

Regional and latitudinal variation in the diversity, dominance and abundance of microphagous microgastropods and other benthos in intertidal beds of dwarf eelgrass, *Nanozostera* spp.

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Abstract The smaller macroscopic members of the epifauna and shallowly-burrowing infauna of comparable intertidal beds of dwarf eelgrass and associated areas of non-vegetated sediment were investigated with uniform methodology in the cool-temperate English southern North Sea (*Nanozostera noltii*), warm-temperate southern coast of the Western Cape, South Africa (*N. capensis*) and in subtropical southern Queensland, Australia (*N. muelleri capricorni*), together with equivalent seagrass sites in tropical Sulawesi, Indonesia, and Seychelles, Western Indian Ocean. Epifaunal microphagous microgastropods dominated both the eelgrass and non-vegetated cool- and warm-temperate sites with >80% of macrofaunal individuals, but decreased markedly in density and dominance with decreasing latitude, down to near zero in the tropics; microgastropod species diversity in the *Nanozostera* increased with decreasing latitude, whilst their species richness per core sample was highest in the warm temperate zone. Other co-existing—largely infaunal—taxa (mainly annelid worms, bivalve molluscs and crabs), however, showed less marked latitudinal variation in density and no relationship of taxon diversity with latitude. With few exceptional cases, microgastropod density, dominance, species richness and diversity were greater in the eelgrass beds than in adjacent non-vegetated sediments, as were the densities and taxon diversities of the associated faunal groups, although within the beds themselves there were no significant correlations between seagrass density and the density or diversity of either the microgastropods or their associated fauna. The extent to which the presence or absence of seagrass influenced the underlying community

composition of the benthic fauna varied between localities. These results are consonant with an increasing effect of predation in low latitudes on small epifauna.

Keywords Gastropoda · Latitudinal gradients · Littoral ecology · Seagrass · Zoobenthos

Introduction

Seagrass beds support an abundant and relatively well-known macrofauna, the density and diversity of which often exceed those present in adjacent areas of non-vegetated sediment (Edgar et al. 1994; Lee et al. 2001; Blanchet et al. 2004; Klumpp and Kwak 2005; Boström et al. 2006; etc.). Mega- and macrofauna range in size from dugong (de Iongh et al. 2007) and green turtles (Aragones and Marsh 2000) to the meiofaunal size boundary (de Troch et al. 2006). Most studied are the nektonic fish and prawn species that use seagrass beds as nursery areas (Tomascik et al. 1997; Hemminga and Duarte 2000; Skilleter et al. 2005a), but prominent amongst the other taxa present, living on the seagrass leaves or on or in the underlying sediment, are benthic molluscs (e.g. Honkoop et al. 2008), amphipod, isopod and brachyuran crustaceans (e.g. Glancy et al. 2003; Orth et al. 2007) and oligochaete and polychaete annelids (e.g. Blanchet et al. 2004; Klumpp and Kwak 2005).

Most research on the gastropod molluscan fauna has been devoted to the commercially valuable conchs (see e.g. NOAA Fisheries 2008) and other large species, but it is now known that macroscopic species are often the tip of the iceberg in intertidal and subtidal aquatic gastropod communities: epifaunal microgastropods (less than, and often much less than, 10 mm in shell height) may be much more abundant and much more diverse than their more obvious

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larger relatives (Bouchet et al. 2002; Strong et al. 2008; Hickman 2008; Geiger and Ruthensteiner 2008), and such largely mesograzers species can have an important ecological impact (Klumpp et al. 1992; Philippart 1995; Fong et al. 2000; Jaschinski and Sommer 2008). In the past, however, judging from their fauna lists, most ecological surveys of seagrass beds have completely ignored this size category, with the notable exception of the northern Atlantic and its associated semi-enclosed seas in which the seagrass beds and soft sediments are clearly dominated by relatively large hydrobiid microgastropods (Muus 1967; Asmus and Asmus 1985; Boström and Bonsdorff 1997; Barnes and de Villiers 2000).

This paper describes an assessment of the extent to which freely-mobile microphagous microgastropods dominate the numbers and diversity of the smaller seagrass-associated benthic animals in four of the regional seagrass floras recognised by Hemminga and Duarte (2000): the North Atlantic, South Atlantic, South Australian, and Indo-Pacific. Seagrasses vary considerably in their size and habitat (Phillips and Meñez 1988; Waycott et al. 2004), and clearly, to have any value, like must be compared with like. The seagrass species sampled in this study were therefore ecologically equivalent and systematically closely related. In all but the two Indo-Pacific sites, the beds investigated were those dominated by geographically replacing species of the dwarf eelgrass *Nanozostera*¹ that occur on intertidal flats of fine sand with admixed silt in sheltered bays and estuaries. There they form dense, largely monospecific beds extending up over the upper shore to (and occasionally beyond) the extreme low high-water neap tidal interface with salt marsh or mangrove dependent on latitude. The Indo-Pacific seagrass sites did not support *Nanozostera*, as the bipolar Zosteraceae is absent from most of the tropics (see Tanaka et al. 2003), but they did contain at least semi-equivalent seagrasses.

The certainties of 50 years ago of the manner in which benthic marine densities and diversities vary across the globe (Thorson 1957) have largely disappeared, to be replaced by considerable contention (Clarke 1992; Clarke and Crame 1997; Gray 2002; Willig et al. 2003). The latitudinal range covered by this study, as augmented by the Indo-Pacific localities, therefore presented the opportunity to explore the contribution of seagrass microgastropods and other equivalently sized organisms to generalities on the effect of distance from the equator on the point diversity, density and degree of dominance of various elements of the shallow-water zoobenthos.

