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Small-scale effect of intertidal seagrass (*Zostera muelleri*) on meiofaunal abundance, biomass, and nematode community structure

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Seagrass beds are common features of coastal ecosystems worldwide, and their associated infauna are often more productive and diverse than in unvegetated habitats. Little is known, however, about the ecology of meiofaunal communities living in seagrass sediments. We compared the abundance and biomass of sediment meiofauna inside and outside an intertidal Zostera muelleri *bed in southern New Zealand to assess the impact of seagrass cover on meiofaunal distribution. Nematode community structure, diversity, and feeding groups were also compared between habitats and sediment depths (0–2, 2–5 and 5–10 cm) to evaluate the effect of seagrass on nematode communities. Meiofaunal biomass was significantly higher inside than outside the Z.* muelleri *bed, but secondary productivity inside the bed is likely to have been limited by the availability of labile organic matter. There were significant differences in nematode community structure between unvegetated, sparsely vegetated, and densely vegetated sites (10^2 m scale), as well as between sediment depths (cm scale). No significant differences were found in depth-integrated (0–10 cm) nematode diversity between sites, but vertical gradients in diversity differed between vegetated and unvegetated sites. Epistrate feeders were the most common feeding group in unvegetated sediments whereas most feeding groups were common inside the seagrass bed. Findings from this study indicate that seagrass beds can have a marked impact on infaunal structure and function over small spatial scales through their effect on sediment characteristics and organic matter input. Some unexpected trends observed in the present study, i.e. low meiofaunal biomass at the vegetated sites, and lower abundance of copepods inside than outside the seagrass bed, suggest that the nature of seagrass–invertebrate interactions may depend on habitat characteristics and the identity and ecology of species considered.*

Keywords: meiofauna, nematodes, *Parastenhelia megarostrum*, seagrass, biomass, sediment benthos, trophic groups, New Zealand

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INTRODUCTION

Seagrass beds constitute a conspicuous feature of sheltered soft-shores worldwide, and are amongst the most productive marine communities (Duarte & Chiscano, 1999; Mateo *et al.*, 2006). As a result, the ecology of seagrass beds and their associated macrofaunal communities has attracted considerable attention in recent decades (Kikuchi, 1980; Hemminga & Duarte, 2000). Research to date suggests that the presence of seagrass positively influences macrofaunal abundance, biomass, and diversity through: (1) enhanced particulate organic matter (POM) deposition and retention within vegetated beds; (2) enhanced larval settlement; (3) provision of greater surface area and habitat complexity; (4) provision of food resources; and (5) protection from predators (Fonseca *et al.*, 1982; Heiss *et al.*, 2000; Kharlamenko *et al.*, 2001; Gacia *et al.*, 2003; Atilla *et al.*, 2005; Bos *et al.*, 2007).

Seagrass beds are under increasing pressure from environmental stressors such as eutrophication, increased sediment loads, and chemical contaminants (Ralph *et al.*, 2006). The loss of seagrass beds from coastal ecosystems is likely to have a major impact on the structure and functioning of associated invertebrate communities (Kenworthy *et al.*, 2006); however, some components of seagrass-associated fauna, such as meiofauna, are poorly known. Most meiofaunal studies have focused on epiphytic meiofauna (Novak, 1982; Hall & Bell, 1993; De Troch *et al.*, 2001a; Da Rocha *et al.*, 2006), and a few have investigated the meiofauna living in seagrass bed sediments (Bell *et al.*, 1984; Giere, 2009). Nematodes, which typically dominate meiofaunal communities (Heip *et al.*, 1985), are poorly represented in studies of seagrass-associated meiofauna (e.g. Fisher, 2003), even though they may play an important role in the energetics of these ecosystems (Danovaro *et al.*, 2002).

Several authors have argued that the high bacterial standing stock and/or organic detritus content of seagrass bed sediments have a positive influence on meiofaunal abundance and biomass (Castel *et al.*, 1989; Danovaro, 1996; Danovaro & Gambi, 2002). Experimental evidence has also linked changes in nematode abundance with changes in the amount of fine organic particles associated with the presence of seagrass cover (Edgar, 1999). The high abundances of small

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predators such as shrimps and juvenile flatfish found within seagrass beds may, on the other hand, have adverse effects on meiofaunal abundance (Decho *et al.*, 1985). The shallower redox potential discontinuity (RPD) layer sometimes associated with the high organic load of seagrass bed sediments could affect the vertical distribution of meiofauna by restricting their distribution to oxygenated surface sediments (Barron *et al.*, 2004). The concentration of meiofauna near the sediment surface could, in turn, make them more susceptible to predation (Coull & Bell, 1979; Sogard, 1984).

