

Distribution and behaviour of meiofaunal copepods inside and outside seagrass beds

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ABSTRACT: The abundance and species composition of meiobenthic copepods from blades and subcanopy sediments of seagrass *Zostera capricorni* beds has been compared with adjacent unvegetated sediment banks in Pauatahanui Inlet, New Zealand. A range of sampling protocols has established that abundance on blades and on sediments beneath dense growths of *Zostera* is significantly higher than on nearby bare sand substrata. Further away from beds abundance increases to a level approximating that of seagrass beds when individuals on blades and subcanopy sediments are taken together. Species richness is nearly twice as high on blades as on sedimentary substrata either inside or outside beds, although in general there is no close association between abundance or species richness and the surface area of individual *Zostera* blades. Multiple pairwise comparisons of numbers of individuals and species sampled over 4 independent 24 h periods at both high and low tide, day and night, demonstrate that significantly more individuals and species occur on *Zostera* blades at low tide than at high tide irrespective of light regime. In contrast, those on subcanopy sediments show no such tidal variability in abundance. Day or night there are more species on blades than on sediments irrespective of tidal state. Reductions in faunal abundance during high water suggested a migratory behaviour coincident with tidal inundation. Experimentally emplaced emergence traps confirmed that a substantial proportion of the *Zostera* bed copepod fauna actively swim into the water column during high water, explaining the reductions in abundance found when sampling blades and sediments alone. Significantly more copepods enter traps emplaced over *Zostera* beds compared with unvegetated sites. Over 70 % of the trapped fauna is derived from blades or as phytal itinerants, establishing an important difference between copepod faunas from vegetated and unvegetated habitats. An earlier view that the appearance of meiofaunal copepods in the water column was due primarily to passive hydrodynamic resuspension needs revision in the light of pronounced swimming activities amongst seagrass inhabitants. Observations on fish predators in seagrass systems were made and the ecological implications of active benthic-pelagic exchanges of seagrass copepods are discussed.

INTRODUCTION

In recent years, there has been a surge of interest in the faunal composition and ecology of invertebrates inhabiting seagrass beds, with most studies being centred in tropical systems dominated by *Thalassia*, *Halodule* and *Syringodium*. In more temperate regions of N. America, Europe and Australasia, work is in progress in grassbeds dominated by *Zostera* and *Posidonia* and there is now a substantial literature concerning the determinants of macrobenthic species abundance, composition and diversity in these habitats (see Heck & Orth 1980, Lewis 1984, Summerson & Peterson 1984 for a summary of pertinent references). The impetus for such research effort has largely been based upon a recognition of the role seagrass beds play in the energy or trophic status of estuarine systems,

either through their release of dissolved organic carbon directly into the water column (Penhale & Smith 1977), or, after defoliation and fragmentation of leaves, by contributing to the detritus pool (Mann 1972). Moreover, the use of seagrass beds as nursery and feeding areas for the young of many commercially important fish species has added to the presumed importance of vegetated habitats in estuaries (see Pollard 1984).

Despite the plethora of investigations concerning macrofauna in seagrass habitats, there are few involving components of the meiobenthos. Studies on seagrass meiofauna have largely been descriptive (see Bell et al. 1984 for review), and only recently (e.g. Robichaux et al. 1981, Novak 1982, 1984, Sogard 1984, Thistle et al. 1984, Decho et al. 1985) have attempts been made to more critically evaluate some of the

causative factors to pattern and composition of grassbed meiofaunal populations. Thistle et al. (1984), for example, concluded that the structural imposition to sandflats of *Syringodium* plants had the effect of creating localized patches of increased sediment bacterial activity. It is believed that these patches act as attractants to, and therefore enhance the abundance of, bacterivorous harpacticoid copepods. Sogard (1984) demonstrated that while meiofaunal harpacticoids from seagrass habitats comprised by far the dominant fraction of the diet of a grassbed fish, predation by this animal did not significantly affect the population dynamics of copepod prey. This finding supports similar conclusions from studies conducted in unvegetated habitats (Alheit & Scheibel 1982, Hicks 1984, 1985b, Gee et al. 1985).

In order to confirm the universality, or otherwise, of some of the patterns exposed during studies of macrobenthic organisms, especially crustaceans (e.g. Stoner 1983, Lewis 1984), the copepod fauna (primarily harpacticoids) associated with *Zostera capricorni* Aschers. beds has been compared with adjacent unvegetated sediment banks. Preliminary tidal and diel sampling has also presented a new view on the behaviour of the residents of grassbeds compared with their bare sand counterparts. Observations on predatory fishes in this environment add to our understanding of seagrass beds as refuges from predation.

MATERIALS AND METHODS

Study site. Four sampling stations for sediment and one for seagrass blades were established on an intertidal fine sand bank (Mana Bank) in Pauatahanui Inlet, the eastern arm of Porirua Harbour, Wellington, New Zealand (41°06' S, 174°54' E). Tidal sea level change within the inlet is semidiurnal and near symmetrical, with mean spring range 1.25 m and mean neap range 0.4 m (Read 1984). Local sea level and tidal range are commonly influenced by ambient meteorological conditions (pers. obs.). Salinity and temperature values are typically within an annual 17 to 34 ‰ and 7 to 25 °C, respectively (Hicks 1984).

Station 1 was located amongst fine sand surface ripples, a site detailed elsewhere (Hicks 1984). Station 2 was positioned some 150 m east on open unvegetated fine sand with a featureless surface microtopography. Station 3 was from sand areas between sparsely occurring plants in monotypic stands of the rhizomatous eelgrass *Zostera capricorni*. Station 4 was 15 m further east from small (subcanopy) sand areas amongst plants in a dense bed of *Zostera*. Plant densities at Stn 4 were roughly 10 times that at Stn 3 (Table 1). Samples of eelgrass blades were taken in dense *Zostera* adjacent to Stn 4, and will henceforth be referred to as Stn 5. At low tide, water drains from the beds, but ponding in depressions amongst the seagrass occurs and it is from the margins of such shallow depressions that blades were sampled. Water depth over these sites at MHW is about 1.2 m.