Methods

Three areas of *Nanozostera*-covered intertidal flat, each within an important regional concentration of the species concerned, were sampled:

1. Monospecific *Nanozostera noltii* (= *nana*) beds fronting saltmarsh within the shelter of the north Norfolk barrier-island chain on the cool-temperate coast of the southwestern North Sea, United Kingdom (see Bridges 1998), where the biology of microgastropods has been studied for a number of years in a system otherwise largely structured by the polychaete *Arenicola marina* (Serventy et al. 1960; Barnes and de Villiers 2000; and see Philippart 1994). The East Anglian + Thames Estuary region of England contains one of the largest continuous areas of *N. noltii* in Europe (Berry 2009).
2. Effectively monospecific *N. capensis* beds (though with some *Halophila ovalis*) fronting saltmarsh along the eastern shore of the marine outer basin (sensu Largier et al. 2000) of the warm-temperate Knysna estuarine system (the 'Knysna Lagoon'), Western Cape, South Africa, where salinities rarely fall below 30 (Allanson et al. 2000). The Knysna system contains half of South Africa's total seagrass area (Maree 2000; Bandeira and Gell 2003) and its flats are otherwise dominated by the decapods *Callinassa kraussi* and *Upogebia africana* (de Villiers et al. 1999; Allanson et al. 2000; and see Siebert and Branch 2006).
3. *N. muelleri capricorni* beds, with some *Halophila ovalis* and *Halodule uninervis*, fronting *Avicennia* and *Rhizophora* mangrove along the sheltered north-western shore of North Stradbroke Island in the subtropical marine Moreton Bay, Queensland, Australia, which contains almost 90% of southern Queensland's seagrass (Davie 1998; Coles et al. 2003). Here *N. m. capricorni* occurs on intertidal flats otherwise engineered by the decapods *Callinassa australiensis* (Skilleter et al. 2005b; Berkenbusch and Rowden 2007), *Mictyris longicarpus* and, to a lesser extent, *Macrophthalmus crassipes* (Stephenson 1961; Davie 1998). [Most recent literature has followed Les et al. (2002) in regarding *N. capricorni* and the cool-temperate *N. muelleri* (and two other Australasian species) as being conspecific, and has followed Jacobs et al. (2006) in granting priority to the name *muelleri*, but this synonymy is not accepted by all (see den Hartog and Kuo 2006).]

In Atlantic Europe, though not in associated enclosed seas and lagoons, *Nanozostera noltii* is a thoroughly intertidal eelgrass (den Hartog 1970), whilst *N. capensis* and *N. m. capricorni* both occur intertidally in the form of specific, shorter-, finer- and often darker-leaved varieties

¹ *sensu* Tomlinson and Posluszny (2001), though see den Hartog and Kuo (2006); dwarf eelgrasses are the *Zostera*, subgenus *Zosterella*, of various other authors

with many shoots per unit area (Phillips and Meñez 1988; Coles et al. 2003; Waycott et al. 2004).

The two tropical, Indo-Pacific, non-*Nanozostera* seagrass sites sampled were:

1. A *Halophila ovalis* and *Cymodocea rotundata* bed sampled in July/August 2008 in the Tukangbesi Islands, Sulawesi Tenggara, Indonesia
2. a *Halophila ovalis* bed, backed by *Thalassia hemprichii*, sampled in January 2009 on the island of Curieuse, Seychelles

In higher latitudes, *H. ovalis* (dugong grass) often occurs in the same high-level intertidal beds as *N. capensis* and *N. muelleri* (Young and Wadley 1979; Phillips 1999; and above) and hence to some extent can be considered to indicate comparable ecological conditions, although the tidal height of both the Indonesian and Seychellois seagrass beds sampled were somewhat lower than those of *Nanozostera*, being located at the extreme landwards margin of the reef flats where they interfaced with the base of the steeply sloping, sandy beaches. *C. rotundata*, at least, has confusingly similar leaves to those of fine-leaved *Nanozostera* (Beentje 1999) and is at least in that respect equivalent. The tropical sites also differed from the *Nanozostera* ones in containing carbonaceous rather than siliceous sediments, as is often the case in low latitudes (Alongi 1990).

At each locality, samples were taken within the landwards section of the *Nanozostera* bed according to the following protocol. At each station, 20 core samples of 60-mm diameter were taken 1 m apart from each other to a depth of 50 mm, ten in the seagrass bed itself and ten in immediately adjacent areas of bare sediment; earlier preliminary studies in Norfolk and Knysna having indicated that (1) ten cores of that diameter would yield an Index of Precision of <10% in estimation of the mean numbers of both microgastropods and total fauna, well within the 20% value regarded by Elliott (1977) as being “a reasonable error in most bottom samples”, and (2) each core sample could be expected to contain up to 200 faunal individuals. Three such stations at least 100 m apart were worked at each site, and, except in the Indo-Pacific region, two sites at least 1 km apart were sampled at each locality (see Table 1). The data from each of the major localities were therefore obtained from 120 individual core samples, those from Scolt Head Island and both South African sites during the local autumn (September 2008 and February/March 2009 respectively) and those from Wells-next-the-Sea and the Queensland sites during the local spring (May 2009 and October/November 2008 respectively). The Indonesian and Seychellois localities were each represented by only one site (Table 1), and therefore by 60 core samples.

Each core sample was gently sieved through 710- μ m mesh (a procedure that removed all sand grains), and was

Table 1 Location of the seagrass beds sampled

SOUTHERN NORTH SEA (NORFOLK), UK	
Cockle Bight, Scolt Head Island	N 52° 59'; E 00° 41'
Harbour Entrance, Wells-next-the-Sea	N 52° 58'; E 00° 52'
KNYSNA LAGOON, WESTERN CAPE, SOUTH AFRICA	
Rexford/Hunters Home Marshes	S 34° 03'; E 23° 04'
Leisure Isle East	S 34° 04'; E 23° 04'
MORETON BAY, QUEENSLAND, AUSTRALIA	
Dunwich, North Stradbroke Island	S 27° 30'; E 153° 24'
Myora Springs, North Stradbroke Island	S 27° 28'; E 153° 25'
PULAU HOGA, SULAWESI TENGGARA, INDONESIA	
Panti Kamboa	S 05° 28'; E 123° 46'
CURIEUSE, SEYCHELLES	
Baie Laraie	S 04° 17'; E 55° 44'

transported alive to a field laboratory where the number of seagrass shoots was counted and the living fauna was extracted by eye against a white background, all seagrass shoots being shaken vigorously to dislodge any attached animals. Extraction continued until no further living animal could be seen after a 3-min search. A rough field estimate of the siltiness of the muddy sand sediment within each station was obtained volumetrically (Briggs 1977): a 50-mm deep, 30-mm diameter sediment core was placed in a 0.25-m \times 30-mm glass measuring cylinder after removal of any seagrass rhizomes etc., local rain or tap water was added to fill the cylinder, and the system shaken until the sediment was thoroughly suspended. It was then allowed to stand for 2 h, after which time the proportion of fine particles (2–63 μ m) was determined.

