All core samples were refrigerated 1–4 days prior to processing. Preliminary sampling indicated no difference in sediment volume collected in the cores by the divers or snorkelers when corers were deployed adjacent to each other.

The pop-up net was deployed in the seagrass beds to capture fauna living among and on the seagrass plants. Sampling stations ($n = 8$) that differed from the core sampling stations were used to ensure no disturbance from prior activity. The pop-up net was 0.5 m long × 0.5 m wide and made of 300-μm Nitex mesh. The net extended from the sea bottom upwards 0.9 m, with the net bottom attached to a weighted PVC quadrat and the top attached to a quadrat with floats. The net was deployed by dropping it from above the seagrass canopy, allowing the weighted quadrat to sit on the sea bottom and the net to extend into the water column. Trapped fauna were sampled using a dip-net (by snorkelers) or suction (by divers) sampler and stored in a plastic bag with water. Any fishes, crabs, or shrimps captured in the pop-up net were released,

Fig. 1 a East coast of North America. Nova Scotia (*NS*) is indicated by the *box*. **b** Field sites in Nova Scotia, Canada. *PJ* Port Joli, *PH* Port l'Hebert, *Keji* Kejimkujik Seaside National Park, *CresB* Crescent Beach, *SecPen* Second Peninsula, *CrouchI* Croucher Island, *Sambro* Inner Sambro Island, *L3F* Lower Three Fathom Harbour, *EastPet* East Petpeswick, *CableI* Cable Island
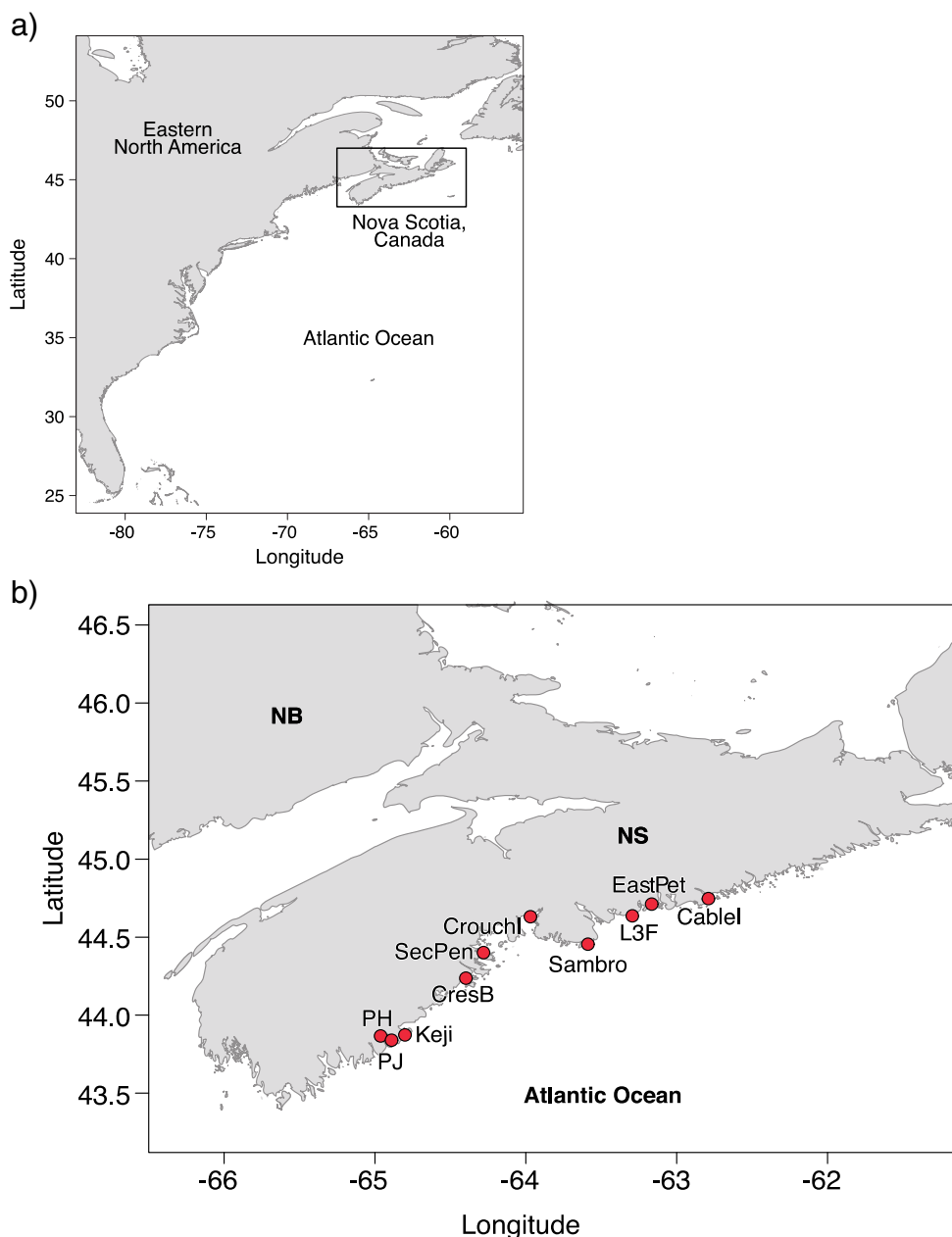
because the procedures would not have properly sampled these larger fauna. All pop-up net samples were refrigerated for 1–4 days prior to processing. Data were calibrated to account for differences in sampling by the dip-net and suction sampler and also to account for different dip nets used in 2012 and 2013 (further details provided in the Appendix Report A1 and Table A1).

Measuring Environmental Variables

Plant characteristics were measured at each core sampling station prior to collection of the core sample. Canopy height was determined by measuring the height of the tallest 80% of leaves (Duarte and Kirkman 2001). Seagrass shoot density was determined by counting all shoots within a 0.25 × 0.25 m quadrat. Above- and belowground plant components were collected by the hand corer when the benthic infauna were sampled.

Cores to determine sediment particle size and organic content were taken at every second station sampled in 2013 and at every station sampled in 2009 with a small hand corer in both habitat types, after collection of the faunal core. Sampling was conducted using two 3-cm-diameter × 5-cm-long plastic syringes with the tips removed. Samples were combined in a plastic bag and frozen for ~1 month prior to analyses.

