



Macrobenthic assemblage structure in a cool-temperate intertidal dwarf eelgrass bed in comparison with those from lower latitudes

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Received 14 April 2011; revised 23 May 2011; accepted for publication 23 May 2011

The evolution and ecology of latitudinal patterns in marine macrofaunal biodiversity and assemblage structure are contentious. With the aim of investigating the occurrence of such patterns in intertidal dwarf eelgrass beds (*Nanozostera* spp.), those at cool-temperate Scolt Head Island, UK (latitude 52°N), were examined and compared with equivalent systems in warm-temperate Knysna, South Africa (34°S), and subtropical Moreton Bay, Australia (27°S): systems that had earlier been examined using an identical methodology. The Scolt Head bed supported the highest faunal density (mean 6568 0.1 m⁻²), lowest observed and estimated species richness (32 and 33 spp., respectively), lowest species diversity (Simpson's index of diversity 0.34), highest mean constancy index (23.0), lowest proportion of total numbers contributed by singletons or doubletons (0.06%), largest Berger–Parker dominance index (0.81), and least degree of variability between component samples. The beds at Knysna were intermediate between those at Scolt Head and at Moreton Bay in all those respects, as well as in nature and composition of the fauna. Similar dwarf eelgrass beds at Arcachon, France, likewise appear intermediate between those of Scolt Head and Knysna. Community variance in all three regions was greatest at the smallest spatial scale of ≤ 1 m, at which scale two of the three sites also displayed randomly organized faunal assemblages, although this changed to non-random at larger spatial scales. Assemblages were deterministically structured at all spatial scales at Knysna. A consistent series of changes in structural characteristics of macrofaunal dwarf-eelgrass assemblages therefore occurred along the latitudinal sequence of Scolt Head (53°), Arcachon (45°), Knysna (34°), and Moreton Bay (27°). Community assembly patterns did not change with latitude, however, but did so with spatial scale in two of the three regions. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, 104, 527–540.

ADDITIONAL KEYWORDS: benthic – community – diversity – richness.

INTRODUCTION

Seagrass beds are among the most productive (Duarte & Chiscano, 1999), most threatened (Duarte *et al.*, 2008; Waycott *et al.*, 2009), and richest (Williams & Heck, 2001) of shallow marine habitats, yet in comparison with more charismatic systems such as coral reefs (Duarte *et al.*, 2008) their value is often unappreciated (Unsworth & Cullen, 2010), and much of their ecological adaptations, structure, and functioning is poorly understood (Holmer & Marba, 2010). This includes latitudinal and other spatial patterns in macrofaunal assemblage structure, largely because data in the available literature are bedevilled by the

use of differing individual methodologies and sizes of areas sampled (Barnes, 2010a; Konar *et al.*, 2010).

The abundance, diversity, and faunal composition of the smaller surface and near-surface macrobenthos of intertidal dwarf eelgrass beds (*Nanozostera* spp.), and their spatial variation over horizontal distances of between 1 m and 4 km, have however been investigated with uniform methodology in the landward horizons of intertidal meadows of *Nanozostera muelleri capricorni* in Moreton Bay, 27°S, in eastern Australia (Barnes & Barnes, 2011) and of *Nanozostera capensis* in Knysna, 34°S, in southern South Africa (Barnes, 2010b). Both these systems in shallow, sheltered marine bays exhibited marked patchiness, with abundance, diversity, and faunal composition showing significant variation at all

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spatial scales, but with variance at the smallest distance between samples (1 m) being greatest and with variance at the largest scale (≥ 1 km) being least.

The faunas of beds of the equivalent intertidal dwarf eelgrass in cool-temperate regions, *Nanozostera noltii* (= *Nanozostera nana*), have also received attention, especially in the Bassin d'Arcachon of Atlantic France (e.g. Bachelet *et al.*, 2000; Blanchet *et al.*, 2004), although using different methodology and sampled area. As in *N. capensis* in the marine outer basin of the Knysna estuarine bay, South Africa (Barnes, 2010b), these authors found more than one type of faunal assemblage at Arcachon, ranging from annelid-dominated systems in the more exposed beds to mollusc-dominated meadows in more sheltered and/or brackish situations. The small sheltered bay of Cockle Bight on the leeward side of the offshore barrier island of Scolt Head on the south-western coast of the North Sea, UK, also contains a well-established bed of *N. noltii*. Like many other Atlantic beds of this and related eelgrasses north of the Mediterranean Sea (e.g. Blanchet *et al.*, 2004; Cacabelos, Quintas & Troncoso, 2008), its fauna is dominated by the rissooidean mudsnail *Hydrobia ulvae*, and is abundant though not diverse: on average, the density of *H. ulvae* was 43 300 m⁻² out of a faunal total of 51 300 m⁻² in September 2008 (Barnes, 2010a), and closely similar values were obtained in September 2007 (R.S.K. Barnes, unpubl. data).

To effect a comparison of the ecological structure of *Nanozostera* beds in warm-temperate and subtropical latitudes with an ecologically equivalent system in the cool-temperate zone, this paper investigates the diversity, abundance, and composition of the smaller elements of the surface and near-surface macrobenthos (< 10 mm) of *N. noltii* beds at Scolt Head (53°N), part of a National Nature Reserve and Ramsar site on the east coast of England, using exactly the same methodology as earlier applied to those lower-latitude systems (Barnes, 2010b; Barnes & Barnes, 2011).

MATERIAL AND METHODS

DATA COLLECTION

Nanozostera noltii occurs over the Cockle Bight intertidal zone on Scolt Head in the form of two beds, to the north-west and south-east, each of some 3 ha in area, separated by an *Arenicola*-structured bare mudflat. Upper horizons (at or above the mean sea level) of the two beds ('localities'), centred on 52°59'08"N, 0°40'25"E and 52°59'00"N, 0°40'43"E, were sampled from June 2009 to August 2010, each by means of two 'sites' centred some 100 m apart. Three stations some 60 m apart were sampled at each site, and each station was sampled by means of a series of