Meiofaunal diversity and community structure are likely to be affected by the presence of seagrass. Seagrass may affect meiofaunal composition through its effect on sediment characteristics (Ndaro & Olafsson, 1999), organic content (Castel *et al.*, 1989), exposure to currents (Steyaert *et al.*, 2003), and the availability of food sources such as bacteria and benthic microalgae (Danovaro & Gambi, 2002; Fisher, 2003; Fisher & Sheaves, 2003). Meiofaunal assemblages may also be influenced by the complex structure of seagrass rhizomes and the release of oxygen and dissolved organic matter in the sediments by the roots (Osenga & Coull, 1983; Marba *et al.*, 2006).

Nematodes provide a good model for investigating the impact of seagrass on the structure of invertebrate communities due to their high diversity and sensitivity to environmental conditions (Bongers & Ferris, 1999; Moreno *et al.*, 2008). The small size and limited dispersal capabilities of nematodes also make them ideal organisms for studying changes in environmental conditions over small spatial scales. Studying sites over small spatial scales (which differ mostly in the presence or absence of seagrass cover) may provide more meaningful comparisons than studies comparing sites further apart, which may be subject to contrasting environmental conditions (e.g. hydrology and water depth) (Mills & Berkenbusch, 2009). In addition, the effect of seagrass cover on nematode community structure and diversity can be studied both horizontally (metre scale) and vertically (centimetre scale) (e.g. Steyaert *et al.*, 2003).

Nematodes can be assigned to feeding types based on buccal structures (Moens & Vincx, 1997), allowing the effect of seagrass on benthic trophic pathways to be evaluated. Several authors have reported high abundance of microbial- and deposit-feeding nematodes in seagrass meadows, which suggests that detritus is an important food for meiofauna of vegetated sediments (Hopper & Meyers, 1967; Danovaro & Gambi, 2002; Fisher, 2003; Fisher & Sheaves, 2003). This is in agreement with the suggestion that seagrass cover enhances the input of detritus to the benthos relative to bare sediments (Marba *et al.*, 2006). Few studies, however, have compared the diet of meiofauna in seagrass beds and adjacent unvegetated sediments (Leduc *et al.*, 2009).

The paucity of data on the distribution of meiofauna in seagrass beds and adjacent unvegetated sediments makes any generalization about the effects of seagrass cover on the ecology of meiofauna difficult. In the present study, the abundance and biomass of meiofauna in an intertidal *Zostera muelleri* meadow and adjacent unvegetated sediments in Papanui Inlet, southern New Zealand, were compared to test whether the presence of seagrass has a positive effect on meiofaunal abundance and biomass. In addition, nematode community structure, diversity, and feeding groups were compared between habitats, and at different sediment depths, to investigate the effect of *Z. muelleri* on nematode species distribution and feeding ecology. This investigation was part of an integrated study on the role of meiofauna in the energy flows of intertidal benthic communities (Leduc *et al.*, 2009).

MATERIALS AND METHODS

Study location

The study was carried out in Papanui Inlet, southern New Zealand, as described in Leduc *et al.* (2009). Papanui Inlet is an unpolluted sheltered inlet with an area of 3.5 km^2; tides are semidiurnal with a mean tidal range of 1.15 m (Albrecht & Vennell, 2007). Most of the inlet is exposed at low tide and consists of a patchwork of unvegetated sediments and *Zostera muelleri* beds. Three 10 × 10 m sampling sites were used during the study: an unvegetated site (45°50′53.1″S 170°42′40.9″E), a sparsely vegetated site (1250 shoots m^{-2}; 45°50′46.8″S 170°42′35.1″E) and a densely vegetated site (8920 shoots m^{-2}; 45°50′48.1″S 170°42′35.7″E). The sites were within 150 m of each other, and situated at least 30 m from the edge of the *Z. muelleri* meadow. The unvegetated site and the densely vegetated site were sampled in June 2005 and January 2006. The sparsely vegetated site was added in January 2006 to provide comparison between densely and sparsely vegetated habitats.