Table 1 Characteristics of field sites

Site (abbreviation)	Water temp (°C)	Water depth (m)	REI
Port l'Hebert (PH)	19.8 ± 2.5	1.0, 1.0	1307.6
Port Joli (PJ)	20.4 ± 2.3	1.0, 1.0	1475.4
Kejimkujik Seaside (Keji)	22.0 ± 2.6	1.0, 1.0	285.4
Second Peninsula (SecPen)	17.3 ± 1.45	2.5, 2.5	317.2
Lower Three Fathom Harbour (L3F)	22.2 ± 1.56	1.0, 1.0	311.9
Crescent Beach (CresB)	18.7 ± 1.83	2.5, 1.5	1038.6
East Petpeswick (EastPet)	16.9 ± 3.3	1.5, 1.5	2002.2
Cable Island (CableI)	13.7 ± 1.5	3.0, 3.0	1965.5
Inner Sambro Island (Sambro)	13.4 ± 2.98	4.0, 8.0	1653.7
Croucher Island (CrouchI)	18.0 ± 1.64	3.0, 3.7	2427.5

Water depth at mean high tide: first value is for seagrass and second for adjacent bare sediments. Water temperature (temp) is the mean temperature for July and August in the year sampling took place. CableI, Sambro, and CrouchI were sampled by scuba diving and all other sites by snorkelling. Sites are listed according to similar environmental conditions, determined from an nMDS (see Appendix). Further habitat characterization is provided in Fig. 2

REI relative exposure index

Water temperature was recorded continuously using temperature loggers (TidbiT v2; Onset Computer Corporation, Bourne, MA, USA) deployed at each site from late spring to early fall. Mean water temperature was calculated for July and August. Water depth at mean high tide was obtained from field measurements.

Wave exposure at each site was calculated using a relative exposure index (*REI*) modified from Keddy (1982) and used in Fonseca et al. (2002):

$$REI = \sum_{i=1}^{8} (V_i \times T_i \times F_i)$$

where i is the compass heading in 45° increments (i.e. centred on north, northeast, and east), V is the average annual wind speed (km h^{-1}), T is the proportion of time that the wind blew from the ith direction, and F is the effective fetch (km) for the ith direction. Wind speed data were obtained from the Shearwater weather station (44.63 N, 63.51 W) located in Eastern Passage, Nova Scotia (Canadian National Climate Archives). The data were recorded hourly (as 2-min averages of wind speed and direction for each hour) for 2011 and 2012. To determine effective fetch, the distance from the sampling site to land along a given compass bearing (Shore Protection Manual 1975) was determined for four 11.25° increments centred on the ith compass heading. Then, effective fetch for each compass heading i was determined as

$$F_i = \frac{\sum_{j=1}^{9} X_j \times \cos\alpha_j}{\sum_{j=1}^{9} \cos\alpha_j}$$

where j is the 11.25° increments on either side of and including the compass heading i, X is fetch (km), and α is the angle of jth departure from the ith compass heading (Shore Protection Manual 1975).

Sample Processing

Samples collected by the corer and pop-up net were rinsed individually over a 500-μm sieve using sea water. Fauna entangled or attached to plant material were removed and added to the sieve. Plants from the core samples were removed, separated into above- and belowground components, dried at 60 °C for 24–48 h, and weighed to determine dry biomass per square metre (Duarte and Kirkman 2001). Material on the sieve was fixed in 5% buffered formalin for 2 weeks and then preserved in 70% ethanol until sorted. Samples were sorted under a dissecting microscope, and animals were identified to the lowest possible taxonomic resolution (usually species) and counted. Biomass was determined by drying each species per sample at 60 °C for 24–48 h and then weighing. Shelled molluscs were acidified using 10% HCl prior to drying. Dry biomass was converted to ash-free dry mass (AFDM) using conversion factors from Brey (2001). Density and biomass for each taxon was determined for each corer and pop-up net sample. Total density and biomass per sample were determined by summing across all species within that sample.

To determine the percent organic matter within sediments, 1 g of each sample was dried at 60 °C for 24–48 h, weighed to determine total dry mass, combusted at 500 °C for 6 h, and reweighed to determine ash mass (Luczak et al. 1997). To determine percent particle distribution, samples from most sites were analysed using a Beckman Coulter Laser (further described in Wong et al. 2016). Samples containing gravel

were wet sieved on a 2-mm sieve to remove the gravel prior to use of the Coulter Laser. The gravel fraction was added to the total final weight of the sample. Samples from three sites (Keji, PH, and PJ) were analysed by wet sieving (Bale and Kenny 2005; Wong and Dowd 2015). For all samples, percent fractions of gravel, sand, and silt (i.e. silt + clay) were determined as 100% × (total dry mass − size category mass) / (total dry mass). Analysis of subsamples using both the Coulter Laser and wet sieving indicated no difference between the two methods. Due to logistical constraints, only three samples were processed for particle size for each habitat and site combination.

Estimates of Secondary Production

I estimated secondary production using the empirical model of Edgar (1990)

$$P = 0.0049B^{0.80}T^{0.89} \qquad (1)$$

where P is the production of an individual macrobenthic animal (μg day^{-1}), B is the body size (μg AFDM), and T is the water temperature (°C). In a departure from Edgar's method, where body size is the mean biomass of all individuals retained on sieves with different mesh sizes, I calculated body size by dividing total AFDM per taxon by total abundance of that taxon (Brey 2001; Wong et al. 2011; Sturdivant et al. 2014). Here, big differences in body size within a species may have influenced production estimates (Banse and Mosher 1980); however, these effects were likely minimal because species with the potentially greatest differences in body size (i.e. molluscs) were only captured as small juveniles. Secondary production for each taxon per replicate was estimated as $P_l \times N_l$, where l is the taxon and N is the abundance (m^{-2}). I then summed across taxa to estimate community secondary production for both corer and pop-up net samples separately.