According to Healy (1980, p. 138), above-ground biomass of *Zostera* in Pauatahanui is lost in winter. On the contrary, my observations spanning 3 yr confirm that it is a perennial at this locality. Seasonal defoliation and blade fragmentation occurs to some degree in winter but does not lead to complete wastage of above ground structures (Table 1). Blades average 127.61 ± 26.23 mm long with a near uniform width of 2.81 ± 0.37 mm ($n = 125$ in both cases), tapering only slightly apically.

Unlike many of the tropical seagrass species (Heck 1979, Lewis & Hollingworth 1982), *Zostera* in Pauatahanui Inlet does not support large and diverse assemblages of macroalgae growing epiphytically on the blades. Surface-borne bacteria and microalgae such as diatoms are, however, readily observed on *Zostera* as they are on other seagrasses (see Novak 1984).

Sampling. Copepods were collected from each substratum covering the 5 stations. Between 3 and 5 samples were taken during daylight hours at low tide at Stns 1 to 3, in December 1983, January, March and June 1984. Within the dense *Zostera* bed (Stns 4 & 5), additional samples were made; sampling frequency, tidal and diel state, number and type of sample during each period are summarized in Table 2. Sediment samples at Stn 1 were taken from the troughs of sand

Table 1. Summer (February), winter (August) comparison of plant density and biomass between areas of sparse and dense seagrass stands, Pauatahanui Inlet

<i>Zostera</i> beds	No. <i>Zostera</i> plants m ⁻² ($n = 10$)		Biomass (g m ⁻²) ($n = 3$)	
	Summer	Winter	Summer	Winter
Sparse	48.31 ± 21.4	41.0 ± 19.0	3.93 ± 0.61	0.8 ± 0.03
Dense	402.10 ± 78.0	370.0 ± 48.0	42.10 ± 1.06	29.03 ± 0.58

Table 2. Summary of samples collected from dense *Zostera* bed 1982–1984. DS: sediment beneath plants; BP: clipped 10 × 10 cm plot of blades; BI: individual blades; ET: emergence traps. *n* = sample number. See text for sampling protocol

Date	Tidal state	Day/night	Sample (<i>n</i>)
15 Nov 1982	Low	Day	DS (3), BP (1)
20 Dec 1983	Low	Day	DS (4), BP (2)
20 Jan 1983	Low	Day	DS (3), BP (2), BI (10)
25 Jan 1984	Low	Day	BI (10)
30 Jan 1984	Low	Night	DS (6), BP (1), BI (10)
31 Jan 1984	High	Day	DS (6), BP (1), BI (10)
31 Jan 1984	High	Night	DS (6), BP (1), BI (10)
31 Jan 1984	Low	Day	DS (6), BP (1), BI (10)
23 Feb 1984	High	Night	DS (6), BP (1), BI (10)
23 Feb 1984	Low	Day	DS (6), BP (1), BI (10)
23 Feb 1984	High	Day	DS (6), BP (1), BI (10)
23 Feb 1984	Low	Night	DS (6), BP (1), BI (10)
23 Mar 1984	High	Night	DS (6), BP (1), BI (10), ET (2)
23 Mar 1984	Low	Day	DS (6), BP (1), BI (10)
23 Mar 1984	High	Day	DS (6), BP (1), BI (10), ET (2)
23 Mar 1984	Low	Night	DS (6), BP (1), BI (10)
24 May 1984	Low	Day	BP (1)
14 Jun 1984	Low	Day	DS (6), BP (2), BI (10)
14 Jun 1984	High	Day	ET (5)
5 Jul 1984	High	Night	DS (5), BI (8)
5 Jul 1984	Low	Day	DS (5), BI (10)
5 Jul 1984	High	Day	DS (5), BI (10)
5 Jul 1984	Low	Night	DS (5), BI (10)

ripples with a brass corer of 23 mm internal diameter (area = 4.15 cm²). As shown previously (Hicks 1984), ripple troughs contain higher copepod densities than crests or surrounding sediment of more uniform microtopography. Sediment samples at Stns 2 to 4 were taken with the same corer; surface ripples did not occur at these sites. Care was taken not to include any part of fresh *Zostera* blades, especially at Stn 4. All cores were sampled to the depth of the relevant RPD (ca 6 cm at Stn 1; ca 2 cm at Stns 2 to 4). Extruded cores were placed in plastic storage jars containing 70 % alcohol and Rose Bengal stain. Collection of copepods was on a 63 µm sieve after multiple swirl-decantations.

Two methods were chosen to sample the fauna on seagrass blades. First, large samples were obtained by clipping blades at the base of the blade sheaths within a 10 × 10 cm quadrat. This procedure was undertaken with great delicacy to minimize disturbance to resident blade fauna and to ensure the least possible contamination of blades by sediment-dwelling species. Blade samples were subsequently placed into plastic bags containing 70 % alcohol. Second, individual blades were sampled by sliding a plastic tube (15 mm internal diameter) over the blade, clipping it as close as possible to the base of the blade sheath, and sealing the end with a shallow bung. The opposite end was unsealed but covered with 63 µm mesh. This prevented a bow wave effect when the tube was emplaced, yet denied escape of animals.

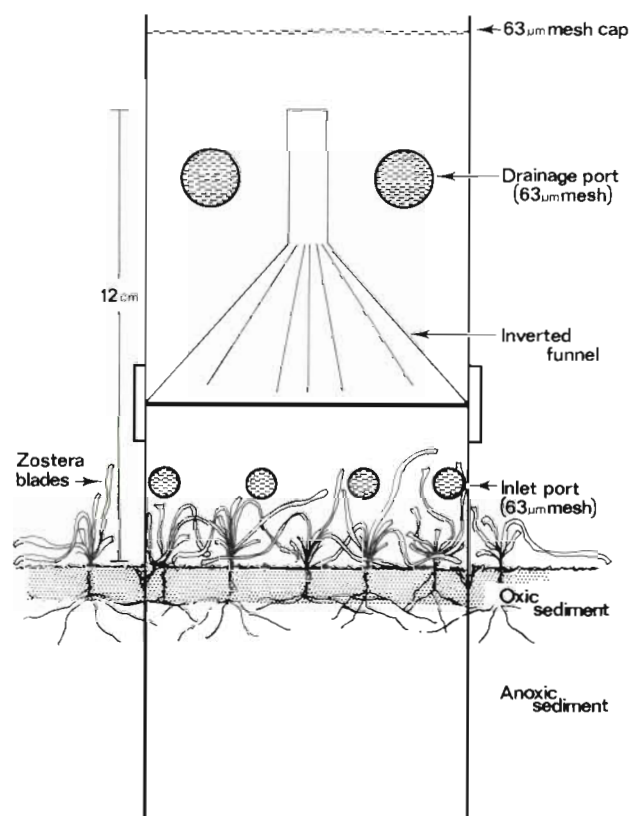


Fig. 1. Schematic illustration of emergence trap. See text for details of emplacement