ten core samples at 1-m intervals, yielding totals of 30 samples per site and 60 samples per locality. This series of 120 cores is termed as 'standard core samples' hereafter. Each core sample was of 60 mm in diameter and 50 mm in depth. Pilot studies at the site indicated that: (1) ten cores of that diameter would yield an acceptable standard error < 10% of the arithmetic means in the estimates for numbers of both the dominant *H. ulvae* and the total fauna; and (2) each core sample could be expected to contain a mean of ≈ 100 faunal individuals. A 50-mm depth was selected because most benthic macrofauna in seagrass beds are known to occur in the top few millimetres of sediment (e.g. 98% in the top 5 mm in the study by Klumpp & Kwak, 2005). Sampling was conducted only in areas free of blanket weed (*Ulva prolifera* and *Ulva flexuosa*), as pilot studies have shown that chlorophycean cover caused a decrease in the species pool of 40% and a drop in faunal numbers of 84% (Mann-Whitney $Z = 6.8$; $P < 0.0001$), with numbers of the dominant *H. ulvae* being depressed by 92% (and see Soulsby, Lowthion & Houston, 1982; Raffaelli, Raven & Poole, 1998). Each sample was collected at low tide, soon after the tidal ebb from the site, and was gently sieved through 710- μ m mesh. All retained material: (1) was placed in a large polythene bag of seawater and shaken vigorously to dislodge all but firmly attached sessile animals from the seagrass before it was discarded (earlier testing having shown that no motile species remained within the seagrass after such treatment); (2) was then re-sieved and transported to a local field laboratory; and (3) was then placed in a large white tray from which the living fauna was extracted by eye, with extraction continuing until no further animal could be seen after a 3-minute search, which preliminary trial runs had indicated was sufficient to remove all live individuals. All collected fauna was identified to species level and counted, excluding sessile animals formerly attached to the seagrass leaves (e.g. *Sagartia* anemones) but dislodged during the shaking process.

To investigate the spatial variation at the smallest of scales, an additional series of core samples was taken in September 2010 between the two south-eastern sites in the form of a 5-m transect parallel with the shoreline, with one core sample taken every 12.5 cm (i.e. 41 cores in total, with a unit gap of 6.5 cm between adjacent samples). The sampling procedure was otherwise identical to that of the standard core samples described above.

Seagrass shoot density was not recorded because earlier data from the sampled region (Barnes, 2010a) showed no significant correlation between *N. noltii* shoot density and either the total number of faunal individuals (Spearman $r_s = 0.17$; $P > 0.3$) or Simpson's index of diversity of faunal groups (Spearman $r_s = 0.08$; $P > 0.6$), but sampling was confined to areas

of 100% *Nanozostera* cover. Field estimates of silt content of the sediment within each station were obtained, however, as the same data set yielded a small correlation verging on significance between an index of the proportion of sedimentary fines and total faunal abundance (Spearman $r_s = 0.36$; $P = 0.053$), and a significant negative correlation between the same index and faunal group diversity (Spearman $r_s = -0.6$; $P = 0.03$). As previously described (Barnes, 2010a), a standard series of 50-mm deep \times 30-mm diameter sediment cores were placed in a 0.25 m \times 30 mm glass measuring cylinder after the removal of any seagrass rhizomes, etc., local rain water was added to fill the cylinder, and the system was shaken until the sediment was thoroughly suspended. It was then allowed to stand for 2 h, after which time the proportion of fine particles (of 2–63 μm in diameter) was determined volumetrically.

ANALYSES

As described previously (Barnes, 2010b; Barnes & Barnes, 2011), species diversity was assessed using Simpson's index of diversity ($1 - \lambda$) and Simpson's evenness index [$(1 - \lambda)/S$]. Constancy indices (CIs) are percentage frequencies of occurrence, categories of faunal rarity are defined *sensu* Colwell & Coddington (1994), and indices of dispersion are variance-to-mean ratios, with significance of departures from unity being tested by a Fisher's χ^2 index of dispersion test. Potential area effects on diversity were avoided because the same area was investigated at all nested sampling units.

The comparison of faunal characteristics of cool-temperate *N. noltii* beds with those of lower latitude *Nanozostera* sites used part of the faunal databases of Barnes (2010b) and Barnes & Barnes (2011) for the lower latitude *Nanozostera* sites. The Scolt Head dwarf eelgrass fauna belongs to the subset of *Nanozostera* faunas that are dominated by microgastropods (Barnes, 2010b). As 12 microgastropod-dominated stations were previously sampled in the South African *N. capensis* beds (the 'enclosed' and 'sheltered' Knysna sites of Barnes, 2010b), to facilitate our comparison the number of Scolt Head stations and total area sampled were therefore set to equal the South African ones, and likewise equivalent data sets were selected for comparison from the Moreton Bay *N. m. capricorni* beds (taken from the two Myora Springs and North Dunwich locations). The precise areas of the three geographical regions to be compared were selected so as to be ecologically as equivalent as possible, setting latitudinal-related differences aside, and besides using the same sampling methodology and protocols, samples were all taken from the same shore horizon (at or about the mean sea level), at the same

time of year (from late spring to early autumn), and all in areas of 100% *Nanozostera* cover. [The precise tidal height and time of sampling during the summer months may not actually be critical, as previous work at the Scolt Head localities has shown that macrofaunal abundance did not change significantly over the summer (as gleaned from the database of Barnes & de Villiers, 2000), and that neither macrofaunal abundance nor species diversity vary significantly with tidal height within the *Nanozostera* at Knysna (R. S. K. Barnes & M. D. F. Ellwood, unpubl. data)] All three areas are also subject to nature reserve legislation in which all disturbance except limited bait-collection activities is prohibited, and all are pollution-free regions of high water quality.

No individual species was common to any two regions, let alone to all three regions. Therefore, to compare faunal composition statistically across regions, faunas were apportioned between 59 taxa, generally at the level of superfamily/order (as recognized by the World Register of Marine Species, <http://www.marinespecies.org>) for speciose and/or abundant groups, but at higher taxonomic levels for groups contributing few individuals to the total. Data sets from two other ecologically equivalent but non-microgastropod stations were also included to ground the analysis: a polychaete-dominated *Nanozostera* faunal assemblage at Knysna (polychaetes = 92% of individuals) and a polychaete- and amphipod-dominated (69% of total) *Halophila/Halodule* site at tropical (5°S) Ambeua, Taman Nasional Wakatobi, Indonesia.