Production estimates from core samples are referred to as $P_{\text{Total fauna}}$, because they include production from fauna within sediments, on the sediment surface, and (when sampling in seagrass) among and on seagrass plants. Production estimates from pop-up net samples in the seagrass bed are referred to as $P_{\text{SG fauna}}$ (where SG is seagrass) and include fauna living among and on the seagrass plants. Note that the production estimates include invertebrate fauna ≥500 μm but exclude large crabs, shrimps, or fishes. I also estimated production per family for core samples by summing production across all taxa in each family and referred to these community data as $C_{\text{Total fauna}}$.

I chose Edgar's model because of its theoretical basis in the metabolic theory of ecology, which posits that a constant fraction of metabolism tends to be allocated to production (Brown et al. 2004). Additionally, the temperature range on which the model is based (5–30 °C) is appropriate for my study. Furthermore, the model is not based on data of mean annual biomass as is the case for several other empirical models (e.g. Tumbiolo and Downing 1994; Brey 2001; Cusson and Bourget 2005). Validation exercises have shown that estimates from Edgar's model are similar to those from other empirical models and direct measurements (Wilber and Clarke 1998; Hagy 2002; Cowles et al. 2009). I further validated Edgar's model by comparing estimates from the model to those estimated from Brey (2001)'s empirical model and found high agreement between the two (linear regression: $R^2 = 0.728$; $p < 0.0001$; Appendix Fig. A1).

Data Analyses

Estimates of total community production ($P_{\text{Total fauna}}$) were compared across habitat types (two levels: seagrass and bare soft sediment) and sites (ten levels) using two-way fixed factor ANOVAs. Site was included as a fixed factor because each site represents a particular set of environmental conditions. Sediment metrics (i.e. percent organic matter, sand, or silt) were similarly analysed. Plant metrics (i.e. shoot density, aboveground and belowground biomass, and canopy height) were compared across sites using one-way ANOVAs. Significant main effects were examined using Tukey's HSD test. Significant interactions were examined by re-running the analyses separately for each level of site (i.e. simple main effects test; Quinn and Keough 2002) to detect habitat-specific differences in dependent variables. In these cases, significant p values were identified after applying the Holm-Bonferroni correction for multiple comparisons (Holm 1979; Quinn and Keough 2002). For sediment metrics, significant interactions split by habitat type were also examined to further illustrate the varying conditions across sites. For all ANOVAs, residual plots were examined to identify violations of the underlying assumptions of normality and homogeneity of variance. Any violations were corrected by data transformations.

Environmental variables at each site were analysed simultaneously to identify differences in environmental conditions among sites and habitats using non-metric multidimensional scaling (nMDS). Mean values of percent sediment organic content or particle size from each habitat and site combination were used for sampling stations where these were not measured. Environmental variables were used to construct a similarity matrix based on Euclidean distance. From this a two-dimensional ordination was constructed. The results of the nMDS were used to order sites based on environmental conditions in the presented figures.

The relationship between total community production ($P_{\text{Total fauna}}$) and environmental variables was explored using multiple linear regression analysis. $P_{\text{SG fauna}}$ was not examined because the explanatory variables were not measured at pop-up net sampling stations. All explanatory variables were

included in the regression for $P_{\text{Total fauna}}$ with the exception of percent gravel (only present in a few samples) and percent silt (high correlation with percent sand). Again, mean values of percent sediment organic content or particle size from each habitat and site combination were used for

$$
\begin{aligned}
P_{\text{Total fauna}} = \beta_0 &+ \beta_1(CanopyH) + \beta_2(ShootD) + \beta_3(AGBM) + \beta_4(BGBM) + \beta_5(Organic) \\
&+ \beta_6(Sand) + \beta_7(Temp) + \beta_8(Depth) + \beta_9(REI) + \beta_{10}(ShootD)^2 \\
&+ \beta_{11}(AGBM)^2 + \beta_{12}(BGBM)^2 + \beta_{13}(Depth)^2 + \beta_{14}(REI)^2 + \varepsilon_i
\end{aligned}
$$

where $P_{\text{Total fauna}}$ is the community secondary production within sediments, on the sediment surface, and (when sampling in seagrass beds) among and on seagrass plants (mg AFDM m^{-2} day^{-1}); $CanopyH$ is the canopy height (cm); $ShootD$ is the shoot density (number m^{-2}); $AGBM$ is the aboveground biomass (dry g m^{-2}); $BGBM$ is the belowground biomass (dry g m^{-2}); $Organic$ is the sediment organic content (%); $Sand$ is the sediment sand content (%); $Temp$ is the water temperature (°C); $Depth$ is the water depth (m); and REI is the relative exposure index. Forward selection regression model building was used to determine the subset of explanatory variables that best explained the observed variation in community production. Residual plots were examined to assess the assumptions of homogeneity of variance and normality. Violations were corrected by weighting the response variable by the inverse of the replicate standard deviation (Draper and Smith 1998), and the use of a square root transformation. ANOVAs and multiple regressions were all implemented in R v3.2.5.

Canonical correspondence analysis (CCA) was used to examine the relationship of community structure ($C_{\text{Total fauna}}$) with the explanatory variables (i.e. environmental variables). CCA is a multivariate constrained ordination technique where major gradients in species community data are extracted and accounted for by measured explanatory variables. This is achieved by combining multiple least squares regression of species community data onto the explanatory variables with ordination, where the ordination axes are linear combinations of the explanatory variables that account for major gradients in the species data (ter Braak 1986; Palmer 1993; Legendre and Legendre 2012). The CCA in this study includes all explanatory variables except percent gravel, percent silt, and aboveground biomass, in order to reduce redundant variables. The data for the community structure used in the CCA were the secondary production of families ($C_{\text{Total fauna}}$) with a square root transformation. Explanatory variables were standardized prior to implementation of the analysis. As for the nMDS and multiple regression, mean values of percent sediment organic content or particle size from each habitat and site combination were used for sampling stations where these were not measured. A forward selection routine was used to identify the

sampling stations where these were not measured. The environmental variables were standardized prior to the analysis. Scatter plots and exploratory regression models were used to identify which variables showed curvature. The initial model was then identified as

subset of explanatory variables that best accounted for the observed variation in community structure of $C_{\text{Total fauna}}$.