Sediment densities and 10×10 cm quadrat blade densities are expressed as numbers of individuals per 10 cm^2 bottom area. Since it is believed that harpacticoids respond directly to surface area of phytal structures (Hicks 1985a), rather than to plant biomass *per se*, the number of individuals and number of species have been compared with the surface area ($\log_e \text{mm}^2$) of individual blades. Blade surface areas were determined arithmetically by length:width measurements using dial calipers to the nearest 0.01 mm, accounting for both surfaces.

At high tide on 2 sampling occasions in March 1984 (Table 2), the water column overlying dense *Zostera* (Stn 4) was sampled with emergence traps; in June 1984, 5 samples of water overlying dense *Zostera* and 5 taken similarly from bare sand at Stn 1 were compared. Emergence traps consisted of a 10.4 cm diameter PVC pipe in 2 sections (Fig. 1). The lower section of 15.5 cm length contained at its top an inverted clear plastic funnel, 2 cm below which were eight $63 \mu\text{m}$ mesh-covered inlet ports to allow water exchange but prevent high flow during a rising tide. The top section fitting tightly into the lower was 15 cm in length and capped with $63 \mu\text{m}$ mesh. At a level 3 cm below the top of the funnel additional $63 \mu\text{m}$ mesh-covered ports allowed drainage as the tide ebbed. The whole structure was forced gently into the substratum enclosing *Zostera* blades (see Fig. 1), allowing approximately 6 cm remaining above the sediment surface. Copepods entering the device had, of necessity, to actively move a distance of some 12 cm from the substratum to the top of the inverted funnel in order to be trapped. Emergence traps were emplaced prior to flood tide and

retrieved 6 h later at low tide, thus sampling a complete high water phase.

RESULTS

Comparison between vegetated and unvegetated substrata

Since regular samples from each subhabitat over all seasons of the year were not undertaken, temporal aspects of abundance and species richness will not be treated. That such variability does occur, however, is evident in the raw data and in Fig. 2 where summer and winter values have been plotted independently. Both abundance and species richness on blades and on sediments beneath dense *Zostera* are significantly higher in June (early winter) than in January (early summer) (ANOVA, $P < 0.001$ in both cases). Summing data from all stations and samples, an inverse parabolic pattern of abundance can be demonstrated with high densities at Stn 1, declining drastically to the margins of *Zostera* beds and beneath sparse plants, but increasing on sediment beneath dense plants and on the blades themselves (Table 3). Taking these latter 2 components together, the abundance of copepods in *Zostera* beds is only slightly below ($P = 0.05$) that on the rippled sand bank (Stn 1). There are, however, significantly more species on the margins and associated with beds than at Stn 1 (ANOVA, $P < 0.001$). About twice as many species occur on blades as opposed to sedimentary substrata either inside or outside beds (Table 3). Taken as a whole, dense grassbeds

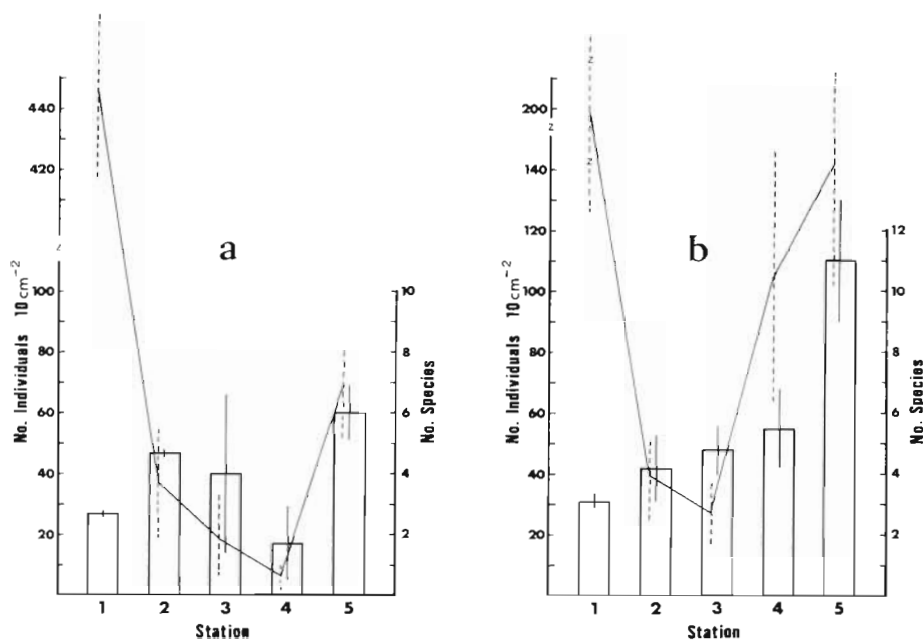


Fig. 2. Mean number (± 1 SD) of individuals (solid line) and mean number (± 1 SD) of species (bar histograms) of meiobenthic copepods from 5 stations in Pauatahanui Inlet. Stn 1 = open sand dominated by surface ripples; Stn 2 = open, featureless sand; Stn 3 = sediment amongst sparse *Zostera* plants; Stn 4 = sediment amongst dense *Zostera* plants; Stn 5 = *Zostera* blades. Samples were taken at low tide during the day (a) in summer, 20 January 1984, and (b) in winter, 14 June 1984.