All microgastropods were identified to species, where ‘microgastropod’ was taken to include all small (<10 mm in largest dimension) deposit-feeding or algal/seagrass-grazing species, together with the juveniles of larger microphagous species within the same size range. Sedentary limpet-like species, such as *Siphonaria compressa*, known to occur at one of the localities were never encountered, and being firmly attached to the seagrass leaves would have required special techniques to be included in the samples (Allanson and Herbert 2005). Most such species were members of the superfamilies Cerithioidea and Rissosoidea, but the muricoid *Nassarius* was included because, although the genus is mainly carrion-feeding, some (e.g. the South African *N. kraussianus*, feed on detritus (Branch and Branch 1981), and the cerithioid turritellids were also included because, although essentially suspension feeders, they probably also deposit feed (Allmon 1988). Predatory or ectoparasitic gastropods in the same size range were considered separately, and other faunal elements were assigned to one of the following eight categories: bivalve mollusc, amphipod crustacean, isopod + tanaid crustacean,

anomuran + brachyuran crustacean, errant polychaete, sedentary polychaete, oligochaete, and ‘others’ (which included the occasional polyclad flatworm, ophiuroid or asteroid echinoderm, nemertine, sipunculan, chironomid or tipulid insect larva, juvenile stomatopod or alpheid crustacean, etc.). Sessile animals attached to the seagrass leaves were not included in the survey.

Diversity, both of the microgastropods and of the faunal categories (i.e. the nine above plus the microgastropod one—termed ‘taxon diversity’ below), was assessed using Simpson’s index of diversity: $1-\lambda$, where $\lambda = \sum p_i^2$ and p_i is the decimal proportion of the total individuals comprised by the i th species or taxon. Potential area-dependent effects on diversity (Rosenzweig 1995) were avoided because exactly the same area was sampled at all stations. Multivariate statistics [ordination by non-metric multidimensional scaling, hierarchical clustering analysis using Bray-Curtis similarity, analysis of similarities (ANOSIM), similarity percentage analysis (SIMPER), and similarity profiling (SIMPROF)] were carried out using PRIMER (Plymouth Routines in Multivariate Ecological Research version 6); other statistical analysis was via StatPlus: mac 2008 or 2009.

Results

Non-metric multidimensional scaling of the superimposed significantly different group-average Bray-Curtis clusters (derived from similarity analysis of the faunal composition data from all individual stations after 4th root transformation) showed that stations within each locality occupy discrete and exclusive areas of Euclidean space (Fig. 1). The cool-temperate North Sea, and tropical Seychellois and Indonesian stations each form single clusters regardless of whether individual stations were from seagrass beds or from adjacent non-vegetated sediment; at these sites geography clearly has a more important effect on taxonomic composition of the fauna than the presence or absence of vegetation cover. In contrast, the warm-temperate South African and subtropical Queensland stations formed a system of adjacent clusters with patterns of similarity that were, to a large extent, based on the presence or absence of seagrass, as previously found for another temperate South African site by Siebert and Branch (2007). Four such adjacent clusters of significantly similar stations occur at a mean similarity of >75%; three of them being themselves grouped (though at $P > 0.05$) at a mean similarity of >60%. The three grouped clusters are (1) the South African bare sediment stations, (2) the South African *Nanozostera* stations, and (3) the Queensland *Nanozostera* stations together with one Queensland bare sediment station; whilst the fourth, relatively isolated cluster contains the remaining five Queensland bare sediment stations. This is partly a result

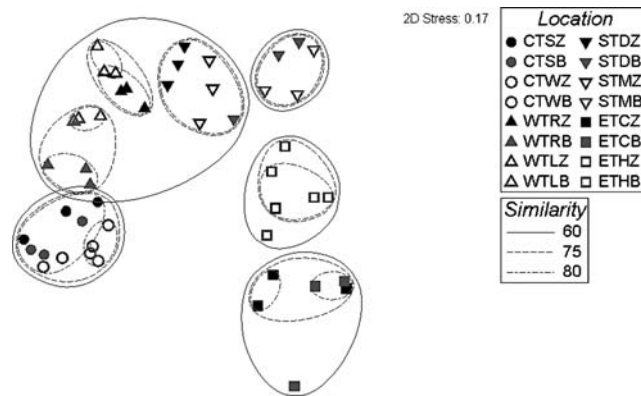


Fig. 1 Non-metric multidimensional scaling of the superimposed group-average Bray-Curtis clusters obtained after 4th root transformation of data on the abundance of different taxa in the faunas of all stations sampled (i.e. numbers of individuals in each of the ten taxonomic categories of the text). All stations clustered at a similarity of >75% are significantly similar at $P < 0.05$ (SIMPROF). In the station codes, the *first two letters* indicate region (CT cool temperate, WT warm temperate, ST subtropical, ET equatorial tropical), the *third letter* indicates regional site (S Scolt Head, W Wells, R Rexford, L Leisure Isle, D Dunwich, M Myora Springs, C Curieuse, H Pulau Hoga) and the *final letter* whether with (Z) or without (B) seagrass cover; each site is represented by three replicate stations

of the 4th root transformation strongly down-playing the significance of the microgastropod component which numerically dominates the South African sites but is much less important at the Queensland ones; one-way ANOSIM indicates that the faunal composition of the South African and Queensland sites did differ at $P < 0.001$ (and see Tables 2, 3).

Microgastropods dominated the seagrass faunas of four sites; they were a significant component of those of a further two, and were effectively absent from the remaining two, which were largely polychaete dominated (Table 2). The same situation applied to the adjacent areas of non-vegetated sediment at those sites (Table 3). SIMPER showed that over 40% of the similarity of stations within each of the North Sea and South African sites was attributable to their microgastropod faunas; over 75% of the similarity of stations within the tropical sites was due to polychaetes; whilst similarity within the Queensland sites was largely due to the sedentary polychaete (22%) and microgastropod (21%) components. Dissimilarity of the cool- and warm-temperate clusters was mostly attributable to the oligochaete fauna of the former (22%) and the isopod + tanaid (13%) component at the latter.