The proportion of variability in the community structure data explained by the CCA was calculated as the sum of all eigenvalues of each constrained canonical axis divided by the total inertia (sum of eigenvalues of both the constrained and unconstrained axes). The significance of the overall CCA and of each axis was determined using permutation tests (Legendre et al. 2011). To identify the environmental variables that determined major environmental gradients through their correlation with CCA axes, inter-set correlations were calculated (ter Braak 1986).

The ordination was visualized using site scores (weighted averages (WAs) of taxon scores), taxon scores, and explanatory variables (represented by vectors) for the first two canonical axes (ter Braak 1986; Legendre and Legendre 2012). In the ordination plot, vector length indicates the relative importance of each environmental variable, vector direction the association with constrained canonical axis 1 or 2, and the angle between vectors the correlations between explanatory variables (where smaller angles indicate higher positive correlation). Further, the location of taxa and site scores relative to the vectors indicates relationships with the explanatory variables, and orthogonal projection of taxon scores onto a vector indicates the approximate centre of the taxon distribution along that particular environmental gradient. Location of site scores indicates their compositional similarity to each other. Plots were scaled by taxon to emphasize relationships among them. The CCA was conducted using the vegan package in R v3.2.5, in which implementation follows Legendre and Legendre (2012). Further explanation of CCA is found in ter Braak (1986), Palmer (1993), and Legendre and Legendre (2012).

Results

General Plant and Sediment Properties

The nMDS ordination for environmental conditions showed clear separation of all sites based on habitat type, with all

seagrass habitats located on the positive side of axis 1 and all bare sediment on the negative side (Appendix Fig. A2). Sites in both seagrass and bare sediment were generally grouped in a similar manner along axis 2. This axis describes a gradient of conditions where sites with high sediment organic content, warm and shallow water, and low exposure are on the positive side of the axis, while sites with low sediment organic content, cool and deep water, and high exposure are on the negative side of the axis. Sites were ordered according to similarity in environmental conditions in all following figures, based on these nMDS results.

ANOVAs indicated that all seagrass metrics were significantly different across field sites ($F_{9,87} = 8.15$ to $F_{9,90} = 82.8$, $p < 0.0001$; Appendix Table A2; Fig. 2a–d). Mean seagrass canopy height ranged from 23.6 to 63 cm and tended to be highest at less-exposed sites (PH, PJ, Keji, SecPen, L3F). Mean shoot density ranged from 57.6 to 1246 shoots m^{-2}, mean aboveground biomass from 143.9 to 519.4 dry g m^2, and mean belowground biomass from 65.1 to 1317.4 dry g m^2. The highest belowground biomass was observed at the more-exposed sites (EastPet, CableI, Sambro, CrouchI).

Mean percent organic content in sediments ranged from 0.7 to 25.6% across all habitat types and sites (Fig. 2e). An ANOVA indicated that differences in organic content between habitat types were site dependent (Appendix Table A2; habitat × site: $F_{9,78} = 8.955$, $p < 0.0001$), with some sites showing higher organic content in seagrass compared to bare sediments (CableI, CresB, CrouchI, PH), some sites showing the opposite pattern (EastPet, L3F), and still others showing no difference between habitat types (Keji, PJ, Sambro, SecPen). High organic content (10–25%) was observed in both habitat types at most shallow and low *REI* sites (PH, PJ, Keji, SecPen) (Table 1). Large ranges in mean percent silt (0–90%) and percent sand content (9.7–100%) were observed (Fig. 2f, g). Small amounts of gravel (<12%) were present at only a few sites (Fig. 2h). Not surprisingly, patterns in percent silt across habitat types were similar to those for organic content, while percent sand showed the opposite pattern.

General Properties of Macrobenthic Invertebrates

A total of 168 taxa of macrobenthic invertebrates (≥500 μm) in 74 families was observed across all sites and habitat types (Appendix Table A3). Cores captured 139 taxa while pop-up nets captured 98 taxa; 73 were only in cores and 32 only in pop-up net samples. Mean total density per core ranged from 1.0×10^3 to 2.7×10^4 individuals m^{-2} and biomass from 430.1 to 2.0×10^4 dry mg m^{-2} (Appendix Fig. A3). Mean density and biomass collected by the pop-up nets were typically much lower and ranged from 851.0 to 8.6×10^3 individuals m^{-2} and from 291.4 to 1.6×10^3 dry mg m^{-2} for density and biomass, respectively.

Habitat-Specific Differences in Community Secondary Production

Mean community secondary production ($P_{\text{Total fauna}}$) ranged from 5.69 to 170.2 mg AFDM m^{-2} day^{-1}. The ANOVA showed that habitat-specific differences in $P_{\text{Total fauna}}$ were dependent on site (habitat × site: $F_{9,179} = 4.687$, $p < 0.0001$; Fig. 3a). $P_{\text{Total fauna}}$ was significantly higher in seagrass than in bare sediment at four sites (CresB, EastPet, Sambro, and CrouchI), with one additional site (CableI) showing a similar trend. These sites are mostly characterized by high exposure, sandy sediments with low organic content, deep and sometimes cool water, and high belowground plant biomass. Sites where habitat-specific differences in secondary production were not evident (i.e. PH, PJ, Keji, SecPen, L3F) tended to be more protected, shallow, and warm and had silty sediments with high organic content.

Mean secondary production from fauna among and on seagrass plants ($P_{\text{SG fauna}}$) ranged from 5.28 to 22.8 mg AFDM m^{-2} day^{-1} and was 7–30% of $P_{\text{Total fauna}}$ in seagrass beds at all sites (Fig. 3b). Patterns in $P_{\text{SG fauna}}$ across sites did not match those for $P_{\text{Total fauna}}$, suggesting that different mechanisms influenced the production of each.

For $P_{\text{Total fauna}}$, annelids made the largest contributions to community production at seven bare soft-sediment sites and three seagrass sites (Fig. 3c). Molluscs were also important and dominated $P_{\text{Total fauna}}$ at two bare sites and four seagrass sites. Arthropods and other fauna were also sometimes important, contributing 1–38% of total production except at one site (SecPen seagrass) where arthropods contributed 70% of production. The majority of $P_{\text{SG fauna}}$ was derived from arthropods and molluscs (Fig. 3d).