Table 3. Mean values for numbers of individuals (no. 10 cm⁻²) and species compared over 5 estuarine substrata (see 'Materials & Methods') at low tide during daylight, Pauatahanui Inlet (underlined values: no significant difference in means; ANOVA and SNK test, P > 0.05)

	Stn 1	Stn 2	Stn 3	Stn 4	Stn 5
Individuals 10 cm ⁻²	230.5	<u>46.5</u>	<u>37.8</u>	<u>85.5</u>	<u>68.3</u>
Number of species	3.0	<u>4.8</u>	<u>4.4</u>	<u>4.7</u>	8.9

(i.e. blades and subcanopy sediments), support significantly higher numbers of copepod species, with a number of individuals within the range of values recorded from unvegetated sediment habitats (i.e. Stn 1).

Patterns of copepod abundance within larger 100 cm² plots of clipped *Zostera* are well predicted by abundances on individual blades. There is a close correlation between these variables in each sample ($r = 0.833$, $P < 0.001$); thus abundance of copepods on vegetation has been assessed as a function of surface area of individual blades. Using each blade from all collection dates ($n = 125$, see Table 2), there was a highly significant relation between log surface area, and the logarithms of abundance ($r = 0.353$, $P < 0.001$), and number of species ($r = 0.364$, $P < 0.001$). However, because of the high n value and clear residual variability, this relation is considered somewhat spurious. If each sampling date is analysed independently, then only in July is a significant correlation obtained between surface area and numbers of species ($r = 0.772$, $P < 0.001$) and individuals ($r = 0.483$, $0.02 > P < 0.05$, $n = 17$ in both cases). Degrees of freedom on other sampling dates varied between 6 and 18 and the strength of the relation varied similarly, but always non-significantly. Thus in general, copepods are responding to some characteristic of seagrass beds unable to be determined at the level of surface area of individual blades.

Comparison with tidal and diel state

Multiple pairwise comparisons of numbers of individuals and species sampled over 24 h at different stages of the tide (high tide; low tide) and day (night; day), reveal a pattern of dynamic tidally-coupled changes (Table 4). Significantly more individuals and species of copepods are collected from *Zostera* blades at low tide than at high tide (Mann Whitney U-test, $P < 0.001$), irrespective of light regime (day vs night). In direct contrast, copepods occupying the subcanopy sediments in dense beds show no such significant tidal

variability in abundance; there is also no difference in relation to diel state. There is a greater number of species on blades than on sediments irrespective of both tidal or diel state. Data collected over 24 h periods in January, February, March and July covering 2 semi-diurnal tidal events (Tables 2 & 4), are consistent in showing significant reductions in total (i.e. blade plus subcanopy sediment) copepod abundance during high water, contributed to primarily by the phytal component. Significant reductions in the blade fauna at high tide irrespective of time of day is strongly suggestive of a migratory behaviour coupled to tidal inundation.

In an attempt to 'locate' animals that seemingly depart *Zostera* beds at high water, a series of incidental samples were taken from a range of adjoining alternative substrata. Random high tide samples included sediments adjacent to beds, attached and drift algae such as *Gracilaria* and *Ulva*, and cockle-shell rubble from nearby shellfish beds. At none of these additional sites could the 'overflow', determined primarily by species composition and relative abundance, be accounted for. It was therefore decided to sample the water column immediately overlying seagrass beds (see 'Materials and Methods').

Table 4. Mean numbers of individuals and species (in parentheses) from 24 h samples of *Zostera* blades and subcanopy sediments, January to July, 1984. Samples circumscribe a low and a high tide each during daylight and at night. LT = low tide; HT = high tide. Values are expressed as numbers per individual *Zostera* blade (A) and number 10 cm⁻² of sediment (B). Absolute values are therefore not comparable

	Low tide Day	High tide Day	Low tide Night	High tide Night
(A) <i>Zostera</i> blades				
Jan	7.2 (1.1)	0.2 (1.0)	9.5 (2.0)	0.8 (1.2)
Feb	9.7 (1.3)	1.0 (1.2)	8.4 (2.1)	1.4 (1.4)
Mar	15.7 (3.0)	3.5 (1.4)	13.4 (2.8)	0.9 (1.6)
Jul	7.8 (2.0)	0.5 (1.0)	4.3 (1.6)	3.1 (1.5)
Individuals LT vs HT = $P < 0.001$, Mann Whitney U-test Individuals Day vs Night = NS Species LT vs HT = $P < 0.001$, Mann Whitney U-test Species Day vs Night = NS				
(B) Subcanopy sediments				
Jan	57.1 (4.3)	43.4 (4.2)	105.3 (4.2)	88.4 (3.8)
Feb	122.5 (5.5)	127.8 (4.8)	165.9 (5.3)	62.6 (4.2)
Mar	114.1 (4.8)	77.9 (4.7)	98.0 (4.3)	68.7 (4.7)
Jul	106.6 (6.4)	115.2 (5.6)	103.6 (5.4)	97.4 (5.0)
Individuals LT vs HT = NS Individuals Day vs Night = NS Species LT vs HT = NS Species Day vs Night = NS				

Abundance in emergence traps

The sequence of high-low tide and low-high tide abundances during both day and night was investigated by analysis of emergence trap data. In March 1984, substantial numbers of copepods were collected in a preliminary duplicate set of traps sampling the water column at both high tide night (\bar{x} individuals = 72.5 ± 71.4), and high tide day ($\bar{x} = 81.0 \pm 49.5$). To assess the contribution to trap fauna of the underlying substrata, the mean number of copepods from sediments together with those on blades were pooled and expressed as number of individuals per 100 cm². The internal area of the emergence trap is equivalent to 104 cm². By direct proportionality of abundance on the substratum during the preceding low tide, the number of copepods collected in traps over the following high water phase accounted for 3.8 % of the 'available' fauna on sediments and blades at high water night and 3.6 % at high water day. The similarity in these 2 values confirms the absence of significant day-night variability in the faunas resident on blades and sediments (see above). The trap collections also verify the movement of copepods into the immediately overlying water column as suggested by sampling blades and sediment alone. Refinements have been made to this preliminary sampling strategy and many more samples have since been taken which confirm this fundamental pattern. Details of these aspects will form the basis of a forthcoming account (Bell, Hicks & Walters unpubl.).