Sampling

Sediment characteristics were measured in June 2005 and January 2006. Sediment samples ($N = 5$) were obtained using randomly allocated cores (2.6 cm diameter) taken to a depth of 5 cm. Samples were split into 0–2 and 2–5 cm depth fractions and stored in dark plastic containers. Separate cores were taken for water and organic matter content, sediment granulometry and pigment analyses.

Meiofauna samples ($N = 3–4$) were obtained using randomly allocated cores (2.6 cm diameter) to a depth of 5 cm in June 2005 and to a depth of 10 cm in January 2006. Samples were split into 0–2 and 2–5 cm depth fractions in June 2005 and 0–2, 2–5, and 5–10 cm depth fractions in January 2006. Seagrass blades were cut at the sediment surface prior to taking the cores at the vegetated sites. An aluminium casing with handles was used to help penetration of the core into the sediment at the densely vegetated site, which was characterized by a dense seagrass rhizome mat. Meiofauna samples were stained with rose Bengal and fixed in warm (70°C) 5% formalin.

Laboratory procedures

Sediment water content was determined by weight loss after drying at 60°C for 48 hours, and organic content was measured by loss on ignition of dried samples at 550°C for 5 hours. Sediment granulometry was determined by wet (silt fraction) and dry sieving (sand fraction) of fresh sediment samples no more than 2 days after collection (Bale & Kenny, 2005). Chlorophyll-*a* and phaeophytin were extracted by boiling homogenized and freeze-dried sediment samples in 90% ethanol. The extract was analysed using a spectrophotometer (Beckman DU-70) and included an acidification step to separate degradation products from chlorophyll-*a* (Sartory, 1982).

Meiofauna samples were washed on a 500 μm sieve to remove large particles and macrofauna, and on a 45 μm sieve to retain meiofauna. Meiofauna were extracted from the sieved sediments by Ludox flotation, transferred to pure glycerol, and mounted onto permanent slides (Somerfield & Warwick, 1996). Meiofauna were counted and identified to major taxa under a compound microscope (100× magnification). A sub-sample of 100 individuals (or all individuals if fewer were present in the sample) of each taxon was randomly selected and used for biomass determination. Meiofaunal biomass was measured using video image analysis (Grove *et al*., 2006). Body volumes were converted to dry weight by assuming a relative density of 1.13 and a dry:wet weight ratio of 0.25 (Feller & Warwick, 1988). Foraminiferans and soft-bodied taxa such as turbellarians are not quantitatively extracted using the Ludox method and were excluded from the analysis.

In January 2006 at least 150 nematodes (or all individuals if fewer were present in the sample) from each site and depth fraction (0–2, 2–5 and 5–10 cm) were randomly selected and mounted separately for community structure analysis. Three replicates were analysed for each site and depth combination. Specimens were identified to genus/putative species using the descriptions by Platt & Warwick (1983, 1988) and Warwick *et al.* (1998), as well as the primary literature. Nematodes were assigned to feeding groups based on their buccal structures using the modified classification of Wieser (1953) proposed by Moens & Vincx (1997): microvores (M), deposit feeders (DF), epistrate feeders (EF), ciliate feeders (CF), facultative predators (FP) and predators (P).

Data analysis

Data were assessed for normality and homogeneity of variance using the Anderson–Darling normality test and Levene's test, respectively (Quinn & Keough, 2009). When necessary, data were log(x + 1)-transformed to meet assumptions for parametric analyses. Sediment characteristics within each depth fraction and sampling time were compared using *t*-tests (June 2005) and one-way ANOVA with Tukey's *post-hoc* test (January 2006).

Nematode, copepod, and total meiofaunal abundance and biomass in the top 5 cm of sediments were compared between the unvegetated and densely vegetated sites and between sampling times (June 2005 and January 2006) using two-way ANOVA. A comparison of nematode density (ind. cm^{-3}) was carried out on the January 2006 data across all three sites and sediment depths using two-way ANOVA with a split-plot design (replicates nested within sites but not within depths) (Steyaert *et al*., 2003). Nematode diversity indices (i.e. Hill's diversity N_1, species evenness J', and expected number of species in a sample of 50 individuals ES(50)) were compared between sites and sediment depths in the same way. Depth-integrated diversity indices in January 2006 were compared between sites using one-way ANOVA. Nematode community structure from the three sites and sediment depths (January 2006) was compared by constructing Bray–Curtis similarity matrices from square-root transformed relative abundance data in PRIMER v6 (Clarke, 1993). Differences in community structure were tested using two-way ANOSIM.