## Relationships of Secondary Production with Environmental Variables

Community Secondary Production

The multiple regression model for $P_{\text{Total fauna}}$ explained 56% of the variance in the data ($R^2 = 0.562$, $p < 0.0001$). Shoot density, belowground plant biomass, sediment organic content, water temperature and depth, and exposure were all retained as important determinants of secondary production, while aboveground biomass and sediment percent sand content were excluded from the model (Table 2).

Community Structure Based on Secondary Production

The final canonical correspondence analysis (CCA) model for $C_{\text{Total fauna}}$ included all the environmental variables in the original model. These variables were shoot density, canopy height, belowground biomass, sediment organic and sand content, water temperature and depth, and exposure. The inertia

Fig. 2 Mean (+1 SE) *Zostera marina* and sediment properties across field sites. *AGBM* aboveground plant biomass, *BGBM* belowground plant biomass. *n* = 10 (*Z. marina*), *n* = 5 (organic content), and *n* = 3 (particle size). *PH* Port l'Hebert, *PJ* Port Joli, *Keji* Kejimkujik Seaside National Park, *SecPen* Second Peninsula, *L3F* Lower Three Fathom Harbour, *CresB* Crescent Beach, *EastPet* East Petpeswick, *CableI* Cable Island, *Sambro* Inner Sambro Island, *CrouchI* Croucher Island
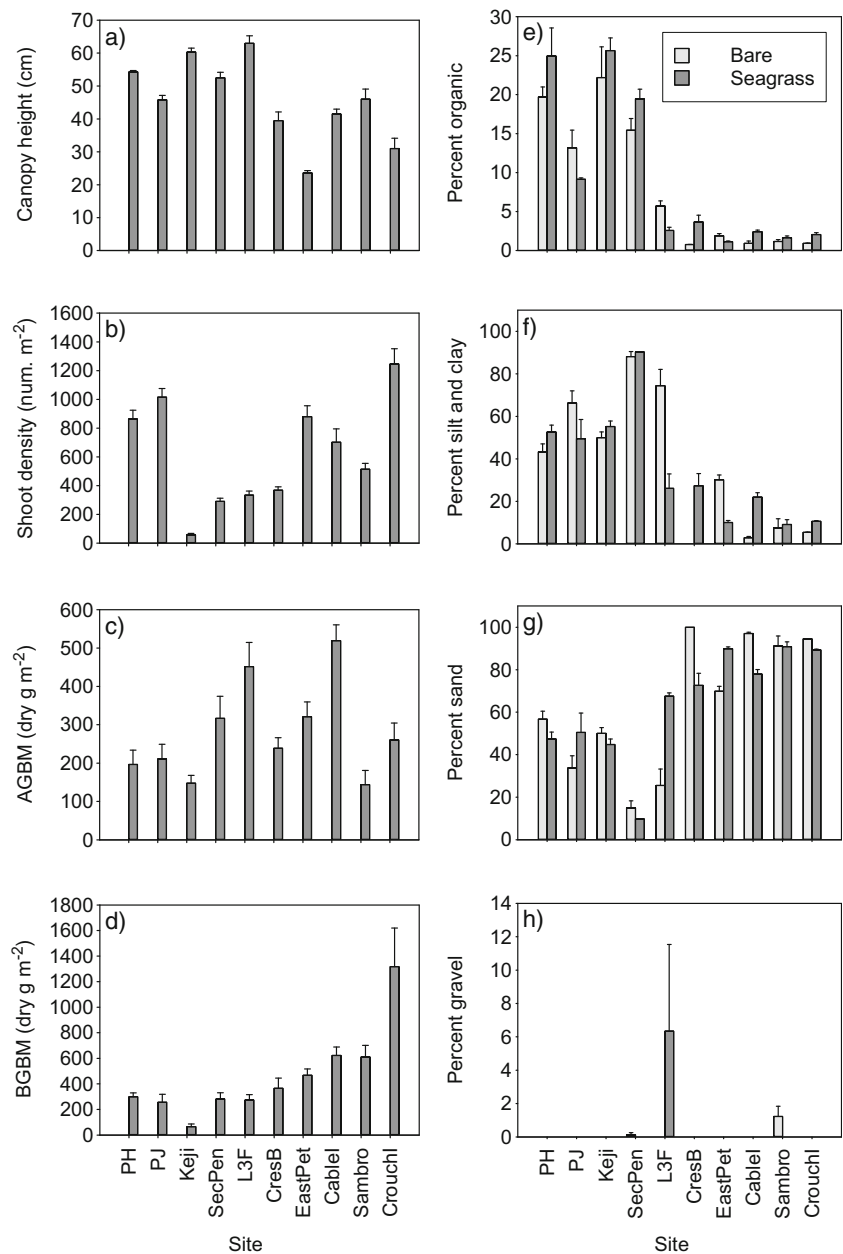

value of the constrained axes was 1.504 and explained 16.4% of the variance in the data, with the first two constrained axes explaining 8.4% of the variance (Table 3). Seven of eight constrained axes were statistically significant for the CCA model.

All constraining variables were similar in magnitude and their contribution to the ordination except for belowground biomass and canopy height (Fig. 4a). The environmental variables correlated with the first CCA axis indicate a gradient across increasing water depth, sediment sand content, and exposure with decreasing water temperature and sediment organic content when moving from the positive to negative side of the axis. The second CCA axis was strongly correlated with shoot density, which increased from the negative to the

positive side of the axis. Examination of site scores indicated that community structure based on secondary production differed between habitat types mainly at deeper, cooler sites that were exposed and had sandy sediments with low organic content (i.e. CableI, CresB, CrouchI, EastPet, and Sambro; Fig. 4a). These were the sites and conditions where community production ($P_{\text{Total fauna}}$) also differed between habitat types. At protected, warm, shallow sites where sediments were high in organic content (Keji, L3F, SecPen), community structure did not differ between habitat types. However, differences became apparent when shoot density was high under these conditions (i.e. PH, PJ).