To test that these tidal migrations are indeed active phenomena of copepods associated with seagrass habitats rather than the result of passive resuspension as found over unvegetated sediments (*sensu* Palmer 1984, Palmer & Gust 1985), 5 traps were set in June 1984 on open unvegetated sand (Stn 1), and 5 over dense *Zostera* beds (Stn 4). Results are presented in Table 5, establishing a highly significant difference (ANOVA, $P < 0.001$) between the 2 subhabitats. Over an order of magnitude more copepods were retrieved from traps emplaced over a vegetated bottom, compared with those from an unvegetated site.

Species composition

Thirty copepod species have been collected from the 364 samples covering all substrata (see 'Materials and Methods'; Table 2). Most of these are in need of critical taxonomic verification. Numerically, *Porcellidium* sp. and *Bulbamphiascus* sp. were the most abundant species on seagrass blades and subcanopy sediments, respectively (Table 6). On sediments amongst sparse plants and on closely adjacent unvegetated sites there was no clear dominant; instead the bulk of the fauna was contributed to by *Paralaophonte* sp., *Bulbamphiascus* sp., *Parastenhelia mearnsi*, and to a lesser extent *Halectinosoma hydrofuge*. All sediment-dwellers so categorized are either epibenthic or shallow burrowers, but an interstitial species, *Paraleptastacus* sp., attained high localized densities at Stn 1 during this sampling period. Some species, e.g. *Ectinosoma melaniceps* and *H. hydrofuge*, have been categorized as phytal itinerants since their abundance is roughly shared between blades and subcanopy sediments; in the case of the former, there was no statistical difference between abundance on both substrata. Other species exhibit distinct distribution patterns in relation to the presence of seagrass. Stn 1 is clearly optimal for *Paraleptastacus* sp.; clean fine sand becoming progressively more silt laden towards seagrass beds, presumably occluding necessary pore space required by this strictly interstitial species. *Parastenhelia mearnsi*, *Robertsonia propinqua* and *Paralaophonte aenigmaticum*, also found predominantly on the clean fine sand bank at Stn 1 (see Hicks 1984), decline in absolute abundance towards the edges of seagrass beds. Conversely, abundance of *Bulbamphiascus* sp. increases proportionally from open unvegetated sediment (Stn 2) to that beneath dense *Zostera* plants. Relative abundance of *Tisbe furcata* is predictably highest on blades, as it is for other typically phytal species including *Paradactylopodia brevicornis*, *Harpacticus* sp., *Amphiascus pacificus*, *Laophonte inornata* and *Amphiascopsis cinctus*. Together with *Porcellidium* sp., these species are prob-

Table 5. Comparison of migrating copepods between vegetated and unvegetated sites. HW = high water. Abundances on substratum are values taken at preceding low water

Site	Date (1984)	No. samples	Abundance on substratum 100 cm ²	Mean no. caught per 6 h (HW)	% of 'available' fauna
Bare sand (Stn 1)	14 Jun	5	2000 ± 400 ^a	19.5 ± 6.9	0.975
Over <i>Zostera</i> bed (Stns 4, 5)	14 Jun	5	1899 ^b	244.8 ± 159.3	13.1

^a Mean of 5 cores
^b Sum of subcanopy sediment (\bar{x} of 6 cores) plus blade (total of one 10 × 10 cm clipped plot) values

Table 6. Total and relative abundance of copepod fauna collected from 5 microhabitats (Stn 1 = open, sand ripples; Stn 2 = open, featureless sand; Stn 3 = sediment amongst sparse *Zostera* plants; Stn 4 = sediment amongst dense *Zostera* plants; Stn 5 = *Zostera* blades). Arbitrary categories ranked as primarily blade-dwellers (B); sediment-dwellers (S); itinerants (I), see text

Species	Stn 1		Stn 2		Stn 3		Stn 4		Stn 5		Category
	Number	%	Number	%	Number	%	Number	%	Number	%	
<i>Porcellidium</i> sp.							3	0.08	7719	85.3	B
<i>Bulbamphiascus</i> sp.			55	17.7	48	27.3	2185	55.1	76	0.84	S
<i>Halectinosoma hydrofuge</i>			46	14.8	22	12.5	812	20.5	205	2.3	I
<i>Paraleptastacus</i> sp.	794	56.1	8	2.6							S
<i>Paralaophonte</i> sp.	1	0.09	54	17.4	41	23.3	405	10.2	13	0.14	S
<i>Tisbe furcata</i>					1	0.57	34	0.86	397	4.4	B
<i>Ectinosoma melaniceps</i>			2	0.64	3	1.7	239	6.0	352	3.9	I
<i>Parastenhelia megarostrum</i>	578	40.8	97	31.2	18	10.2	6	0.15			S
<i>Halicyclops</i> sp.			19	6.1	6	3.4	176	4.4	25	0.28	S
<i>Paradactylopodia brevicornis</i>			1	0.32	3	1.7	7	0.18	118	1.3	B
<i>Enhydrosoma</i> sp.			7	2.3	15	8.5	76	1.9			S
<i>Robertsonia propinqua</i>	40	3.5	15	4.8	15	8.5	1	0.03			S
<i>Harpacticus</i> sp.							1	0.03	70	0.77	B
<i>Amphiascus pacificus</i>							3	0.08	40	0.44	B
<i>Paralaophonte aenigmaticum</i>	3	0.26	4	1.3	1	0.57	3	0.08			S
<i>Laophonte inornata</i>							4	0.10			I
<i>Amphiascopsis cinctus</i>									8	0.09	B
<i>Psyllocamptus minutus</i>							2	0.05	6	0.07	I
<i>Quinquelaophonte candelabrum</i>			1	0.32	3	1.7	1	0.03			S
<i>Pseudostenhelia</i> sp.	1	0.09	2	0.64							S
<i>Mesochra</i> sp.							2	0.05	1	0.01	I
<i>Metis</i> sp.									2	0.02	B
Ameiridae									2	0.02	B
<i>Enhydrosomella</i> sp.							1	0.03	1	0.01	I
<i>Stylicletodes</i> sp.							2	0.05			S
<i>Amphiascus ?gracilis</i>									1	0.01	B
<i>Harpacticus</i> sp. A.									1	0.01	B
<i>Brianola</i> sp.									1	0.01	I
<i>Typhlamphiascus</i> sp.							1	0.03			S
<i>Halectinosoma otakoua</i>							1	0.03			S
Total no. copepods	1416		311		176		3965		9046		
Total no. species	6		13		12		22		20		

ably so localized because of feeding preferenda from vegetative rather than clastic surfaces.