RESULTS

Sediment characteristics

Sediment at the study sites consisted of well-sorted fine sand (Table 1). Sediments at the densely vegetated site had higher silt, water, organic matter content, and phaeophytin concentrations than at the unvegetated site ($P < 0.05$). Differences were more pronounced in January 2006 than June 2005. Sediment characteristics at the sparsely vegetated site were intermediate between those of the unvegetated and densely vegetated sites. The depth of the redox potential discontinuity (RPD) layer was deeper than 10 cm at the unvegetated and sparsely vegetated sites, and approximately 2 cm at the densely vegetated site.

Meiofaunal abundance and biomass

Mean meiofaunal abundance and biomass in the top 5 cm of sediments ranged from 2519 to 4979 ind. 10 cm^{-2} and from 251 to 528 mgDW m^{-2}, respectively (Table 2). There was

Table 1. Sediment characteristics at the unvegetated, sparsely vegetated, and densely vegetated sites at Papanui Inlet in winter (June 2005) and summer (January 2006). Results are mean (SD) (N = 5). Within each sampling time, values followed by different letters were statistically different ($P < 0.05$) from corresponding values at the other site(s) for that sediment depth interval (*t*-test or one-way ANOVA with Tukey's *post-hoc* test).

	Depth (cm)	Mean grain size (μm)	Silt content (%)	Water content (%)	Organic matter content (%)	Chlorophyll-*a* (μg/gDW)	Phaeophytin (μg/gDW)
June 2005							
Unvegetated	0–2	160.9 (2.3)^{a}	0.63 (0.18)^{a}	22.4 (0.5)^{a}	0.25 (0.05)^{a}	4.01 (0.66)^{a}	0.71 (0.23)^{a}
	2–5	163.4 (1.3)^{a}	0.95 (0.18)^{a}	21.6 (1.1)^{a}	0.29 (0.06)^{a}	3.10 (0.63)^{a}	0.86 (0.22)^{a}
Densely vegetated	0–2	161.9 (6.1)^{a}	5.90 (1.46)^{b}	26.8 (2.4)^{b}	1.00 (0.28)^{b}	5.74 (2.33)^{a}	3.12 (1.62)^{b}
	2–5	159.0 (4.4)^{a}	3.97 (0.98)^{b}	30.5 (3.9)^{b}	1.10 (0.43)^{b}	4.76 (0.90)^{a}	1.74 (0.63)^{b}
January 2006							
Unvegetated	0–2	162.7 (1.1)^{a}	0.64 (0.09)^{a}	21.7 (0.3)^{a}	0.34 (0.03)^{a}	2.39 (0.50)^{a}	1.31 (0.39)^{a}
	2–5	161.9 (2.3)^{a}	0.92 (0.29)^{a}	21.3 (0.3)^{a}	0.33 (0.06)^{a}	1.02 (0.16)^{a}	0.99 (0.27)^{a}
Sparsely vegetated	0–2	164.9 (1.6)^{a}	3.13 (0.72)^{b}	22.6 (1.0)^{a}	0.41 (0.07)^{a}	2.91 (0.14)^{a}	2.81 (0.51)^{b}
	2–5	164.4 (0.8)^{a}	2.54 (0.56)^{b}	21.8 (0.8)^{a}	0.46 (0.11)^{a}	2.15 (0.22)^{b}	1.70 (0.31)^{b}
Densely vegetated	0–2	125.9 (2.6)^{b}	15.88 (1.26)^{c}	33.1 (2.9)^{b}	1.36 (0.39)^{b}	7.85 (0.88)^{b}	10.69 (2.30)^{c}
	2–5	153.5 (1.2)^{b}	9.40 (0.21)^{c}	26.4 (2.1)^{b}	0.93 (0.26)^{b}	3.61 (0.44)^{b}	2.99 (0.58)^{c}

Table 2. Meiofaunal abundance (ind. 10 cm^{-2}) and biomass (mgDW m^{-2}) at the three study sites at Papanui Inlet. Results are mean (SD) (N = 3–4). Nd, no data.