Observation of taxon scores relative to environmental variables provided insight into taxa contributing to habitat

Fig. 3 Mean (+1 SE) community secondary production for **a** total fauna ($P_{\text{Total fauna}}$) captured by corers, which includes invertebrates (≥500 μm) within the sediments, on the sediment surface, and (when in seagrass beds) among and on seagrass plants, and **b** seagrass fauna ($P_{\text{SG fauna}}$) captured by pop-up nets, which includes invertebrates among and on seagrass plants. Proportion contribution of invertebrates to $P_{\text{Total fauna}}$ and $P_{\text{SG fauna}}$ is provided in **c, d**, respectively. In **c**, bare sediments are the *first bar* and seagrass the *second bar* within each site. $n = 8$ ($P_{\text{SG fauna}}$) and 10 ($P_{\text{Total fauna}}$). The *asterisks* indicate a significant difference between habitat types within each site; the *tilde* indicates a similar trend that was non-significant due to low statistical power. Site abbreviations as in Fig. 2
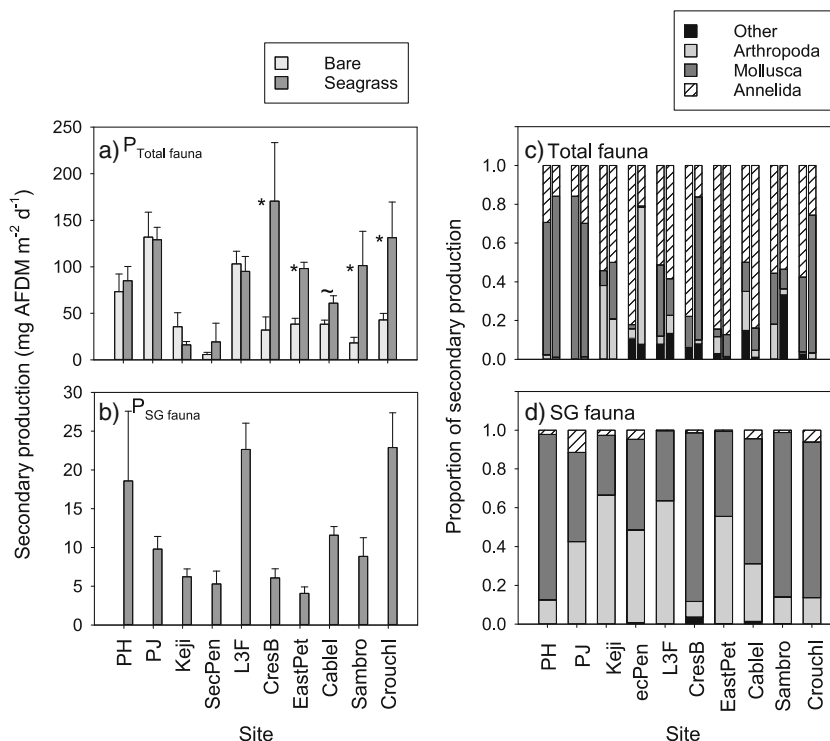
differences in community structure and their relationships to environmental conditions. For example, taxa present in communities strongly associated with protected sites in shallow, warm water with silty sediments and high shoot density include those in the families Janiridae, Nassariidae, and Hydrobiidae (points 39, 52, and 36 in quadrant 1 of Fig. 4b, respectively), while taxa in these same conditions but with low density (or absent) seagrass included the Skeneopsidae,

Table 2 Results of multiple linear regression analysis for community production ($P_{\text{Total fauna}}$; mg AFDM m^{-2} day^{-1}). $P_{\text{Total fauna}}$ includes fauna within the sediments, on the sediment surface, and among and on seagrass plants

Dependent variable	Factor	Coefficient	SE	t	p
$P_{\text{Total fauna}}$	Intercept	8.760	0.385	22.725	<0.0001
	ShootD	0.841	0.251	3.351	0.001
	Organic	−1.445	0.237	−6.098	<0.0001
	Temp	1.973	0.228	8.659	<0.0001
	REI	0.714	0.246	2.900	0.004
	REI^2	−1.327	0.273	−4.867	<0.0001
	Depth^2	−0.168	0.084	−1.998	0.047
	BGBM	0.612	0.330	1.853	0.065

SE = standard error, *ShootD* = shoot density (number m^{-2}), *Organic* = sediment organic content (%), *Temp* = water temperature (°C), *REI* = relative exposure index, *Depth* = water depth (m), *BGBM* = belowground plant biomass (dry g m^{-2}). $R^2 = 0.562$; $F_{7,191} = 37.26$, $p < 0.0001$

Table 3 Results of the CCA analysis for community structure of $C_{\text{Total fauna}}$, based on the secondary production of families

	$C_{\text{Total fauna}}$		
Total inertia	9.173		
Constrained inertia	1.504		
Proportion constrained inertia	0.164		
	CCA1	CCA2	CCA3
Eigenvalue	0.472	0.306	0.215
Proportion explained	0.051	0.033	0.023
Cumulative proportion explained	0.051	0.084	0.108
ANOVA for constrained axes			
$F_{1,188}$	11.57	7.502	5.271
P	0.001	0.001	0.001
Inter-set correlations			
Sand	−0.807	−0.149	−0.084
ShootD	−0.328	0.613	0.362
REI	−0.732	0.363	−0.299
Temp	0.774	0.201	−0.019
Depth	−0.763	−0.246	0.005
BGBM	−0.399	0.370	0.450
CanopyH	−0.027	0.192	0.532
Organic	0.566	0.287	−0.072