No one species showed any positive association with surface area of individual seagrass blades.

Similar pairwise comparisons to those made on total numbers of species and individuals (see above) have been carried out on the 6 most abundant species from blades and subcanopy sediments. As expected, results for total fauna are reflected in individual species with both blade and itinerant forms showing significant differences in abundance at low compared to high tide (Table 7). The reduction in abundance at high tide demonstrated for *Porcellidium* sp., *Tisbe furcata*, *Ectinosoma melaniceps* and *Halectinosoma hydrofuge*, is not supported in those species categorized as primarily sediment-dwellers. Although exhibiting similar tidal variability, results for *Bulbamphiascus* sp. are not quite significant at the 95 % confidence level.

Of all species associated with seagrass beds, only *T. furcata* shows any indication of a greater loss of individuals at high tide during the day, compared to the same tidal state at night. These data, however, suffer the same fate as those for *Bulbamphiascus* sp. (see Table 7). Examination of relative abundances of the commonest species suggests that only a proportion of the population of each species is moving off plants or subcanopy sediments at high tide, rather than the entire population of 1 or 2 species alone. This is supported by the emergence trap catches which are sampling all of the common species occupying both blade and subcanopy sediments (Table 8). Note that of the species undergoing active migration from the substratum into the water column, over 70 % of the fauna (discounting unidentifiable nauplii), is derived directly from blades or as phytal itinerants. *Bulbamphiascus* sp. is the only sediment-dweller to contribute

Table 7. Mann-Whitney probabilities of significant differences in both diel and tidal abundances of the 6 most abundant species associated with seagrass beds

Species	Low tide/High tide	Day/Night
Blade dwellers		
<i>Porcellidium</i> sp.	P < 0.001	NS
<i>Tisbe furcata</i>	P < 0.001	0.05 > P < 0.10
Itinerants		
<i>Ectinosoma melaniceps</i>	P < 0.05	NS
<i>Halectinosoma hydrofuge</i>	P < 0.05	NS
Sediment-dwellers		
<i>Bulbamphiascus</i> sp.	0.05 > P < 0.10	NS
<i>Paralaophonte</i> sp.	NS	NS

at all substantially to trap results. Full species analysis of emergence trap data will be presented at a later date (Bell, Hicks & Walters unpubl.).

DISCUSSION

In this examination of estuarine copepods, dense beds of *Zostera capricorni* supported an average of twice as many sediment-dwelling individuals as the sparsely vegetated fringes of beds and immediately adjoining unvegetated sediments. Together, dense bed blade and subcanopy sediment densities can approximate abundances in a nearby unvegetated sand ripple system (Stn 1), which has been shown to maintain very high peak harpacticoid densities (Hicks 1984). Furthermore, *Zostera* blades alone are capable of supporting more than double the number of species than other sites elsewhere on Mana Bank. It is now axiomatic that areas of increased floristic density,

architecture or biomass contain more species and greater abundance of epibenthic and phytal invertebrates than do areas of reduced floristic equivalents (see Heck & Orth 1980, Hicks 1985a for reviews). The practical operation of such a relation exists in the provision, via higher levels of complexity or heterogeneity, of an increased habitable space (= number of microhabitats), and the formation of protected living centers (refuges) from predators and/or hydrodynamic disturbance. Initial analyses here, using surface area of individual blades, a technique employed successfully in other studies on phytal meiofauna (Hicks 1980, Coull & Wells 1983), show little in the way of a direct relation linking copepod abundance and species richness to blade surface area. In certain circumstances (e.g. highly turbid waters) it is known that the sensitivity of surface area measures is impaired (Hicks 1980), and in this instance surface area of individual blades would seem to be an inappropriate technique. Seagrass biomass has commonly been used for correlative assessments of macrofaunal abundance and diversity (Heck & Wetstone 1977, Stoner 1980, Lewis 1984), and a gross measure such as this, although biologically less meaningful than surface area (at least to superficially sensitive copepods!), may prove to be a more useful measure of habitat 'abundance' against which to evaluate the number and diversity of meiofaunal copepods. The only time at which a significant abundance and species richness relation with blade surface area was found was during winter (July) when *Zostera* biomass is reduced on Mana Bank, yet copepod abundance and number of species is high. It may be that at this time, reduced availability of the phytal substratum impacted upon

Table 8. Mean and relative abundances of the copepod fauna collected in emergence traps (n = 5), emplaced over dense *Zostera* bed, Pauatahanui Inlet, 14 June 1984. Categories are those in Table 6. Values integrate an entire 6 h high tidal phase

Species	Mean number per 104 cm ² trap	SD	%	Category
<i>Halectinosoma hydrofuge</i>	60.4	38.0	24.6	I
<i>Tisbe furcata</i>	57.0	27.7	23.2	B
<i>Bulbamphiascus</i> sp.	46.5	25.6	15.2	S
<i>Ectinosoma melaniceps</i>	32.4	26.1	13.2	I
<i>Porcellidium</i> sp.	25.6	28.2	10.4	B
Unidentified nauplii	16.4	21.9	6.7	-
<i>Paralaophonte</i> sp.	14.3	15.1	4.6	S
<i>Haliclyps</i> sp.	3.7	1.5	0.90	S
<i>Paradactylopodia brevicornis</i>	2.3	1.5	0.73	B
<i>Amphiascus pacificus</i>	2	-	0.16	B
<i>Halectinosoma otakoua</i>	1	-	0.08	S
<i>Quinquelaophonte candelabrum</i>	1	-	0.08	S
Total no. species	11			
Total no. individuals	1226			