	Unvegetated			Sparsely vegetated			Densely vegetated		
	Nematodes	Copepods	Total	Nematodes	Copepods	Total	Nematodes	Copepods	Total
Abundance									
June 2005									
0–2 cm	1227 (798)	1081 (212)	2385 (1012)	nd	nd	nd	3956 (2076)	39 (25)	4032 (2077)
2–5 cm	2020 (1676)	39 (37)	2062 (1717)	nd	nd	nd	1275 (350)	1 (1)	1282 (349)
January 2006									
0–2 cm	1280 (252)	463 (91)	1747 (231)	2987 (638)	89 (77)	3129 (685)	3528 (1251)	17 (7)	3545 (1246)
2–5 cm	772 (354)	0 (0)	772 (354)	1630 (287)	0 (0)	1634 (289)	1428 (736)	0 (0)	1434 (740)
5–10 cm	381 (162)	0 (0)	381 (162)	1222 (505)	0 (0)	1225 (505)	185 (154)	0 (0)	187 (153)
Biomass									
June 2005									
0–2 cm	93 (58)	167 (35)	262 (85)	nd	nd	nd	312 (135)	11 (8)	323 (134)
2–5 cm	73 (63)	2 (2)	75 (63)	nd	nd	nd	125 (16)	0 (0)	125 (16)
January 2006									
0–2 cm	102 (16)	91 (42)	193 (55)	215 (25)	20 (19)	235 (52)	369 (74)	6 (2)	375 (73)
2–5 cm	58 (20)	0 (0)	58 (20)	174 (42)	0 (0)	174 (42)	153 (82)	0 (0)	153 (82)
5–10 cm	27 (12)	0 (0)	27 (12)	98 (44)	0 (0)	98 (44)	16 (16)	0 (0)	16 (16)

no significant difference in total meiofaunal abundance between sites or sampling time (two-way ANOVA, $P > 0.05$), but meiofaunal biomass was significantly higher at the densely vegetated site than at the unvegetated site (483 versus 294 mgDW m^{-2}, $P < 0.05$; Table 3). Nematodes and copepods represented over 95% of meiofaunal abundance and biomass at the study sites; other taxa were therefore excluded from further statistical analysis. Nematode abundance and biomass were significantly higher at the densely vegetated site than at the unvegetated site (two-way ANOVA, $P < 0.05$), whereas copepod abundance and biomass showed the opposite trend ($P < 0.001$).

Nematode abundance, diversity, and community structure

Two-way ANOVA revealed the presence of significant site, sediment depth and interaction effects on nematode density (expressed as ind. cm^{-3}) in January 2006 (Table 4). Mean nematode density decreased with depth at all sites, but most markedly at the vegetated sites (Figure 1). Nematode density at 0–2 cm depth was 2–3 times greater at the vegetated sites than at the unvegetated site, but little between-site difference was observed at 2–5 and 5–10 cm depths.

A total of 84 nematode species was identified: 45 at the unvegetated site, 59 at the sparsely vegetated site and 57 at the densely vegetated site. The unvegetated site had 10 species exclusive to that site while the sparsely and densely vegetated sites had 8 and 13 unique species, respectively. Two-way ANOVA comparing nematode diversity across sites and sediment depths revealed significant interaction effects for all diversity indices (Table 4). Diversity increased with depth at the unvegetated site, whereas the opposite trend was observed at the vegetated sites (Figure 1). There was no significant difference in depth-integrated diversity indices between sites (one-way ANOVA, $P > 0.05$).

The nematode community at the unvegetated site was dominated by *Metachromadora* sp., *Microlaimus falciferus* and *Microlaimus* sp. 1 (Table 5 & Appendix). The most common species at the sparsely vegetated were *Chromaspirinia* sp. 1, *Chromaspirinia* sp. 2, *Paramonohystera* sp. 2 and *Microlaimus* sp. 1. At the densely vegetated site, *Desmolaimus courti*, *Chromaspirinia* sp. 1, *Paracanthonchus* sp. and *Aponema subtile* dominated. The two-dimensional MDS ordination plot and two-way ANOSIM showed a

Table 3. Two-way ANOVA testing for differences in meiofauna, nematode, and copepod abundance and biomass across the study sites and sampling times. Probability for main effects and interactions shown in bold type are significant at α = 0.05.