Ordination by non-metric multidimensional scaling (nMDS), hierarchical clustering analysis using S17 Bray–Curtis similarity, and similarity percentage analysis (SIMPER) were carried out via CAP 4 (Pisces Conservation Ltd), permutational analysis of variance (PERMANOVA) including partitioning of variance components was carried out using PRIMER 6 (PrimerE Ltd), and species-richness estimation (Chao2) and species accumulation analysis using the Mao τ expected richness function (Colwell, Mao & Chang, 2004) were carried out using EstimateS [Colwell RK. 2006. EstimateS: Statistical estimation of species richness and shared species from samples, Version 8; downloadable from <<http://viceroy.eeb.uconn.edu/estimates>>]. PERMANOVA and nMDS were carried out on Bray–Curtis similarity matrices with untransformed, and square- and fourth-root transformed versions of the data; transformation did not materially affect any results. Observed patterns of species co-occurrence were compared with statistical randomizations of the original species occurrence data using ECOSIM 7 simulations [Gotelli NJ, Entsminger GL. 2010. EcoSim: Null models software for ecology, Version 7; Acquired Intelligence Inc. & Kesey-

Bear, Jericho, VT 05465; downloadable from <http://garyentsminger.com/ecosim.htm>]. As recommended by Fayle & Manica (2010), 30 000 random matrices were simulated for each analysis to avoid type-1 errors. The randomization algorithm in ECOSIM 7 maintains fixed sums for row and column totals, so each matrix generated had the same number of species and samples as the original. Differences between simulated and observed co-occurrence patterns were tested using the Stone & Roberts (1990) *C*-score index.

RESULTS

SCOLT HEAD FAUNA

The 20 807 faunal individuals present in the standard core samples from the Scoln Head *N. noltii* beds represented 32 species, of which the microgastropod *H. ulvae* (81% of the total) and the tubificid oligochaete *Tubificoides benedii* (9%) were the two most abundant species (see Appendix). Although only two species dominated, ten (31%) had CIs ≥ 25 , and seven (22%) had CIs ≥ 40 (Appendix). Several species were rare, in the sense of occurring as singletons (four), doubletons

(four), uniques (four), or duplicates (five) (*sensu* Colwell & Coddington, 1994), but these comprised an insignificant proportion of the total faunal individuals (< 0.1%). Little regional differentiation of fauna was evident across the sampled area (Fig. 1; Table 1). The

Table 1. Ecological characteristics of the smaller surface and near-surface macrobenthos at the four *Nanozostera noltii* sites sampled on Scoln Head

Site	<i>N</i>	<i>S</i>	1- λ	<i>E</i>	<i>G</i>
South-east 1	5357	22	0.291	0.064	84.3
South-east 2	8029	25	0.195	0.050	89.6
North-west 1	6846	18	0.526	0.117	66.4
North-west 2	6040	17	0.304	0.084	83.2

All numbers are estimated from 30 core samples per site; *N*, total number of individuals in an area of 0.1 m²; *S*, total number of species; 1- λ , Simpson's index of diversity; *E*, Simpson's evenness index; *G*, percentage of the total individuals that are gastropods (> 99.6% of which were *Hydrobia ulvae*).

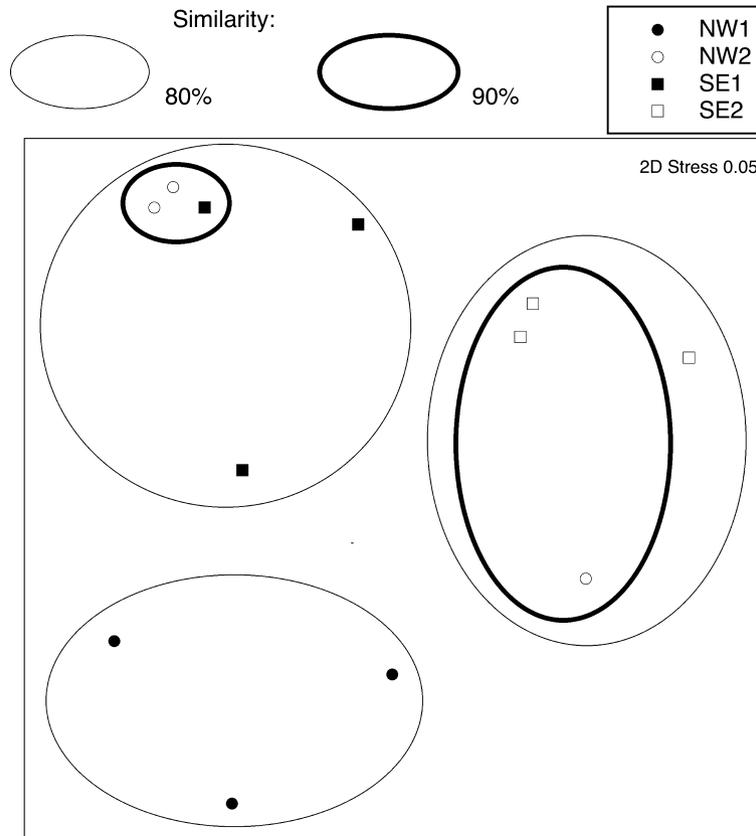


Figure 1. Non-metric multidimensional scaling plot of the superimposed group-average Bray-Curtis similarity clusters of square-root transformed abundances of the various faunal species at the 12 stations (four sites) sampled in the *Nanozostera noltii* beds on Scoln Head, UK. The 80 and 90% envelopes are Bray-Curtis similarities.

Table 2. Partitioning of variance components in the Scolt Head data at the nested levels of site (Si), station (St), and core sample (Co) using fourth-root transformed data (PERMANOVA)

Scale	d.f.	MS	Pseudo- <i>F</i>	<i>P</i>	UP	√EV	V
Lo	1	6098	0.92	0.67	3	–	–
Si	3	6458	3.62	0.003	958	12.48	27.9%
St(Si)	8	1786	4.25	0.001	998	11.69	26.2%
Co[St(Si)]	108	420				20.49	45.9%
Total	119						

The level of locality (Lo) was excluded from the final analysis, because it had no significant effect and resulted in an 'illogical' negative estimate of variance (EV) in the preliminary run; relevant data were then pooled (Underwood, 1997); MS, mean square; UP, unique permutable units; EV, estimate of variance; V, variance component as percentage of total.

two separate localities did not differ in the nature and relative abundance of their species (PERMANOVA pseudo-*F* = 0.92; *P* > 0.6); all stations had > 70% Bray–Curtis similarity, and only one of the four sites occupied its own exclusive area of Euclidean space in the nMDS plot (Fig. 1).

The partitioning of variance components (Table 2) showed that most variation occurred on the 1-m spatial scale. The six most abundant species (see Appendix) that together comprised > 97% of the individuals sampled all showed contagious distributions (χ^2 all > 300; d.f. 119; *P* < 0.01), with indices of dispersion of 2.6–23.0.