Regional patterns of microgastropod abundance and dominance at all 24 seagrass and non-vegetated stations are shown in Figs. 2 and 3: there are marked regional differences (Kruskal-Wallis ANOVA $H^* > 18$; $P < 0.0005$) and significant correlations between latitude and both their density per unit area and their relative importance in the fauna (Spearman Rank $r_s > 0.8$; $P < 0.0001$), abundance and dominance decreasing towards the equator. The equivalent position in respect of the density of the associated faunal

Table 2 Decimal proportions of the total faunal individuals of different taxa in the sampled seagrass beds

	UK		WESTERN CAPE		QUEENSLAND		SULAWESI	SEYCHELLES
	Scolt	Wells	Rexford	Leisure	Dunwich	Myora	Hoga	Curieuse
Microgastropods	0.85	0.84	0.93	0.90	0.33	0.35	0.02	<0.01
Oligochaetes	0.09	0.04	0	0	0	0	0	0
Sedentary polychaetes	0.04	0.10	0.01	0.02	0.27	0.21	0.59	0.92
Bivalves	0.01	0.02	<0.01	<0.01	0.03	0.03	0.21	0
Anomurans & brachyurans	0.01	0	0.01	0.01	0.18	0.20	0.05	<0.01
Errant polychaetes	<0.01	<0.01	<0.01	0.01	0.03	0.03	0.07	0.06
Predatory gastropods	<0.01	<0.01	0.01	<0.01	0.01	0.02	0.04	0
Amphipods	0	0	0.02	<0.01	0.08	0.09	0.01	0
Isopods & tanaids	0	0	<0.01	0.03	0.05	0.02	0	0
Others	<0.01	0	<0.01	0.01	0.01	0.05	0.02	0.01

taxa is displayed in Fig. 4; here there was also significant regional differentiation (Kruskal-Wallis ANOVA $H^* > 10$; $P < 0.02$), consequent on the richer cool-temperate seagrass stations and on the richer temperate non-vegetated sites. The correlation with latitude, however, was much less marked, especially in the seagrass beds, although still significant (Spearman Rank $r_s = 0.5$; $P = 0.02$). Within the seagrass beds there were no significant correlations between ambient density of seagrass shoots and the density or diversity of the fauna, neither of microgastropods nor of the other associated species (Spearman Rank $r_s < 0.3$; $P > 0.1$), as found by a number of other studies (Orth et al. 1984; Attrill et al. 2000; etc.). There was also no significant correlation between the abundance of microgastropods and the volumetric proportion of silt in the sediment, neither within the *Nanozostera* beds (Spearman Rank $r_s < 0.5$, $P > 0.05$) nor in the associated bare sediment ($r_s < 0.4$, $P > 0.15$). As might be expected, in almost all cases the *Nanozostera*-associated sediments contained more silt than the adjacent non-vegetated sands (Wilcoxon matched-pairs signed-ranks $z = 3.0$; $P < 0.003$).

It is also evident from Figs. 2 and 4 that, except in South Africa, the abundances of both microgastropods and their associated fauna were greater in the seagrass beds than within adjacent areas of bare sediment (Wilcoxon matched-pairs signed-ranks $z > 3.2$; $P < 0.001$). The non-conforming South African stations, however, do appear to be special cases. At two of the Rexford stations, there appeared to have been a large recent spatfall of the microgastropod *Rissoa capensis*² on the non-vegetated sediment, in that ca. 1-mm-long juvenile snails were there at some 2.5-times their density within the *Nanozostera capensis* bed. Further, at all three Rexford stations the densities of infaunal

polychaete worms were much larger in the bare sediment than within the eelgrass; and the same was true in respect of the polychaete *Ceratonereis* and the burrowing tanaid *Anatanais* at the Leisure Isle site stations, both being three-times more abundant in the non-vegetated areas.

Up to eight microgastropod species occurred per site, their species richness and species diversity within the *Nanozostera* beds varying regionally (Kruskal-Wallis ANOVA $H^* > 11$; $P < 0.005$) and increasing with decreasing latitude (Fig. 5) (Spearman Rank $r_s > 0.8$; $P < 0.001$). Both microgastropod species richness and diversity were larger within the *Nanozostera* than in the adjacent bare sediment (Wilcoxon Matched-pairs Signed-ranks $z > 2.5$; $P < 0.01$). Although in total number of species the Queensland *N. m. capricorni* microgastropod fauna was equivalent to that in the South African *N. capensis* beds, with eight species and seven respectively, the mean number of species per core (Fig. 6) was greater in the South African warm-temperate sites (Mann-Whitney $U = 25$, $P = 0.009$) and the same was also true of areas of non-vegetated sediment (Mann-Whitney $U = 25$, $P = 0.009$). Several microgastropod species per core was the norm at all *N. capensis* and *N. m. capricorni* stations, but only one species or at most two were abundant, the others being rare (Fig. 7). Only at the Leisure Isle site at Knysna were two species (*Hydrobia knysnaensis* and *Rissoa capensis*) co-dominant. A systematic list of the 19 microgastropod species present in the *Nanozostera* is provided in the Appendix. The tropical non-*Nanozostera* seagrass beds, however, were effectively devoid of microgastropods. In addition, at both Knysna sites the sole species in the predatory/parasitic gastropod category was also in the microgastropod size range (an unidentified ectoparasitic pyramidellid) which occurred at densities of up to $32 \times 0.1 \text{ m}^{-2}$.

Regional variation in taxon diversity of the associated fauna within the seagrass and non-vegetated habitats is shown in Fig. 8. With the exception of the Seychelles site,

² Although described as such, this gastropod is clearly not a species of *Rissoa* nor indeed even a member of the Rissoidae, but its true affinities within the Rissooidea are currently uncertain—see “Appendix”.