the copepod species to force some degree of habitat fractionation on blades. In this way the influence of habitat 'scale' might better predict significant associations between density, species and surface area (see Edgar 1983, Hicks 1985a). Alternatively the more turbulent conditions during winter might resuspend fine particles that had settled on blades over the earlier and more tranquil part of the year. Accumulation of silts on blades would alter the fundamental habitable surface, appreciably reduce the realized surface, and modify the predicted relation between species richness, abundance and surface area (Hicks 1980). Non-significant or even inverse correlations between abundance, diversity and individual blade surface area in summer, when total *Zostera* biomass is higher, implies that either copepod populations are not intimately linked to the 'abundance' (biomass) of *Zostera* (see Nelson 1979), or that such predicted links are out of phase (Stoner 1983), perhaps because of siltation of blades. More experimental work is needed to accurately define which measure of plant abundance might significantly affect density and diversity of the copepod subcommunity. Because of the rather uniform morphology of *Zostera* blades and above ground structures, and the largely unknown behavioural responses of most copepods to vegetative structure, it is conceivable that such relations might not operate in seagrass meiofaunal communities to the extent demonstrated in marine algal systems.

With the revelation here that meiobenthic copepod abundance and species richness are significantly greater inside seagrass beds (blades plus subcanopy sediments) than on closely adjoining unvegetated sand flats, a condition has arisen which reiterates that frequently reported for the macrobenthos (e.g. Kikuchi 1967, Reise 1977, Stoner 1980, 1983, Lewis 1984, Summerson & Peterson 1984 – but see Decho et al. 1985). Hypotheses advanced to explain this pattern include a larval and food accumulation mechanism whereby above-ground seagrass structures (blades, sheaths etc.), act as 'filters' to suspended food and larvae thus concentrating them amongst blades and subcanopy sediments (e.g. Peterson et al. 1984). An alternative view argues inhibition of predatory efficiency with seagrass structures serving to disrupt actively hunting predators such as fish, crab and shrimp. Physical structures of plants provide refuge for prey which are more effectively controlled by predation in habitats without such interrupting structures (see Heck & Orth 1980). Summerson & Peterson (1984) have examined more specifically the distribution of predators inside and outside seagrass beds and propose a modification of this latter hypothesis. It predicts that epibenthic predators themselves use seagrass beds as refuges from higher order predators during daylight, and for safety

reasons, restrict themselves to nocturnal foraging over open unvegetated habitats. The intensity of predation is therefore suspected to be lower the further away from a seagrass refuge used by a predator. While critical field experimental work remains to be done on these aspects as related to meiofaunal populations, results herein have some bearing on this hypothesis.

Sediment-dwelling copepod abundances decline from within dense seagrass beds (Stn 4) to open unvegetated sediment (Stn 2), but increase significantly even further away from beds (Stn 1). At first sight this distribution pattern would tend to support Summerson & Peterson's predictions, with areas immediately adjacent to dense beds (Stns 2 & 3) suffering greatest assumed predatory exploitation (average abundance being half that in dense beds). When account is taken of the natural history of the component species, however, a differing view emerges. First, the species contributing most to total abundance at Stn 1 during this survey was the interstitial form *Paraleptastacus* sp. This species lives deep in the sediment down to the level of the RPD (0 to 6 cm), and does not suffer loss to surface-feeding macrobenthic predators whether or not they reside diurnally in beds. Second, *Parastenhelia megarostrum* is known to be heavily cropped by flatfish predators at Stn 1 (Hicks 1984), and third, those fish species of appropriate size caught from within grass beds have always had guts containing predominantly phytal harpacticoids (pers. obs.). Sediment-dwellers inside dense *Zostera* beds (mainly *Bulbamphiascus* sp., *Paralaophonte* sp. and *Halicyclops* sp.), may thus escape significant predation because of the protective canopy formed by blades (*sensu* Heck & Orth 1980), which may explain the higher mean densities at Stn 4 than in areas with sparser overhead cover (Stns 2 & 3). These features combine to cast doubt on the efficacy of Summerson & Peterson's notion, at least for meiofauna, that predation should decline as a function of increasing distance from seagrass bed refuges utilized by epibenthic predators. Instead it would seem that copepods living on open unvegetated sediments are preyed upon by a suite of either cryptic (e.g. flatfish) or burrowing (e.g. mud crabs) macro-predators whilst seagrass-dwelling species fall prey to a completely different suite of vegetation picker-type predators (*viz.* labrids, syngnathids). The latter are specifically localized amongst the protective cover of seagrass vegetation itself (e.g. Howard & Koehn 1985, pers. obs.). Such a distinction would appear to be more prevalent among macrofauna-meiofauna interactions than the strictly macrofauna-macrofauna interactions alluded to by Summerson & Peterson (1984).

Observations of a sequential 'loss' of individuals from grassbed microhabitats during each high tide necessitated a sampling of the water column immedi-

ately overlying beds. Data accumulated from emergence traps have established conclusively an active swimming of members of the *Zostera* copepod assemblage, with individuals trapped representing the range of species available. During daytime low water periods, high abundances of copepods are generally found associated with the substratum; subsequent daytime high water periods exhibit abundances on sub-canopy sediments and blades that are each reduced when compared to previous low tide values. This same sequence of high-low tide and low-high tide abundances is repeated during night-time tides suggesting a lack of any light-induced emergence cue. The implication from these data is that a substantial component of the fauna was leaving the seagrass bed during the flood tide and returning to it on the ebb. Using similar techniques in an essentially atidal, tropical (Tampa Bay, Florida) seagrass bed dominated by the turtlegrass *Thalassia testudinum*, Bell et al. (1984) have revealed an equivalent emergence phenomenon amongst harpacticoids and to a lesser extent, other components of the meiobenthos. Unlike the tidally-coupled emergence behaviour found in Pauatahanui Inlet, the Tampa Bay data show a pronounced pulse of copepods migrating into the water column at sunset. In the absence of what for the Pauatahanui populations may ultimately prove to be pressure-related cues linked to tidal inundation (Morgan 1984), populations in Florida would seem alternatively to be stimulated by differences in ambient light regime (Walters unpubl.).