The 5-m transect in the south-eastern *Nanozostera* bed yielded an overall picture equivalent to that of the standard core samples taken in the area (see Table 1), i.e. a faunal density of 5685 0.1 m⁻² and a total of 20 species, with gastropods comprising > 80% of the total. There were no differences, however, in the Bray–Curtis similarity of faunas from cores taken 0.125, 0.25, 0.5, and 1.0 m apart (ANOVA *F*_{3,71} = 1.27; *P* = 0.3), with the mean similarities being 72–78% across all of those scales.

There were no significant correlations between the index of sedimentary fines and the density of *Hydrobia* (Spearman *R*_s = -0.15; *P* = 0.46), with densities of the other associated fauna (*R*_s = -0.30; *P* = 0.13), nor with species diversity (*R*_s = -0.19; *P* = 0.34), although the correlation with numbers of species approached significance (*R*_s = 0.37; *P* = 0.06).

COMPARISON OF SCOLT HEAD WITH LOWER LATITUDE *NANOZOSTERA* FAUNAS

The upper horizons of sheltered intertidal *Nanozostera* beds at Scolt Head, Knysna, and Moreton Bay share faunas in which microgastropods comprise ≥ 60% of macrofaunal individuals, and rissoi-deans comprise ≥ 70% of those gastropods. Never-

Table 3. Differences in ecological characteristics of the smaller surface and near-surface macrobenthos in the *Nanozostera noltii* beds of cool-temperate Scolt Head, North Sea, UK (this paper), in microgastropod-dominated areas of the warm-temperate *Nanozostera capensis* beds of the Knysna outer basin, Western Cape, South Africa (from data of Barnes, 2010b), and in equivalent areas of the subtropical *Nanozostera muelleri capricorni* beds of Moreton Bay, Queensland, Australia (from data of Barnes & Barnes, 2011)

	<i>N</i>	<i>S</i> (Chao2)	1 - λ	<i>d</i>
Scolt Head	6568	32 (33)	0.337	0.81
Knysna	2049	44 (60)	0.635	0.55
Moreton Bay	231	70 (91)	0.854	0.35

All data were obtained from the same total sample area (12 stations, each of ten standard core samples); *N*, mean numbers of individuals in an area of 0.1 m²; *S*, total number of species observed and, parenthetically, the mean Chao2 estimate of the number actually present (to nearest integer); 1 - λ, Simpson's index of diversity; *d*, Berger–Parker dominance index.

theless, they displayed marked differences in abundance, species richness, and species diversity (Table 3). A non-metric multidimensional scaling plot (Fig. 2) shows that they also differed in assemblage composition, with the Knysna sites all being located in an intermediate position between those of Scolt Head and Moreton Bay. All three regional clusters in the nMDS plot differed significantly from each other (PERMANOVA pseudo-*F* = 88.54; *P* < 0.001). The Moreton Bay stations actually showed greater similarity to the Sulawesi out-group station (although at only 18%) than they did to the other microgastropod-dominated localities (< 10%).

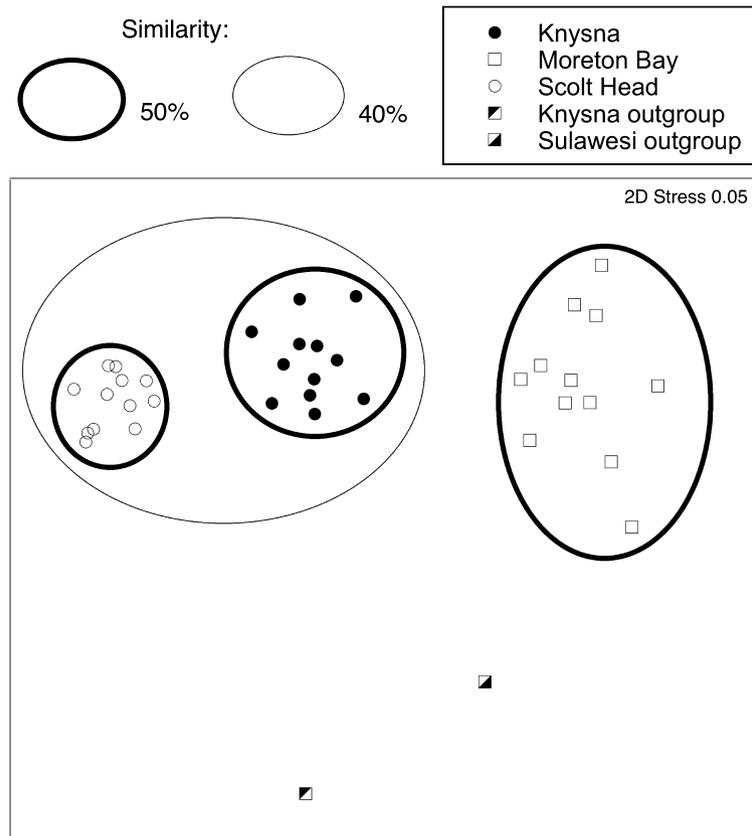


Figure 2. Non-metric multidimensional scaling plot of the superimposed group-average Bray–Curtis similarity clusters of square root transformed abundances of the various taxonomic groups comprising the faunas of microgastropod-dominated *Nanozostera* stations at each of cool-temperate Scolt Head, warm-temperate Knysna, and subtropical Moreton Bay (12 stations from each region), together with two out-group non-microgastropod-dominated stations. Sampling regimes and total areas sampled were the same at each station. The South African and Australian data are from the databases of Barnes (2010b) and Barnes & Barnes (2011); the Indonesian data are from R. S. K. Barnes (unpubl.). Stations clustered at a Bray–Curtis similarity of 50% were not significantly different at $P > 0.05$ (PERMANOVA).

Table 4. Abundance and rarity in the three intertidal *Nanozostera* systems of Table 3

	% singleton spp.	% N	% $CI \geq 25$	mean CI
Scolt Head	12.9	0.06	32.3	23.0
Knysna	27.3	0.25	15.9	14.2
Moreton Bay	33.3	6.43	7.1	9.2

Percentage of smaller surface and near-surface macrobenthic species occurring only as singletons; percentage of the total faunal numbers comprised by singleton and doubleton species; percentage of species with a constancy index (CI) ≥ 25 ; and mean species CI.