Table 3 Decimal proportions of the total faunal individuals of different taxa in the sampled non-vegetated sediments immediately adjacent to the seagrass beds

	UK		WESTERN CAPE		QUEENSLAND		SULAWESI	SEYCHELLES
	Scott	Wells	Rexford	Leisure	Dunwich	Myora	Hoga	Curieuse
Microgastropods	0.84	0.85	0.90	0.71	0.21	0.37	<0.01	0
Oligochaetes	0.10	0.03	0	0	0	0	0	0
Sedentary polychaetes	0.03	0.10	0.05	0.05	0.41	0.22	0.75	0.91
Bivalves	0.02	0.02	<0.01	<0.01	0.09	0.19	0.13	0
Anomurans & brachyurans	<0.01	0	<0.01	<0.01	0.02	0	0	0.02
Errant polychaetes	<0.01	<0.01	0.04	0.06	0.02	0.04	0.09	0.05
Predatory gastropods	0	0	<0.01	<0.01	0.03	0	0.01	0
Amphipods	0	0	0	0	0.10	0.12	0	0
Isopods & tanaids	0	0	0	0.17	0	0	0	0
Others	<0.01	<0.01	0	0	0.12	0.05	0.01	0.02

where polychaetes comprised 98% of all fauna in the seagrass and 96% in non-vegetated sediment (Tables 2 and 3), taxon diversity although showing regional variation (Kruskal-Wallis ANOVA $H^* > 13$; $P < 0.005$) showed no significant correlation with latitude (Spearman Rank $r_s < 0.3$; $P > 0.2$). At a given station taxon diversity of the associated fauna was generally greater in the seagrass beds than in adjacent bare sediment (Wilcoxon matched-pairs signed-ranks $z = 2.3$; $P = 0.02$).

These results then indicate that: (1) the cool temperate Norfolk *N. noltii* sites and the warm temperate Knysna *N. capensis* ones were very similar in microgastropod density and dominance, and the two temperate sites then differed

markedly from the lower latitude, subtropical *N. m. capricorni* beds in which microgastropods were a less significant component of the overall fauna, and where their densities were considerably lower; (2) in the two tropical seagrass sites, abundances and dominance of microgastropods were the lowest of all; and (3) in contrast, densities and taxon diversity of the non-microgastropod fauna were more uniform across all the sampled stations. The two temperate sites did differ, however, in respect of microgastropod species richness and diversity, the warm-temperate ones showing increases in both these measures over the cool-temperate values, so that within the different regional *Nanozostera* beds microgastro-

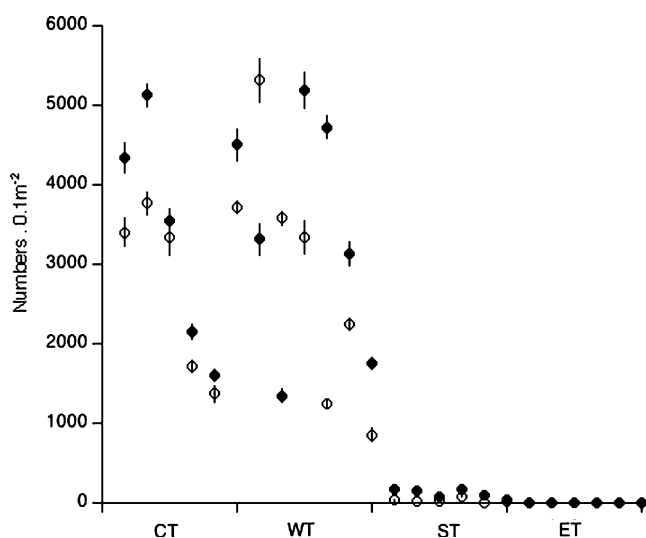


Fig. 2 Variation in mean abundance of microgastropods per core (1) in seagrass beds (*solid circles*) and (2) in adjacent areas of non-vegetated sediment (*open circles*) at the 24 stations in the four climatic zones sampled, arranged according to latitude. Numbers expressed per 0.1 m²; *error bars* standard errors; *CT* cool temperate, *WT* warm temperate, *ST* subtropical, *ET* equatorial tropical

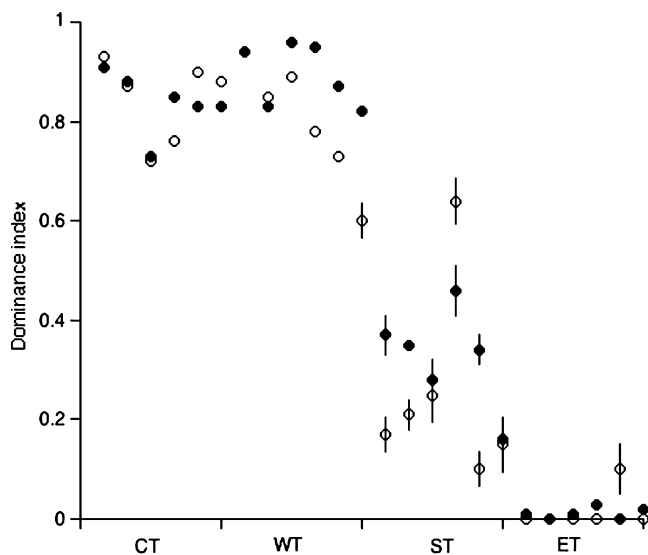


Fig. 3 Variation in the mean dominance of microgastropods per core (1) in seagrass beds (*solid circles*) and (2) in adjacent areas of non-vegetated sediment (*open circles*) at the 24 stations in the four climatic zones sampled, arranged according to latitude. Dominance measured as decimal proportion of total faunal individuals present; only standard errors > 0.05 shown; abbreviations as in Fig. 2

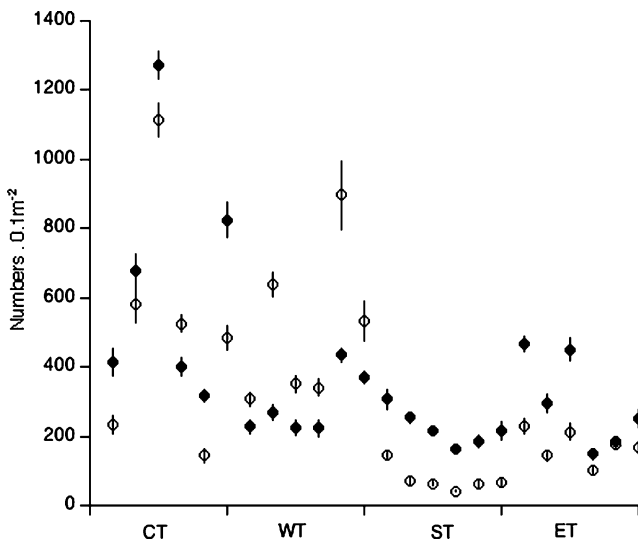


Fig. 4 Variation in mean number per core of faunal elements other than microgastropods present (1) in seagrass beds (*solid circles*) and (2) in adjacent areas of non-vegetated sediment (*open circles*) at the 24 stations in the four climatic zones sampled, arranged according to latitude. Numbers expressed per 0.1 m²; *error bars* standard errors; abbreviations as in Fig. 2

pod species richness and diversity were high in both the warm temperate and subtropical zones.