Source	df	Total meiofauna			Nematodes			Copepods		
		Mean squares	F-ratio	P	Mean squares	F-ratio	P	Mean squares	F-ratio	P
Abundance										
Time	1	0.037	0.87	0.373	0.016	0.17	0.691	0.287	6.69	**0.029**
Site	1	0.134	3.18	0.105	0.379	5.96	**0.035**	0.588	153.71	**<0.001**
Time*site	1	0.023	0.56	0.473	0.006	0.09	0.771	0.029	0.68	0.430
Error	10	0.042			0.063			0.043		
Biomass										
Time	1	0.000	0.00	0.967	0.005	0.39	0.545	0.009	10.97	**0.008**
Site	1	0.121	7.69	**0.020**	0.343	24.47	**0.001**	0.042	47.62	**<0.001**
Time*site	1	0.027	1.71	0.220	0.007	0.52	0.489	0.002	2.46	0.148
Error	10	0.016			0.014			0.056		

Table 4. ANOVA tests for differences in nematode abundance (N), Hill's diversity (N_1), species evenness (J'), and expected number of species (ES(50)) between sites and sediment depths at Papanui Inlet, January 2006. Probability for main effects and interactions shown in bold type are significant at $\alpha = 0.05$.

Variable	Source	df	Mean squares	F-ratio	*P*
N	Site	2	0.40408	8.93	**0.016**
	Depth	2	1.35218	37.46	**<0.001**
	Site*depth	4	0.22278	6.17	**0.006**
	Error	12	0.03609		
N_1	Site	2	0.00787	0.91	0.453
	Depth	2	0.00530	0.64	0.543
	Site*depth	4	0.07096	8.61	**0.002**
	Error	12	0.00824		
J'	Site	2	0.00065	2.43	0.169
	Depth	2	0.00030	1.58	0.246
	Site*depth	4	0.00027	6.23	**0.006**
	Error	12	0.00019		
ES(50)	Site	2	0.00615	1.92	0.227
	Depth	2	0.00893	1.95	0.185
	Site*depth	4	0.01814	3.96	**0.028**
	Error	12	0.00459		

significant effect of site ($R = 0.981$, $P = 0.1\%$) and depth ($R = 0.781$, $P = 0.1\%$) on nematode community structure (Figure 2; Table 6). Pairwise comparisons showed significant differences between all sites and depths. Top (0–2 cm) and bottom (5–10 cm) layers were the most different, whereas middle (2–5 cm) and bottom layers were most similar. Pairwise comparisons, however, should be treated with caution since fewer than 4 replicates were compared (Clarke, 1993).

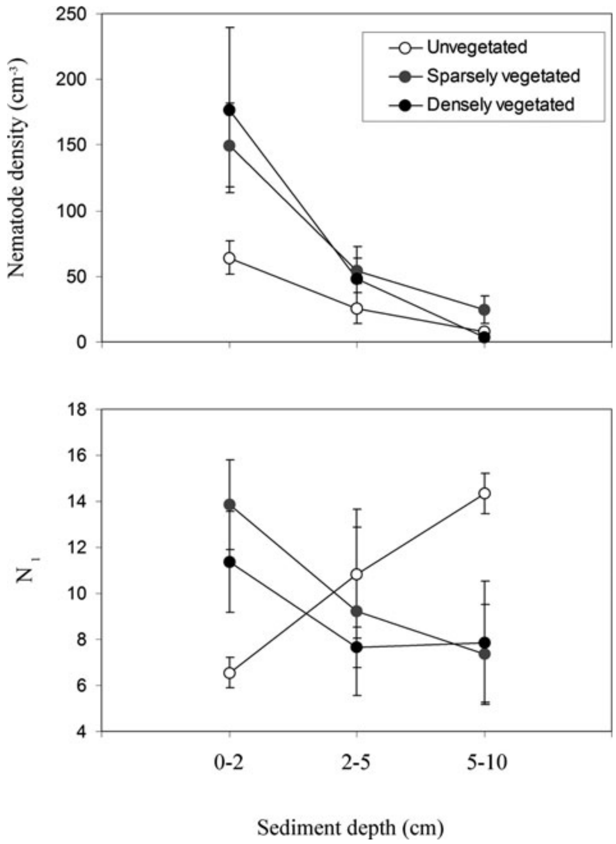

Fig. 1. Mean (N = 3) nematode density and Hill's diversity (N_1) at the three Papanui Inlet study sites and sediment depths, January 2006. Error bars are standard deviation from the mean.