Both the faunal density and degree of dominance by a single species decreased from Scolt Head to Knysna to Moreton Bay, whereas species richness, species diversity, and the contribution of rare species to the fauna all increased in the same order (Tables 3 and 4). The cumulative relative abundance, frequency of occurrence, and species accumulation curves for the faunas of the three localities are shown in Figures 3–5. In each case the individual curves also separated such that Knysna was intermediate in character. Cores from Scolt Head succeeded in sampling most of the species likely to be present, whereas no asymptote was reached for Knysna or Moreton Bay (Fig. 3; Table 3); Scolt Head also showed the largest average frequency of occurrence and Moreton Bay the smallest (Table 4). The variability of individual core and station samples also changed in the same sequence: as predicted by Barnes & Barnes (2011), Scolt Head samples were most similar to each other,

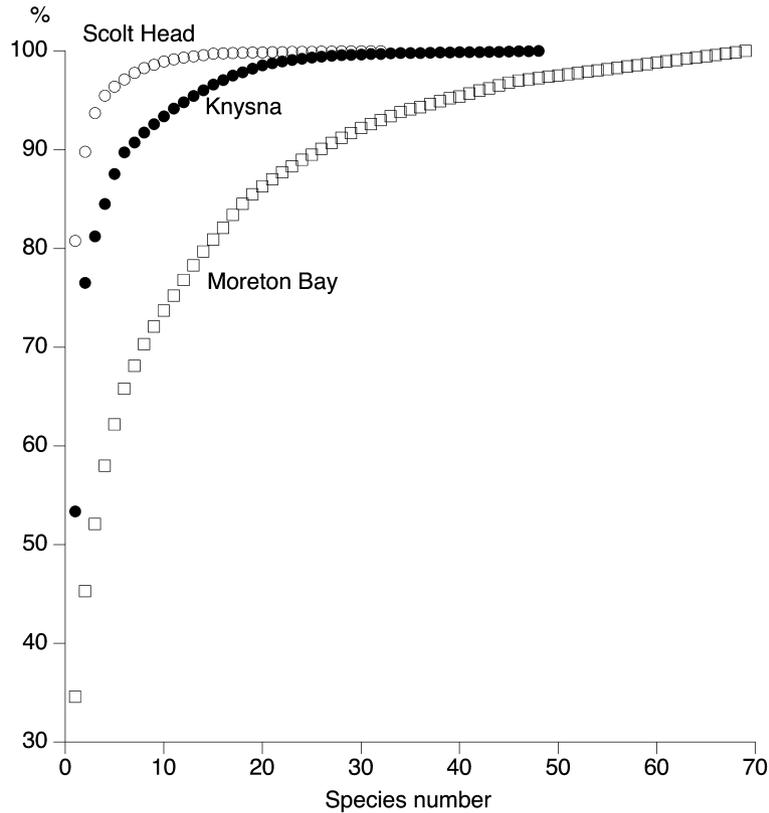


Figure 3. Cumulative logarithmic relative abundance curves of the smaller surface and near-surface macrobenthos in the *Nanozostera noltii* beds of cool-temperate Scolt Head, North Sea, UK (this paper) and in the microgastropod-dominated areas of the warm-temperate *Nanozostera capensis* beds of the Knysna outer basin, Western Cape, South Africa (data from Barnes, 2010b) and the subtropical *Nanozostera muelleri capricorni* beds of Moreton Bay, Queensland, Australia (from data of Barnes & Barnes, 2011). All data were obtained from the same total sample area.

Table 5. Percentage levels of within-group similarity (SIMPER) at the scales of (A) location (groups of 12 stations), (B) station (groups of ten cores), and (C) core sample in the three *Nanozostera* systems of Table 3

	Locations	Stations	Core samples
Scolt Head	72.3	78.5	71.4
Knysna	58.4	69.0	50.5
Moreton Bay	48.9	54.9	18.0

and those from Moreton Bay were least similar (Table 5). The probability of the Knysna site randomly being ranked in intermediate position on all of these measures is $\ll 0.05$.

In respect of the dominant microgastropod element, the population density decreased markedly, and numbers of component species and families (as accepted by the World Register of Marine Species)

increased markedly along the same sequence: Scolt Head supported four gastropod species in a total of three families at a density of > 5400 per 0.1 m^2 ; Knysna Outer Basin supported ten species representing eight families at a density of 1724 per 0.1 m^2 ; whereas Moreton Bay supported 21 species in 17 families at a density of < 140 per 0.1 m^2 .

The C scores for the observed species co-occurrence patterns, compared with random pseudo-communities simulated using null models, are shown in Table 6, together with the associated significance levels of the departures of the observed patterns from random (i.e. $C_{\text{obs}} > C_{\text{sim}}$) at each of three spatial scales in each location. No geographical trends were evident. Communities at the smallest spatial scale at both Scolt Head and Moreton Bay were randomly assembled, but their assemblages became progressively more non-random at greater spatial scales, to become significantly deterministic at the largest scale investigated at each location. Those at Knysna were significantly deterministic (non-random) at all spatial scales.

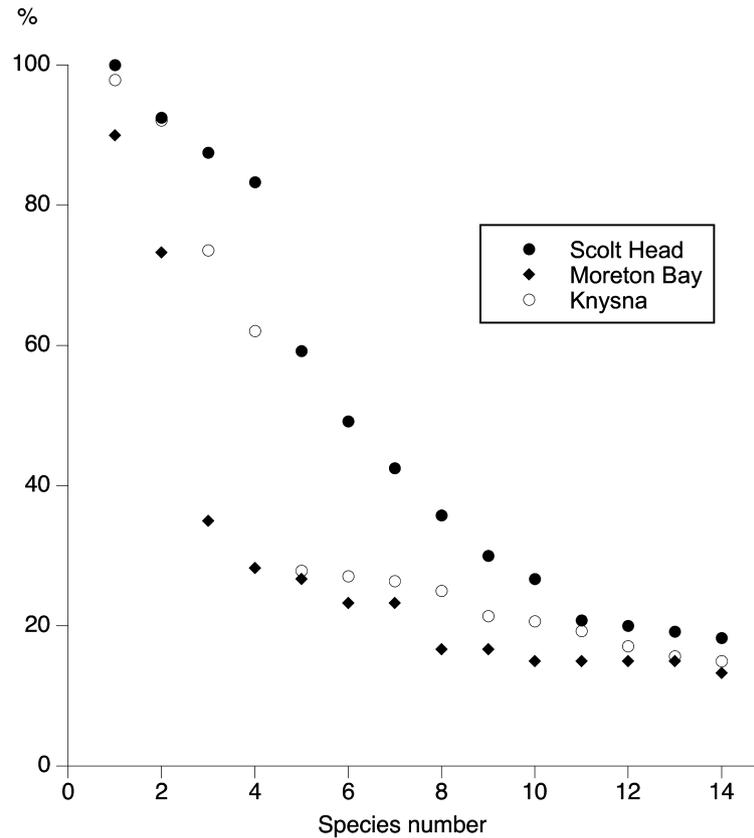


Figure 4. Frequencies of occurrence of the 15 most widespread of the smaller surface and near-surface macrobenthos in the three *Nanozostera* systems of Figure 3. All data were obtained from the same total sample area and same number of core samples, but note that at Knysna the frequencies of the two nereid polychaete species present were pooled.