Discussion

Although latitudinal gradients in various aspects of marine ecology have received much attention, including those

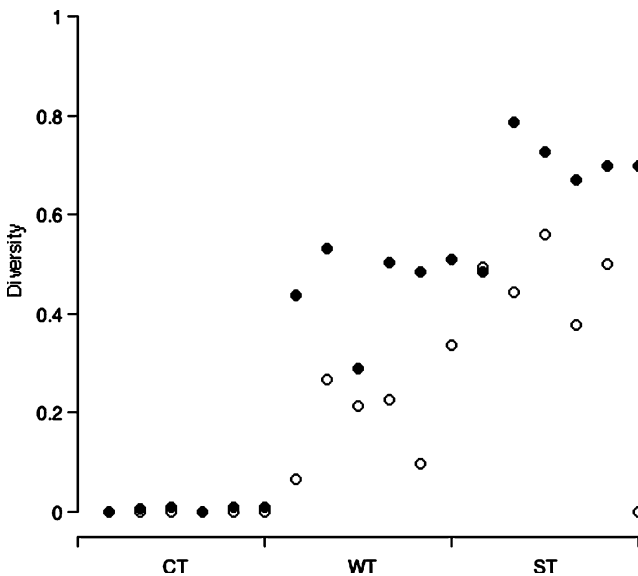


Fig. 5 Variation in species diversity of microgastropods per station (1) in beds of *Nanozostera* species (*solid circles*) and (2) in adjacent areas of non-vegetated sediment (*open circles*), arranged according to latitude. Abbreviations as in Fig. 2

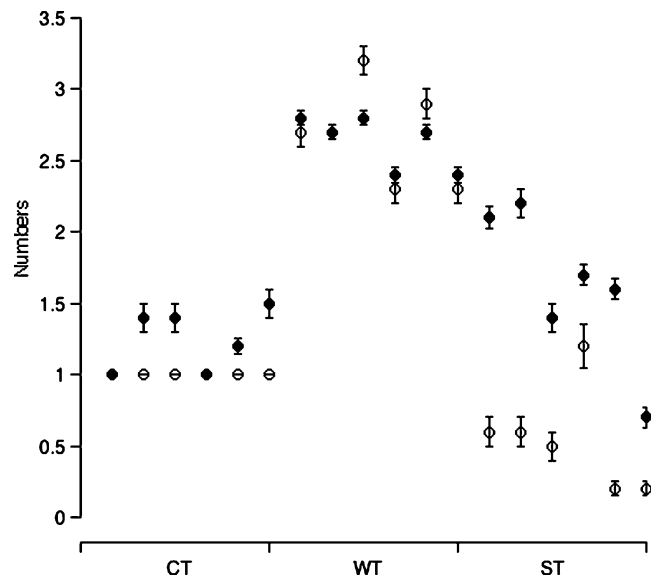


Fig. 6 Variation in the mean number of microgastropod species per core sample (1) in beds of *Nanozostera* species (*solid circles*) and (2) in adjacent areas of non-vegetated sediment (*open circles*), arranged according to latitude. *Error bars* standard errors; abbreviations as in Fig. 2

demonstrated by gastropod molluscs (Roy et al. 1998), little of this has been paid to the macrobenthos of sheltered marine soft sediments, let alone to the smaller members of that fauna, and little has extended beyond a single ocean basin. Such analysis as has been carried out has mainly been achieved by compilation of published information on

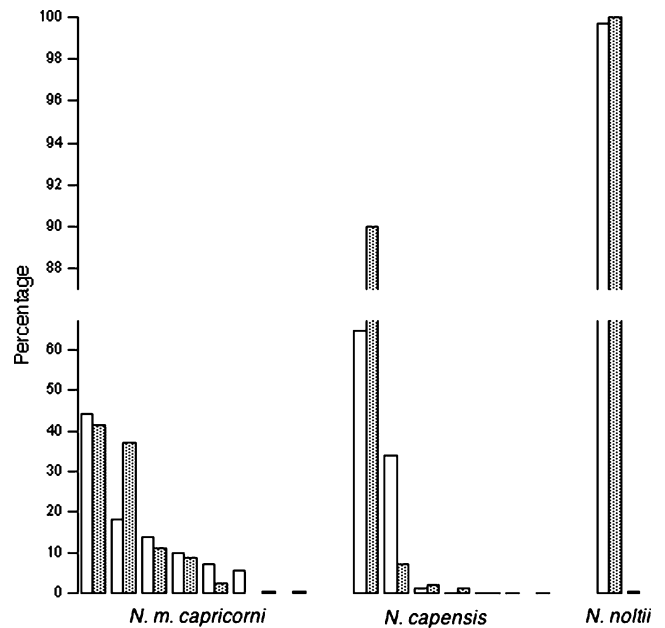


Fig. 7 Proportion (percentage) of the total individuals in each component species of the various microgastropod faunas associated with beds of different regional *Nanozostera* species (*open columns*) and with adjacent areas of non-vegetated sediment (*stippled columns*)

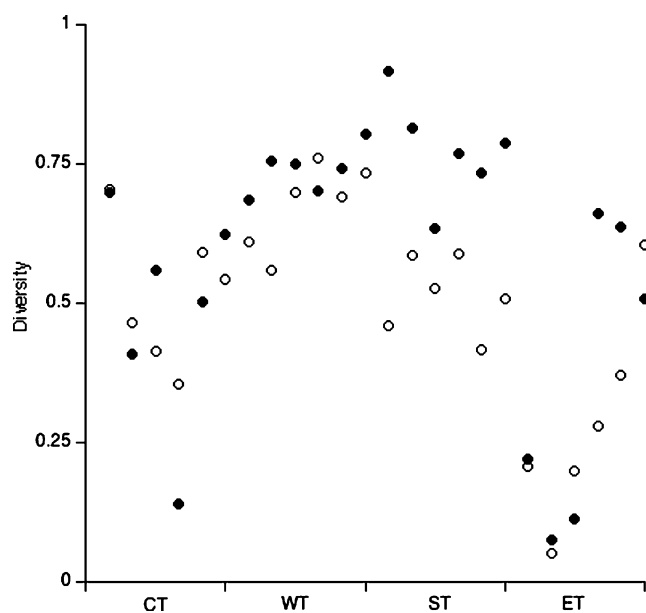


Fig. 8 Variation in taxon diversity per station of faunal elements other than microgastropods (1) in seagrass beds (*solid circles*) and (2) in adjacent areas of non-vegetated sediment (*open circles*) at the 24 stations in the four climatic zones sampled, arranged according to latitude. Abbreviations as per Fig. 2