Over 86 % of the individuals found to be actively swimming and consequently collected in emergence traps belonged to 5 species. Of these, only *Bulbamphiascus* sp. can be categorized as primarily sedimentary in its habitat choice. The remaining 71 % of individuals are comprised of typically phytal or itinerant species (*Ectinosoma melaniceps* herein categorized as itinerant is frequently considered a phytal species – Dahl 1948, Hagerman 1966, Hicks 1980, Coull et al. 1983). That most migrating individuals from seagrass habitats are associated in some way with the vegetation coincides with what is already known of harpacticoid copepods from algal biotopes. In these, a number of species have been documented as exhibiting well-developed swimming capabilities (see Lang 1948, Hauspie & Polk 1973, Pallares & Hall 1974a, b), with, in some cases, the suggestion of pronounced tidal rhythmicity (Wieser 1952). Active swimming in obligatory sediment-dwelling harpacticoids such as epibenthic-burrowing members of the Cletodidae, some Tachidiidae and some Diosaccidae, has yet to be definitively reported. Recent demonstrations of transport into the water column of epibenthic and infaunal species belonging to these families, as a consequence

of mechanical resuspension due to bottom shear currents (Palmer 1984, Palmer & Gust 1985), have forced a reappraisal of the association of these organisms with bottom sediments (see also Bell & Sherman 1980, Palmer & Brandt 1981, Fleeger et al. 1984). Palmer & Gust's (1985) contention, that the occurrence of copepods in the water column is a passive erosional phenomenon rather than active behavioural emergence, unquestionably holds for their open unvegetated mud site, but cannot be sustained for the faunas of vegetated habitats. Emergence trap samples collected concurrently over dense *Zostera* beds and over unvegetated sediments indicate a significantly different behavioural response from the component faunas of each biotope. Bare sand (Stn 1) is dominated epibenthically by *Parastenhelia megarostrum* which, for a similar ambient substratum abundance, is retrieved over an order of magnitude less than species over a vegetated habitat. The insignificant occurrence of bare sand-dwelling copepods in traps through default, in fact, supports Palmer & Gust (1985), i.e. active swimming is not a feature of strictly sediment-dwelling species. Taking regard of the situation over vegetated sites, however, a significant swimming component exists. Moreover, from a taxo-ecological perspective, the majority of migrating animals belong to typically phytal genera and/or species, previously acknowledged for their swimming prowess. Clearly there is a pronounced divergence in the behaviour of copepod faunas from vegetated and unvegetated systems. The view that passive resuspension is the primary way in which meiofaunal copepods enter the water column does not take sufficient account of the unique differences between such habitats and their resident biota. Systems containing an important phytal component could be expected therefore to contribute some of its members to the water column at certain times (tidally and/or diurnally-nocturnally variable). The precedent of behavioural emergence rhythms in small crustaceans has after all been set, and has a long history in the biological literature (see Morgan 1984).

Active benthic-pelagic exchanges have profound implications for the ecological dynamics of seagrass habitats. Vertical migration into the water column of substantial numbers of copepods at each high tide is a pathway of biomass transfer between benthic and pelagic realms. This organic material is a potential energy source for midwater feeding predators (Robertson & Howard 1978, Burchmore et al. 1984). Copepods migrating during daylight high water may become selected food items for visually feeding fishes which move over grassbeds with the rising tide (pers. obs.). Indeed, tidally invading epibenthic predators might 'stimulate' prey to swim as an escape response (Alldredge & King 1977, Ambrose 1984). If this were so,

then preferential night-time movements could equally be interpreted as a strategy for predator avoidance. Most fishes associated with seagrass beds are daytime feeders (Bell & Harmelin-Vivien 1983, Sogard 1984, Howard & Koehn 1985), with some foraging in the water column during the day, and resting or sleeping close to the substratum at night (Bell & Harmelin-Vivien 1983). One of the most important phytal copepod-feeding fishes residing in *Zostera* beds in Pauatahanui Inlet (*Pseudolabrus celidotus*), can be observed sleeping amongst blades at night. Robertson & Howard (1978), on the contrary, found that fish feeding activity was maintained at night over *Zostera* beds in Australia, but with a switch in the predominant predator and the type of prey selected. The present investigation has established that migration of seagrass copepods occurs at high tide not only at night, but also during the day. It would seem therefore that the utility of vertical excursions into the water column as a tactic to reduce risk of predation, particularly when linked to a diurnal versus nocturnal perspective, is not universally important with respect to seagrass copepods.

Bottom feeding copepods would also carry nutrients from sediments and blades into the water column. Bacterial and microalgal biomass, the predominant food of meiofaunal copepods (Hicks & Coull 1983), would be released as excretory products into the water whereas it might otherwise remain bound to bottom deposits. The involvement of seagrass bed faunas as intermediaries in the broader context of nutrient exchange in estuarine systems has yet to be fully assessed. Despite this a parallel exists whereby transfer of nutrients by fish which move nocturnally from open water to rocky reefs (e.g. Bray et al. 1981) can be viewed similarly to migratory activities of seagrass copepods.

There are also important implications for meiofaunal subcommunity structure. Tidally alternating variations in not only absolute but relative abundance, species richness and species composition, indicate that our traditional view of meiofaunal populations being locally static yet varying temporally needs drastic revision. The dynamic nature of these copepod populations over very short time scales (tidal cycles), demonstrate that rigid sampling routines, usually constrained to low tides because of logistical ease, are providing only part of the complex picture. Upon entering the water column, the potential for enhanced dispersal to new habitat patches, particularly for such well-known opportunists as *Tisbe* (Lopez 1982), together with rapid reorganization of microspatial patterns (Findlay 1981, Hicks 1984), emphasizes the great impact benthic-pelagic links of this kind could have on assemblage structure. All of the above implications have yet to be

critically examined, but currently underway is a detailed analysis of individual species migratory patterns (Bell, Hicks & Walters unpubl.), in an attempt to understand the functional rationale behind emergence behaviour of seagrass copepods.

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