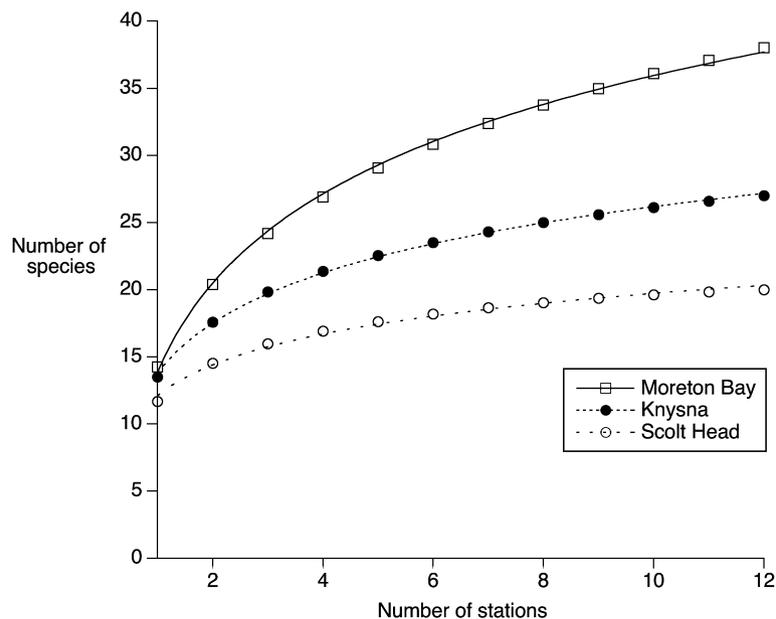


Figure 5. Species accumulation curves for the smaller surface and near-surface macrobenthos in the three *Nanozostera* systems of Figure 3. Curves are derived from the Mao τ expected richness function. All data were obtained from the same total sample area.

Table 6. Stochasticity of macrofaunal assemblage structure at three nested spatial scales in the three *Nanozostera* systems of Table 3

	Small scales (≤ 1 m)	Medium scales (60–150 m)	Large scales (0.4–4.0 km)
Scolt Head	$C_{\text{obs}} = 18.34$ $C_{\text{sim}} = 18.23$ $P = 0.62$	$C_{\text{obs}} = 14.13$ $C_{\text{sim}} = 14.23$ $P = 0.27$	$C_{\text{obs}} = 27.78$ $C_{\text{sim}} = 26.04$ $P < 0.001$
Knysna	$C_{\text{obs}} = 14.61$ $C_{\text{sim}} = 14.23$ $P = 0.01$	$C_{\text{obs}} = 11.33$ $C_{\text{sim}} = 11.12$ $P = 0.02$	$C_{\text{obs}} = 9.67$ $C_{\text{sim}} = 8.82$ $P < 0.001$
Moreton bay	$C_{\text{obs}} = 13.80$ $C_{\text{sim}} = 13.68$ $P = 0.31$	$C_{\text{obs}} = 7.81$ $C_{\text{sim}} = 7.58$ $P = 0.06$	$C_{\text{obs}} = 10.12$ $C_{\text{sim}} = 9.52$ $P < 0.001$

C scores derived from the observed pattern of species co-occurrence (C_{obs}) and the mean expected C score from randomized versions of the data (C_{sim}). Where $C_{\text{obs}} > C_{\text{sim}}$ is significant, the assemblage structure is non-random (i.e. deterministic). Each spatial scale was represented by ten randomly drawn samples. The full data sets of Barnes (2010b) and Barnes & Barnes (2011) were used for Knysna and Moreton Bay, respectively.

DISCUSSION

GEOGRAPHICAL VARIATION IN MACROFAUNAL ASSEMBLAGE CHARACTERISTICS

Both the overall abundance and the individual faunal components of the Scolt Head dwarf eelgrass system fell well within the range of the Atlantic *N. noltii* communities reviewed by Blanchet *et al.* (2004). Although not directly comparable because of differing sampling regimes and areas, macrofaunal species richness at Scolt Head was equal to the median value of the non-Mediterranean beds they reviewed, and the Scolt Head faunal density was of very similar magnitude to that recorded from Königshafen, also in the southern North Sea (55°N) (Reise, Herre & Sturm, 1994). In a number of respects the Scolt Head fauna is particularly similar to that of the group-A stations described by Blanchet *et al.* (2004) for Bassin d'Arcachon on the Atlantic coast of France. In both, the epifaunal microgastropod *H. ulvae* and, to a lesser extent, the infaunal oligochaete *T. benedii* occur at high density and overwhelmingly dominate numbers (together comprising 89% of the total macrofaunal individuals at Arcachon and 90% on Scolt Head), although many species (almost a third of those on Scolt Head) had CIs > 25. Not all species appear to be listed in the tables of Blanchet *et al.*, but their CIs were clearly high: the 32 listed group-A species had a mean CI of 66 (although no species with a CI < 26 appears in the list, so this value is probably inflated).

There were also some consistent quantitative differences: more microgastropod species were present at the French site (45°N), for example. More generally, and in respect of the type of characteristics presented in Table 3, the overall species diversity at Arcachon was 0.55 (calculated from the mean abundance data of group-A stations, with interpolation, although note that this was based on a much larger sampled area than that sampled at Scolt Head; Blanchet *et al.*, 2004: table 2), the mean faunal abundance at the microgastropod-dominated group-A stations was 24 370 m⁻², and Berger–Parker dominance for those sites was 0.59: all values are intermediate between Scolt Head and Knysna. The Scolt Head *N. noltii* faunal data presented here therefore appear to be generally representative of microgastropod-dominated assemblages associated with sheltered cool-temperate beds of this North Atlantic dwarf eelgrass, but the precise quantitative characteristics of the otherwise similar *Hydrobia*-dominated beds located some 8° south at Arcachon are intermediate between those of Scolt Head and Knysna.