Results for the first three canonical axes are shown out of eight in total. *CanopyH* = canopy height, *ShootD* = shoot density, *Sand* = percent sand in sediments, *Organic* = percent organic matter in sediments, *REI* = relative exposure index, *BGBM* = belowground plant biomass, *Temp* = water temperature, *Depth* = water depth. Overall ANOVA results: $F_{8,188} = 4.61$, $p = 0.001$
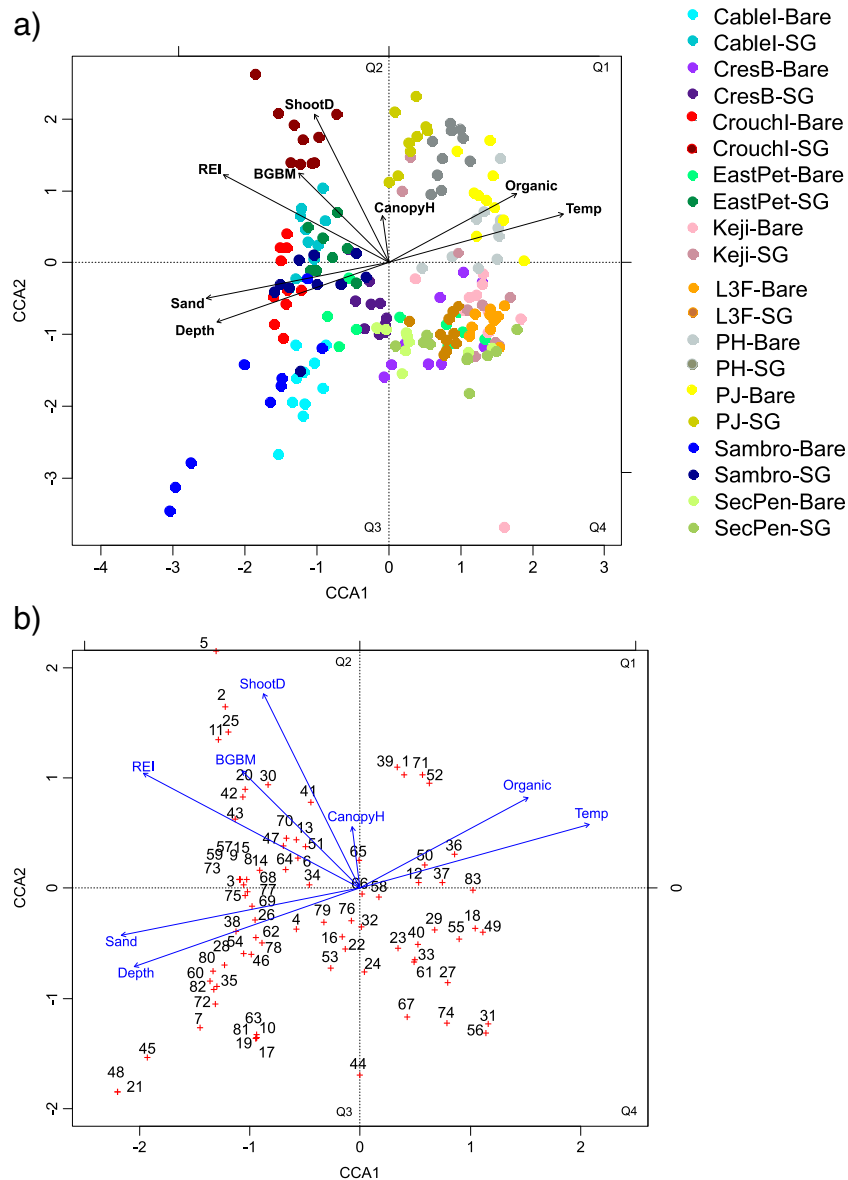
Fig. 4 Canonical correspondence analysis (*CCA*) plots for community structure ($C_{Total\ fauna}$), based on secondary production of families. See Table 3 for statistical results. **a** Site scores (weighted averages) along the first and second CCA axes with overlaid environmental variables (vectors). *Q* quadrant, *CanopyH* canopy height, *ShootD* shoot density, *Sand* percent sand in sediments, *Organic* percent organic matter in sediments, *REI* relative exposure index, *BGBM* belowground plant biomass, *Temp* water temperature, *Depth* water depth, *SG* seagrass. See Fig. 2 for site abbreviations. **b** Taxa scores (*plus sign*) along the first and second CCA axes in relation to environmental variables (vectors). Families represented by *numbers in the plot* are as follows (with the *letters* after each family representing the taxonomic groups: *G* = Gastropoda, *A* = Amphipoda, *P* = Polychaeta, *E* = Echinodermata, *B* = Bivalvia, *I* = Isopoda, *In* = Insecta, *C* = Cumacea, *Cn* = Cnidaria, *H* = Hemichordata, *T* = Tanaidacea): Acteocinidae-G (*1*), Ampeliscidae-A (*2*), Ampharetidae-P (*3*), Amphiuridae-E (*4*), Ampithoidae-A (*5*), Anomiidae-B (*6*), Anthuridae-I (*7*), Arcticidae-B (*8*), Astartidae-B (*9*), Buccinidae-G (*10*), Calyptraeidae-G (*11*), Capitellidae-P (*12*), Caprellidae-A (*13*), Cardiidae-B (*14*), Caudinidae-E (*15*), Cerithiidae-G (*16*), Chaetiliidae-I (*17*), Chironomidae-In (*18*), Cirolanidae-I (*19*), Cirratulidae-P (*20*), Colloniidae-G (*21*), Columbellidae-G (*22*), Corophiidae-A (*23*), Cumacea-C (*24*), Dexaminidae-A (*25*), Dorvilleidae-P (*26*), Fabriciidae-P (*27*), Flabelligeridae-P (*28*), Gammaridae-A (*29*), Glyceridae-P (*30*), Haloclavidae-Cn (*31*), Haminoeidae-G (*32*), Harrimaniidae-H (*33*), Hesionidae-P (*34*), Hiatellidae-B (*35*), Hydrobiidae-G (*36*), Idoteidae-I (*37*), Ischyroceridae-A (*38*), Janiridae-I (*39*), Leptocheliidae-T (*40*), Littorinidae-G (*41*), Lottiidae-G (*42*), Lumbrineridae-P (*43*), Lyonsiidae-B (*44*), Lysianassidae-A (*45*), Mactridae-B (*46*), Maldanidae-P (*47*), Margaritidae-G (*48*), Metridiidae-Cn (*49*), Myidae-B (*50*), Mytilidae-B (*51*), Nassariidae-G (*52*), Nemertea (*53*), Nephtyidae-P (*54*), Nereididae-P (*55*), Nudibranchia (*56*), Oedicerotidae-A (*57*), Oligochaeta (*58*), Opheliidae-P (*59*), Ophiactidae-E (*60*), Orbiniidae-P (*61*), Paraonidae-P (*62*), Paratanaoidea-T (*63*), Pholoidae-P (*64*), Phoxocephalidae-A (*65*), Phyllodocidae-P (*66*), Platyhelminthes (*67*), Polynoidae-P (*68*), Pontogeneiidae-A (*69*), Pyramidellidae-G (*70*), Rissoidae-G (*71*), Serpulidae-P (*72*), Sigalionidae-P (*73*), Skeneopsidae-G (*74*), Sphaerodoridae-P (*75*), Spionidae-P (*76*), Stenothoidae-A (*77*), Syllidae-P (*78*), Tellinidae-B (*79*), Terebellidae-P (*80*), Travisiidae-P (*81*), Unciolidae-A (*82*), Veneridae-B (*83*)