individual sites, with all the problems of interpretation consequent on differing individual methodologies and areas sampled (Kendall and Aschan 1993; Mackie et al. 2005). Perhaps unsurprisingly, results have proved inconsistent (Clarke and Crame 1997; Gray 2002) and whether or not latitudinal gradients in point diversity or abundance occur is still contentious, although the balance of evidence suggests that they do, especially in the epifauna (Hillebrand 2004). This study set out to investigate the smaller members of the seagrass macrofauna across a wide range of latitudes with a single uniform methodology. Of course, this approach is not without its own limitations: the number of sites that can be worked is much more restricted than can be derived from a literature survey, and different sizes of sampling unit may be more appropriate in different circumstances (see e.g. Attrill et al. 2000) not least because different microgastropod species show differing patterns of temporal and spatial variability (Olabarria and Chapman 2002). Nevertheless, clear differences were observed in faunal density, diversity and gastropod dominance between the various locations, and within each of them also in respect of the presence or absence of seagrass cover.

The density and species composition of the fauna of the Norfolk *N. noltii* beds recorded here fall well within the range of the North Atlantic *N. noltii* beds reviewed by Blanchet et al. (2004), and the Scolt Head site in particular is very similar in nature and structure to their Group A stations in the Bassin d'Arcachon on the Atlantic coast of France. In both, the microgastropod *Hydrobia ulvae* and the

oligochaete *Tubificoides benedeni* occurred at high density and totally dominated numbers (together comprising >90% of the total macrofaunal individuals). More microgastropod species were present at the (44° 42' North) French site, but gastropod diversity (calculated from the mean abundance data for the Group A stations in Blanchet et al. 2004, Table 2) was still well below 0.1. Equivalently, the nature and abundance of the benthic fauna of the *N. capensis* beds of the South African Knysna system fall well within the range of those in the suite of Western Cape estuaries and lagoons (with, in some, *Ruppia* instead of *Nanozostera*) that stretch from the cool temperate Great Berg in the west to the warm temperate Keurbooms in the east, especially the nearby Swartvlei Estuary (see e.g. Branch and Day 1984; Whitfield, 1989; Bennett and Branch 1990; Kalejta and Hockey 1991; Barnes 2004; Siebert and Branch 2007). [One notable shared feature of these South African systems is that the abundances of their gastropods may be very patchy in both space and time (see Barnes 2004), and the Knysna abundances recorded here differ significantly from those found there in 2004 and 2005 (Barnes 2004 and unpublished data).] The Norfolk and Knysna sites can therefore be regarded as representative of their type; unfortunately, insufficient information is available to indicate whether the same can be said of the microgastropod fauna of the Moreton Bay *N. m. capricorni* beds.

The various seagrass sites investigated clearly displayed a marked decrease in density of microgastropods from temperate to tropical regions, but although the microgastropod densities imposed such a trend on the fauna as a whole, it was less marked especially within the seagrass beds because densities of the associated faunal taxa were generally of more similar orders of magnitude regardless of latitude. This was in large measure due to the expected lack of a marked trend in the infaunal component (e.g. Piersma et al. 1993; Frouin and Hutchings 2001), particularly the polychaetes and bivalves which, as elsewhere (e.g. Hughes and Gamble 1977; Klumpp and Kwak 2005), dominated the tropical sites. (In this context it is important to note that these are proportional relationships: annelid worms and bivalve molluscs were most abundant per unit area in cool temperate Norfolk, but there they comprised small proportions of the total faunal individuals.)

In respect of differential abundance in relation to latitude, Piersma et al. (1993) assembled data from 19 intertidal mudflats between 57°N and 34°S and detected no latitudinal trend in total prey biomass harvestable by shorebirds. Neither was there a latitudinal trend in either the contribution of gastropods to the total prey biomass (which varied between 0 and 99% of the total) or in their biomass $\times \text{m}^{-2}$ (data from their Table 1). North-temperate flats, however, did support relatively more molluscs than those in the tropics, and flats in the tropics supported more

taxa. Similarly, Virnstein et al. (1984) found that the density of seagrass amphipods did not vary with latitude (though individual size of amphipods did, decreasing with decrease in latitude). In contrast to the present study, that of Piersma et al. (1993) included the infauna down to 150–500 mm depth and the larger benthic species as well. All sites investigated by this study also possessed an abundant fauna of large animals distributed more sparsely than the sub-10-mm component under investigation—burrowing sedentary echiurans, polychaetes, callianassid sand-prawns and holothurians, and relatively mobile epifaunal gastropods and burrowing crabs were in abundant evidence, although none was represented in any core sample—so the point requiring specific explanation is not so much variation in total faunal biomass as variation in the small-sized component alone, and particularly in that of the epifauna, largely comprised by microgastropods.

The variation in abundance seen within sites may be relevant to this picture. Although variation in density, dominance, species richness and species diversity of microgastropods in non-vegetated sediment exactly paralleled those seen within the adjacent seagrass beds, densities and, to a lesser extent, diversities of both microgastropods and the other associated taxa were usually greater within the *Nanozostera* beds than in the non-vegetated sediments (i.e. with the clear exception of the South African stations). Such exceptions notwithstanding, larger densities of small invertebrates in seagrass beds has long been regarded as a consequence of their role as a refuge from epibenthic predation (Summerson and Peterson 1984; Orth et al. 1984). Nevertheless, many of the juvenile prawns (O'Brien 1994), crabs (Ray-Culp et al. 1999) and fish (Nagelkerken et al. 2006) that use seagrass beds as nursery areas, including commercially important species, do feed at least in part and/or at some stage in their development on the small molluscs, crustaceans and other seagrass-associated micro-invertebrates (Edgar and Shaw 1995). The intense predation pressure typifying subtropical and tropical zones (Vermeij 1978; Irie and Iwasa 2005) is therefore likely to be responsible for the relative scarcity of microgastropods and equivalently sized animals from low latitudes.