One population of *N. noltii* occurs in subtropical/tropical latitudes: it dominates extensive areas of the Banc d'Arguin at 20°N in Mauritania (Honkoop *et al.*, 2008). Across the oligotrophic Banc d'Arguin as a whole, intertidal sedimentary macrofaunal biomass and density are low to very low, with the biomass being dominated by the infaunal bivalve *Anadara* [with 48% of the 17 g ash-free dry weight (AFDW) m⁻² total] and by infaunal polychaetes (with 53% of the < 150 per 0.1 m² total) (Wolff *et al.*, 1987, 1993). Gastropods and oligochaetes there contribute only 18% to the total numbers, although *H. ulvae* does comprise almost a third of the gastropods (Wolff *et al.*, 1993). The fauna is rich, however, with more than 100 species, although, as at Arcachon, a larger area was sampled to arrive at this total than on Scolt Head. Most of the Mauritanian species were also rare, with 27% occurring at < 1 m⁻² and with < 10% having a CI $\geq 10\%$. Within the Banc d'Arguin *N. noltii* beds, only the molluscan fauna has attracted specific study (Honkoop *et al.*, 2008), but only three of its 12 gastropod species occurred at a density of > 8 m⁻², and none were found at a density > 22 m⁻²: the dominant molluscs in terms of both density and biomass were all infaunal genera, in this case *Dosinia* and *Loripes*.

Comparing like with like, the basic ecological structure of the microgastropod-dominated macrofaunal assemblages associated with the higher tidal horizons of the intertidal dwarf eelgrass beds studied in the southern North Sea (53°), on the south coast of South Africa (34°), and on the eastern coast of Australia (27°) shows a consistent suite of changes, and, insofar as comparison is possible, published data on the equivalent Arcachon *N. noltii* stations (45°) are also

consonant with the same series of changes, suggesting a direct or indirect association with latitude. As latitude decreases among these regions there are decreases in the overall population density, in the degree of dominance by one or a few species, and in the mean frequency of occurrence of the component species. There are increases in species richness, species diversity, and in the numerical contribution of rare species with decreasing latitude, along with changes in the taxonomic composition of the fauna. The degree of spatial variance in faunal composition also changes along the same sequence, with samples being most uniform on Scolt Head and most variable in Moreton Bay. No such potentially latitudinal relationships are evident, however, in respect of annelid-dominated *Nanozostera* sites (cf. data in Lee, Fong & Wu, 2001; Blanchet *et al.*, 2004; Barnes, 2010b). The dominant microgastropods at Scolt Head, Arcachon, Knysna, and Moreton Bay sites are all epifaunal, whereas the bivalves and/or annelids dominating *N. noltii* beds in the Banc d'Arguin and other regions of Arcachon and Knysna, and those of *N. japonica* at Hong Kong (Lee *et al.*, 2001), are all infaunal. An influence of latitude on the shallow-water epifauna, but not on the infauna, has been suggested for at least 60 years (Thorson, 1952; Hillebrand, 2004). However, 'debate still surrounds the existence of nearshore latitudinal biodiversity trends, especially on the global scale. The reason for this is the lack of studies actually completed at the global scale' (Konar *et al.*, 2010: 33). As Konar *et al.* (2010) also state, because of time and cost constraints, such studies are not easy to achieve, and the three locations of the present study, together with a partial fourth from the literature, clearly do not comprise a large latitudinal sample. Nevertheless, the results are certainly suggestive of an influence of latitude upon the dominant smaller macrobenthos of equivalent microgastropod-dominated intertidal *Nanozostera* beds, and this effect is in greater accordance with the general expectation for this system than in infauna-dominated seagrass systems.

Not all community characteristics of these microgastropod-dominated systems varied with latitude, however. At all three locations, sample variance was greatest at the smallest spatial scales and least at the greatest spatial scales, as often appears to be the case in intertidal and shallow-water rocky marine systems (Fraschetti, Terlizzi & Benedetti-Cecchi, 2005), and community assembly patterns also varied with spatial scale but not with latitude.

SPATIAL VARIATION IN COMMUNITY ASSEMBLY PATTERNS

The relative importance of stochastic and deterministic processes in structuring the nature of seagrass

communities is also contentious: colonization, for example, shows elements of both processes (e.g. Montefalcone *et al.*, 2010), as do mortality patterns (e.g. van der Heide *et al.*, 2010). Both processes are also evident in the assemblages from Scolt Head and Moreton Bay, as both showed stochastic characteristics at small spatial scales but progressively became more deterministic at larger scales, and significantly so on the largest scale. Barnes & Barnes (2011) also drew attention to the remarkable constancy of various community parameters across large spatial scales at the Moreton Bay localities, although the individual species creating those patterns varied markedly from site to site without any clear indication of ecological replacement. Indeed, they also found that in five of the six most numerous species their dispersion pattern changed from random to non-random (clumped) with an increase in spatial scale. Why this change from random to deterministic organisation with spatial scale occurs is not self-evident, although the same phenomenon has been shown in respect of the arthropod decomposer communities of epiphytic rainforest ferns (Ellwood, Manica & Foster, 2009).

Lepori & Malmqvist (2009) argued that, in a similar manner to Connell's (1978) intermediate disturbance hypothesis, stochastically structured communities should be most evident under benign and under very disturbed conditions, and Hubbell's (2001) neutral theory predicts that communities closer in space should be more similar than those further apart (Gilbert & Lechowicz, 2004), neither of which resonate with the present situation. The latter case is the opposite of what we have found in this system, and although seagrass systems are subject to perturbations from a range of sources (e.g. Cardoso, Raffaelli & Pardal, 2007; Viaroli *et al.*, 2008; Barnes, 2010b), the systems studied here by no means appear to sit at the extremes of the perturbation spectra. Leigh (1981) suggested that stochasticity should be expected where populations occur at low density, and are therefore at risk of local extinction (which certainly applies to the Moreton Bay beds, although hardly to those on Scolt Head), and where they are dispersal limited, which is unlikely to apply to many of the seagrass macrofauna. Lepori & Malmqvist (2009), following Hanski's (1982) core and satellite hypothesis, considered that deterministic processes will dominate where the available species pool comprises two types of animal: (1) rare ones likely to be sensitive to disturbance; and (2) common, more robust species. This is probably an apt description of the seagrass faunas in question here (as well as of very many other faunas!), although – like the hypotheses outlined above – it does not seem to explain why deterministic processes only operate on large spatial scales in two of the three seagrass systems studied here, and at all scales in the seagrass

systems of Knysna. Clearly, deterministic controls are likely to select the local pool of species capable of successfully colonizing the available habitats, whereas stochastic effects will operate in the actual colonization process, as well as on a wide range of *in situ* biological interactions (Gilbert & Lechowicz, 2004; Boström, Törnroos & Bonsdorff, 2010). The specific characteristics of habitats are more likely to change as spatial scales increase – as was the case with the nature of the sediment at the Moreton Bay localities (Barnes & Barnes, 2011) and the degree of shelter at Knysna (Barnes, 2010b) – but it may well be that the explanation of the scale effect is not necessarily an ecological one at all, but a consequence of sampling processes in the context of metacommunities (Wootton, 2005).