Nematode feeding groups

Predators and facultative predators represented less than 2% of feeding group composition at all sites and depths, and were excluded from the graphical representation for clarity. Epistrate feeders strongly dominated (84% of total) the surface nematode community at the unvegetated site (Figure 3). Epistrate feeders decreased in deeper sediment layers whereas deposit feeders and microvores increased. Microvores were the most common feeding group (34–38% of total) in surface sediments of both vegetated sites, followed by epistrate feeders (30–33%), deposit feeders (20–23%) and ciliate feeders (10%). Epistrate feeders were dominant in deeper sediment layers at the sparsely vegetated site, whilst microvores and deposit feeders decreased. This pattern was mostly a reflection of the greater abundance of *Chromaspirinia* spp. 1 and 2 in deeper sediments at that site. Epistrate feeders were more abundant at 2–5 cm depth at the densely vegetated site, but decreased again at 5–10 cm depth, where deposit feeders dominated.

DISCUSSION

Sediment characteristics

Higher levels of organic matter, fine particles, chlorophyll-*a*, and phaeophytin in seagrass bed sediments are consistent with enhanced detritus deposition inside vegetated areas (Marba *et al*., 2006). The input of seston to the sediment of Papanui Inlet, however, is likely to have been limited; analysis of the isotopic and fatty acid composition of sediments at the study sites suggests that other organic matter sources, such as macrophyte detritus and benthic microalgae, were the main contributors (Leduc *et al*., 2009).

Between-site differences in sediment characteristics were most pronounced for the unvegetated and densely vegetated site, which suggests that the effect of *Zostera muelleri* on sediment characteristics (and associated benthic communities, see below) varies depending on shoot density (Webster *et al*., 1998). Intertidal beds of *Zostera muelleri* have been shown to baffle currents and promote retention of fine particles (Heiss *et al*., 2000), despite the small length (about 12 cm) of the blades in this species. The shoot density (9000 m^{-2}) recorded from the dense *Z. muelleri* site is close to the maximum densities reported for *Zostera* (Ismail, 2001; Lee *et al*., 2006).

Meiofaunal distribution

The greater nematode abundance and biomass recorded inside relative to outside the *Zostera muelleri* bed in this study is consistent with earlier findings. The evidence available to date suggests that nematodes respond positively to the finer, organically-rich sediments associated with seagrass meadows (Castel *et al*., 1989; Danovaro, 1996; Edgar, 1999; Danovaro *et al*., 2002), as observed in the present study.

Most studies comparing the abundance of copepods inside and outside seagrass beds found higher copepod densities in vegetated than unvegetated areas (Ansari & Parulekar, 1994;

Table 5. Percentage contribution of the eight most dominant nematode species to total nematode community composition at each site and sediment depth, January 2006.

Site	Sediment depth					
	0–2 cm		**2–5 cm**		**5–10 cm**	
	Species	**%**	**Species**	**%**	**Species**	**%**
Unvegetated	*Microlaimus falciferus*	43.6	*Microlaimus* sp. 1	24.6	*Metachromadora* sp.	17.6
	Metachromadora sp.	24.4	*Metachromadora* sp.	20.2	*Odontophora* sp.	11.2
	Chromadorita sp.	3.3	*Paramonohystera* sp. 2	6.3	*Microlaimus* sp. 1	7.3
	Atrochromadora sp.	2.7	*Eubostrichus* sp.	4.9	*Metadasynemoides* sp.	5.6
	Metadasynemoides sp.	2.0	*Pseudochromadora* sp.	4.9	*Eubostrichus* sp.	5.4
	Morlaixia sp.	1.8	*Chromaspirinia* sp. 2	4.6	*Gonionchus* sp.	4.7
	Dasynemoides sp.	1.8	*Daptonema* sp. 2	4.17	*Paramonohystera* sp. 2	4.0
	Paramonohystera sp. 1	1.3	*Metadasynemoides* sp.	3.7	*Campylaimus* sp.	4.0
Sparsely vegetated	*Aponema subtile*	19.8	*Chromaspirinia* sp. 1	30.1	*Chromaspirinia* sp. 2	30.4
	Paramonohystera sp. 2	16.1	*Paramonohystera* sp. 2	15.4	*Chromaspirinia* sp. 1	25.8
	Microlaimus sp. 1	12.4	*Odontophora* sp.	11.7	*Desmolaimus courti*	10.7
	Daptonema sp. 2	9.3	*Microlaimus* sp. 1	11.0	*Microlaimus* sp. 2	8.7
	Odontophora sp.	7.8	*Chromaspirinia* sp. 2	9.7	*Metalinhomoeus* sp. 1	2.9
	Chromadorita sp.	7.4	*Daptonema* sp. 2	5.4	*Microlaimus* sp. 1	2.9
	Desmolaimus courti	2.1	*Cobbia* sp. 2	4.3	*Odontophora* sp.	2.2
	Cobbia sp. 2	2.1	*Microlaimus* sp. 2	1.9	*Eubostrichus* sp.	1.8
Densely vegetated	*Aponema subtile*	18.0	*Chromaspirinia* sp. 1	17.8	*Desmolaimus courti*	33.3
	Paramonohystera sp. 2	11.9	*Paracanthonchus* sp.	16.4	*Diplolaimella* sp.	15.2
	Desmolaimus courti	9.1	*Desmolaimus courti*	12.6	*Chromaspirinia* sp. 2	15.2
	Chromaspirinia sp. 1	8.1	*Chromaspirinia* sp. 2	11.9	*Theristus* sp. 2	5.2
	Odontophora sp.	7.9	*Diplolaimella* sp.	11.7	*Aponema subtile*	3.4
	Paracanthonchus sp.	7.3	*Theristus* sp. 2	8.6	*Chromaspirinia* sp. 1	3.0
	Chromadora sp. 2	6.3	*Odontophora* sp.	5.6	*Cobbia* sp. 3	2.6
	Sabatieria annulata	5.5	*Camacolaimus* sp.	2.3	*Metachromadora* sp.	2.2