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Orbiniidae, and Nereididae (points 74, 61, and 55 in quadrant 4 of Fig. 4b, respectively). Taxa associated with high sediment sand content, greater water depth, more exposure and higher seagrass cover at low water temperature, and low sediment organic content (i.e. quadrant 2 in Fig. 4c) included the Lottiidae, Oedicerotidae, and Lumbrineridae (points 42, 57, and 43 in Fig. 4b, respectively), while taxa associated with these same conditions but with low or absent seagrass cover (i.e. quadrant 3 in Fig. 4b) included the Anthuridae, Hiatellidae, and Lysianassidae (points 7, 35, and 45 in Fig. 4b, respectively).

Discussion

My study found that habitat-specific differences in secondary production were not present across the entire range of environmental conditions in which seagrass beds and bare soft-sediment habitats were examined. This suggests that habitats with emergent structure may not always reflect higher ecosystem functioning than nearby habitat without emergent structure, at least when using secondary production as a metric for functioning. In some cases, habitat-specific differences appear more influenced by environmental conditions than by the habitat structure itself. In particular, I found that community secondary production ($P_{\text{Total fauna}}$) in seagrass beds differed (and was higher) than in adjacent soft-sediment bottom only when conditions included high exposure, sandy sediments low in organic content, high belowground plant biomass, and relatively deep and cool water. Similar patterns were also observed for the underlying community structure ($C_{\text{Total fauna}}$) where shoot density sometimes also played a role. While many studies have found that seagrass beds support higher secondary production than bare sediments (e.g. Heck et al. 1995; Bologna 2006; Wong et al. 2011), others have shown this is not always the case (Asmus and Asmus 1985; Sprung 1994; Edgar et al. 1994), similar to my study. This suggests that when using secondary production to assess ecosystem functioning, habitat structure and environmental conditions should both be considered.

Generally, the estimates of community secondary production in my study were within the range found in other studies of *Zostera* spp., typically 50 to 600 and 15 to 200 mg AFDM m^{-2} day^{-1} in seagrass and bare soft-sediment habitats, respectively (see Appendix Table A5). This was observed even though most previous studies used mean annual biomass to estimate secondary production rather than summer biomass, as in this study. A few estimates from my study were lower than those previously reported, particularly at sites with very low exposure, low shoot density, and very silty sediments with high organic content (i.e. Keji, SecPen). These conditions, combined with low water exchange and high water temperatures (Wong et al. 2013), likely restricted plant growth and

benthic production through consequent high sulphide concentrations in the sediments (Pearson and Rosenberg 1978; Goodman et al. 1995). Other sites with very silty sediments (PH, PJ) had better flushing rates and were more exposed, with high secondary production derived from molluscs in both seagrass and bare sediment habitats. Interestingly, fauna among and on seagrass plants contributed only a small proportion (7–30%) to total community production in seagrass beds. Inclusion of production from shrimps and crabs would have increased contributions from epibenthic invertebrates to community production in both habitat types (Wong and Dowd 2016).

The regression model for community secondary production ($P_{\text{Total fauna}}$) and the environmental variables explained 56% of the variation in the data. Important determinants of secondary production included exposure, plant properties (shoot density, belowground plant biomass), sediment organic content, and water depth and temperature, similar to other studies of seagrass and bare sediments across a range of latitudes and water depths (e.g. Emerson 1989; Tumbiolo and Downing 1994; Edgar and Barrett 2002; Cusson and Bourget 2005; Bolam et al. 2010). The CCA model for community structure ($C_{\text{Total fauna}}$) showed that sediment sand content and canopy height were also important. However, the CCA model explained a relatively low proportion (0.16) of the variance in the data, suggesting that other environmental variables are likely important. One such variable is food availability (Ysebaert and Herman 2002). In my study, sediment organic content partially accounted for food resources, but inclusion of chlorophyll *a* in the sediments and also the water column may have improved the model. Further improvements may have also resulted by including hydrodynamic properties such as water velocity, known to affect seagrass bed structure, plant biomass, and benthic community production (Fonseca et al. 1983; Edgar and Barrett 2002; Peralta et al. 2006; Bolam et al. 2010). Despite these potential improvements, this study still allowed several important environmental determinants of benthic production to be identified. The models allow prediction of community secondary production and its underlying faunal structure based on the surrounding environmental conditions, useful when full-scale field studies to quantify secondary production are not possible.

The findings of my study have important implications not only for our general understanding of ecosystem functioning in the nearshore but also for practical applications such as habitat restoration. Restoration practitioners often preferentially restore structured habitats under the assumption these habitats consistently provide higher ecosystem functioning than non-structured habitats. My study suggests that in addition to habitat structure, the environmental conditions at the restoration site will play an important role in the provision of ecosystem functions and should be carefully considered prior to the initiation of restoration projects. Generally, secondary

production is a useful metric to guide restoration activities in that it allows the scaling and benefits of the restored habitat to be easily quantified (Fonseca et al. 2000; Wong et al. 2011). My study provides some of the first data of benthic secondary production and its relationship with environmental conditions that can inform management decision making in nearshore ecosystems of Atlantic Canada. When evaluated within the appropriate environmental context, secondary production is a useful metric to inform management objectives and practices in nearshore ecosystems.

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