Evolutionary and ecological constraints on the abundance, diversity, and species composition of shallow-water marine assemblages in different latitudes are poorly understood, and the role of top-down (predation) versus bottom-up (competition) controls on seagrass and intertidal flat populations are still debated (e.g. Levinton & Kelaher, 2004; Jaschinski & Sommer, 2008). Of course, top-down and bottom-up controls are not necessarily alternatives in any given system, as they may clearly vary in space and time (Fleeger *et al.*, 2008). Reise (1985), however, made a very strong case for the controlling factor in the southern North Sea being indiscriminate predation by small epibenthic species, and the juveniles of those species that use the system as nursery areas. Vermeij (1978) and Heck & Wilson (1987) have also demonstrated that the importance of predation as a structuring force is likely to increase as latitude decreases. Barnes (2010a) considered the local distribution patterns of the dominant dwarf eelgrass microgastropods to be consonant with the likely effects of predation. Although many studies have investigated top-down effects in seagrass beds (see, e.g. Jorgensen, Ibarra-Obando & Carriquiry, 2007), much remains to be clarified (Canion & Heck, 2009), and the possible roles of predators/consumers within seagrass systems as causal agents of stochasticity and determinism, and the effects of spatial scale on those roles, are largely unexplored territory, particularly in respect of intertidal species like the dwarf eelgrasses (Polte & Asmus, 2006).

Finally, Chase (2010) recently proposed an argument that causally associates latitudinal diversity gradients with stochasticity of community assembly, suggesting that increasing stochasticity correlates with increasing productivity, and that this drives increasing biodiversity. Seagrass productivity, including that of *Nanozostera* spp., increases with decreasing latitude (Duarte & Chiscano, 1999), and our evidence suggests that so does the diversity of sea-

grass macrofauna, but there is no suggestion from our data that the stochasticity of macrofaunal community assembly also increases. But then a simple relationship between latitudinal productivity patterns and ecosystem properties does seem to be a less clear-cut feature of the sea (e.g. Witman *et al.*, 2008) than on land (Harrison & Grace, 2007).

ACKNOWLEDGEMENTS

R.S.K.B. wishes to thank Michael Rooney and Natural England for the use of the facilities of the Watcher's Hut on Scolt Head Island, Jonathan Brown for boat transport to and from the island, and Morvan Barnes for analytical assistance and advice. He is also most grateful to Operation Wallacea and the Coral Reef Research Unit (University of Essex) for financial support for the trip to Laboratorium Pusat Penelitian Bawah Laut, Taman Nasional Wakatobi, Indonesia, during which the Indonesian out-group data presented in Figure 2 were collected. M.D.F.E. is grateful for the support of the University Museum of Zoology and the Department of Zoology, University of Cambridge. We thank Adrian Friday for helpfully commenting on a draft of the article.

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ARCHIVED DATA

Data deposited at Dryad: doi:10.5061/dryad.v8gg2

APPENDIX

Percentage of total individuals ($N = 20\ 807$) contributed by each species to the smaller surface and near-surface macrobenthos of the Scolt Head *Nanozostera noltii* beds, together with their constancy indices (CIs; $N = 120$ core samples). (Nomenclature after Kluijver, Ingalsuo & Bruyne, 2000 and Kluijver *et al.*, 2000).

Species	% of individuals	CI
<i>Hydrobia ulvae</i> (Prosobranchia)	80.8	100.0
<i>Tubificoides benedii</i> (Oligochaeta)	9.01	92.5
<i>Pygospio elegans</i> (Polychaeta)	3.94	83.3
<i>Abra tenuis</i> (Bivalvia)	1.76	87.5
<i>Fabricia stellaris</i> (Polychaeta)	0.88	30.0
<i>Carcinus maenas</i> (Decapoda)	0.74	59.2
? <i>Tubifex costatus</i> (Oligochaeta)	0.68	49.2
<i>Ampharete acutifrons</i> (Polychaeta)	0.47	26.7
<i>Cerastoderma edule</i> (Bivalvia)	0.35	35.8
<i>Macoma balthica</i> (Bivalvia)	0.34	42.5
<i>Aphelochaeta marioni</i> (Polychaeta)	0.22	10.8

APPENDIX *Continued*

Species	% of individuals	CI
<i>Littorina saxatilis</i> (Prosobranchia)	0.16	20.8
<i>Hediste diversicolor</i> (Polychaeta)	0.14	18.3
<i>Scrobicularia plana</i> (Bivalvia)	0.13	20.0
<i>Eteone longa</i> (Polychaeta)	0.13	19.2
<i>Notomastus latericeus</i> (Polychaeta)	0.04	7.5
<i>Heteromastus filiformis</i> (Polychaeta)	0.03	5.0
<i>Retusa obtusa</i> (Opisthobranchia)	0.02	3.3
<i>Crangon crangon</i> (Decapoda)	0.02	3.3
<i>Littorina littorea</i> (Prosobranchia)	0.02	3.3
<i>Malacoceros fuliginosus</i> (Polychaeta)	0.01	2.5
Dolichopodid sp. (larva) (Diptera)	0.01	2.5
<i>Phyllodoce mucosa</i> (Polychaeta)	0.01	2.5
<i>Gammarus locusta</i> (Amphipoda)	0.01	1.7
<i>Lineus ruber</i> (Nemertea)	0.01	1.7
<i>Nephtys hombergi</i> (Polychaeta)	0.01	1.7
Chironomid sp. (larva) (Diptera)	0.01	1.7
Tipulid sp. (larva) (Diptera)	0.01	1.7
<i>Sphaerodoropsis minutum</i> (Polychaeta)	< 0.01	0.8
<i>Arenicola marina</i> (Polychaeta)	< 0.01	0.8
<i>Polydora cornuta</i> (Polychaeta)	< 0.01	0.8
<i>Manayunkia aestuarina</i> (Polychaeta)	< 0.01	0.8

In addition, a singleton *Cephalothrix rufifrons* (Nemertea), not recorded in the standard samples, was present in the additional core sample series.