In this regard, it may be significant that in the sites likely to be most under threat from epibenthic predation—low latitude areas of bare sediment—such microgastropods as were present were to a much greater extent those with relatively thick shells. At the Queensland sites, for example, thick-shelled species such as juvenile *Nassarius* and *Batillaria* comprised 78% of the microgastropod fauna, whilst in the adjacent seagrass areas 67% of individuals were of the more usual thin-shelled, and hence more vulnerable, species typified by *Calopia* and *Smaragdia*. Likewise, the major location of microgastropod faunas at warm temperate Knysna in creeks and pools within blocks

of saltmarsh (Barnes 2004) is consonant with relative shelter from water-borne predators compared with the more exposed intertidal flats fringing the main channels, which are largely free of *Hydrobia knysnaensis* and *Rissoa capensis*, the two thinner-shelled species, but are often dominated by the larger, thicker-shelled *Protomella capensis* and *Nassarius kraussianus*.

In respect of diversity, an analysis of data on the epifauna of seagrass beds (Virnstein et al. 1984), though restricted to crustaceans and fish, found that species richness of amphipod and decapod crustaceans (though not isopods) did increase towards the tropics. Attrill et al. (2001) used published data from 20 mudflat sites and also found a definite increase in total faunal diversity with decrease in latitude. Patterns of diversity are dependent on spatial scale, however: most tropical marine species are rare and are only likely to be encountered if large areas of sediment are sampled (Shin and Ellingsen 2004). Even though Barnes et al. (2009) sampled hundreds of square metres, none of their species accumulation plots from the Seychelles reached asymptote. This can only increase the disparity found here between the diversities within the temperate *Nanozostera noltii* and *N. capensis* beds and those in the lower latitude sites in that sampling larger areas would be unlikely to have increased the diversity of the temperate sites to any appreciable extent because of their known relative faunal poverty. At a small scale, point diversities of mudflat fauna may not show a clear relationship with latitude, but it is likely that at a large scale of sampling they would do so.

With a total of eight sites distributed across only four latitudinal regions, the above data set is relatively small and it is of course possible that some confounding variable/s (other than salinity since this was >30 at all sites, seagrass shoot density or siltiness of the sediment) may be responsible for the patterns observed (as below). Nevertheless, the data for the epifauna and shallowly burrowing infauna in intertidal soft sediments obtained by this survey are broadly consistent with trends towards the equator of a reduction in the numbers of the smaller members of the epifauna, of an increase in the proportion of infaunal animals (bivalves, annelids and crabs), and of a larger differential between the abundance of the smaller elements of the fauna within the seagrass beds and those in adjacent areas of non-vegetated sediment. The possibility raised by this study, that there are considerable differences in the effect of intertidal seagrass beds on the underlying faunal community structure within the sediment, is intriguing and deserving of further study. It seems unlikely that the effect is latitudinally related, but several plausible hypotheses relating to confounding variables suggest themselves. It was evident that the intertidal beds of *N. capensis* and *N. m. capricorni* sampled were composed of longer-leaved

seagrasses than those of *N. noltii* or at the tropical sites, and therefore ground cover was almost certainly greater at those sites—in places it was clearly 100%, a value not achieved at the North Sea, Seychelles or Indonesian intertidal stations. Also, non-vegetated areas of sediment at the warm-temperate and subtropical sites, but not at the cool-temperate or tropical ones, were clearly structured by bioturbating callianassids. Both increasing percentage cover by seagrasses (Irlandi 1994) and the presence of callianassids (Siebert and Branch 2006, 2007) are likely to maximise differences between eelgrass-associated and adjacent bare-sediment benthos.

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Appendix 1

Microgastropods and juvenile macrogastropods occurring in or near *Nanozostera* beds (*S* within the seagrass, *B* on associated non-vegetated sediment)

Trochoidea: Trochidae	
<i>Astela speciosum</i> (juv.)	Queensland (<i>S</i>)
Trochoidea: Phasianellidae	
<i>Tricolia</i> sp.	Queensland (<i>S</i>)
Neritoidea: Neritidae	
<i>Smaragdia souverbiana</i>	Queensland (<i>S</i>)
Rissooidea: Hydrobiidae	
<i>Hydrobia ulvae</i>	UK (<i>S, B</i>)
<i>Hydrobia knysnaensis</i>	Western Cape (<i>S, B</i>)

Rissooidea: Calopiidae	
<i>Calopia imitator</i>	Queensland (<i>S, B</i>)
Rissooidea: Irvadiidae	
<i>Nozoba topaziaca</i>	Queensland (<i>B</i>)
Rissooidea: Vitrinellidae	
<i>Pseudoliotia micrans</i>	Queensland (<i>S</i>)
Rissooidea: family uncertain	
' <i>Rissoa</i> ' <i>capensis</i> ^a	Western Cape (<i>S, B</i>)
Rissooidea: Assimineidae	
<i>Assimineia ovata</i>	Western Cape (<i>S</i>)
<i>Assimineia globulus</i>	Western Cape (<i>S, B</i>)
Littorinoidea: Littorinidae	
<i>Littorina saxatilis</i> (juv.)	UK (<i>S</i>)
Cerithioidea: Cerithiidae	
<i>Cerithium corallium</i> (juv.)	Queensland (<i>S</i>)
Cerithioidea: Batillariidae	
<i>Batillaria australis</i> (juv.)	Queensland (<i>S, B</i>)
Cerithioidea: Scaliolidae	
<i>Finella pupoides</i>	Queensland (<i>B</i>)
Cerithioidea: Litiopidae	
<i>Alaba pinnae</i>	Western Cape (<i>S</i>)
Cerithioidea: Turritellidae	
<i>Protomella capensis</i> (juv.)	Western Cape (<i>S</i>)
Muricoidea: Nassariidae	
<i>Nassarius burchardi</i> (juv.)	Queensland (<i>S, B</i>)
<i>Nassarius kraussianus</i> (juv.)	Western Cape (<i>S, B</i>)

^aThe systematic position of this species is currently being investigated by Winston Ponder and Hiroshi Fukuda of The Australian Museum, Sydney; it may well prove to be an aberrant assimineid

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