Guerrini *et al.*, 1998; Ndaro & Olafsson, 1999; De Troch *et al.*, 2001b). Studies in intertidal habitats of New Zealand, however, have found that copepod densities were either the same (Iwasaki, 1993) or higher in bare sand relative to nearby *Zostera muelleri* beds (Hicks, 1986). It is possible that the small size and simple structure of *Z. muelleri* does not promote high copepod densities to the same extent as larger, more structurally complex seagrass species (Hicks, 1986; De Troch *et al.*, 2001b). Moreover, shallow seagrass beds may not increase meiofaunal densities to the same extent as deeper seagrass beds (De Troch *et al.*, 2001b). The most common species in intertidal soft shores of New Zealand, *Parastenhelia megarostrum*, reaches very high densities in unvegetated habitats (Hicks, 1984), although it is not clear why this species should prefer unvegetated sediments. It is possible that the presence of dense seagrass canopy prevents the growth of preferred food sources such as benthic microalgae (Leduc *et al.*, 2009). Alternatively, the shallower oxic zone associated with the greater amount of fine particles and detritus found in vegetated sediments may negatively impact populations of harpacticoid copepods (Wetzel *et al.*, 2001). Further research

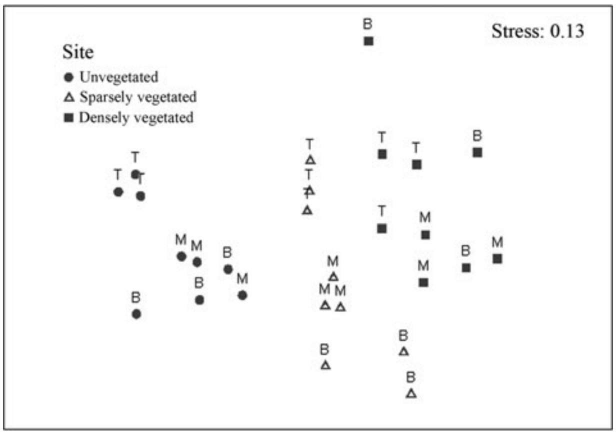

Fig. 2. Two-dimensional multidimensional scaling configuration for nematode species abundance in Papanui Inlet, January 2006. T (top), M (middle), and B (bottom) refer to sediment depths 0–2, 2–5 and 5–10 cm, respectively.

Table 6. Two-way ANOSIM results testing differences in nematode community structure between three sites (unvegetated, sparsely vegetated and densely vegetated) and sediment depths (bottom = 5–10 cm, middle = 2–5 cm, top = 0–2 cm), with details of global and pairwise comparisons; 999 permutations were run for each comparison. Results in bold are significant at α = 0.05 (global R value) or 0.017 (pairwise comparisons with Bonferroni corrections).

Factor	R	Significance level %
Site		
Global ANOSIM	0.981	**0.1**
Unvegetated—densely vegetated	1.0	**0.2**
Unvegetated—sparsely vegetated	1.0	**0.2**
Densely vegetated—sparsely vegetated	0.951	**0.1**
Sediment depth		
Global ANOSIM	0.781	**0.1**
Top—middle	0.889	**0.2**
Top—bottom	0.938	**0.6**
Middle—bottom	0.603	**0.2**

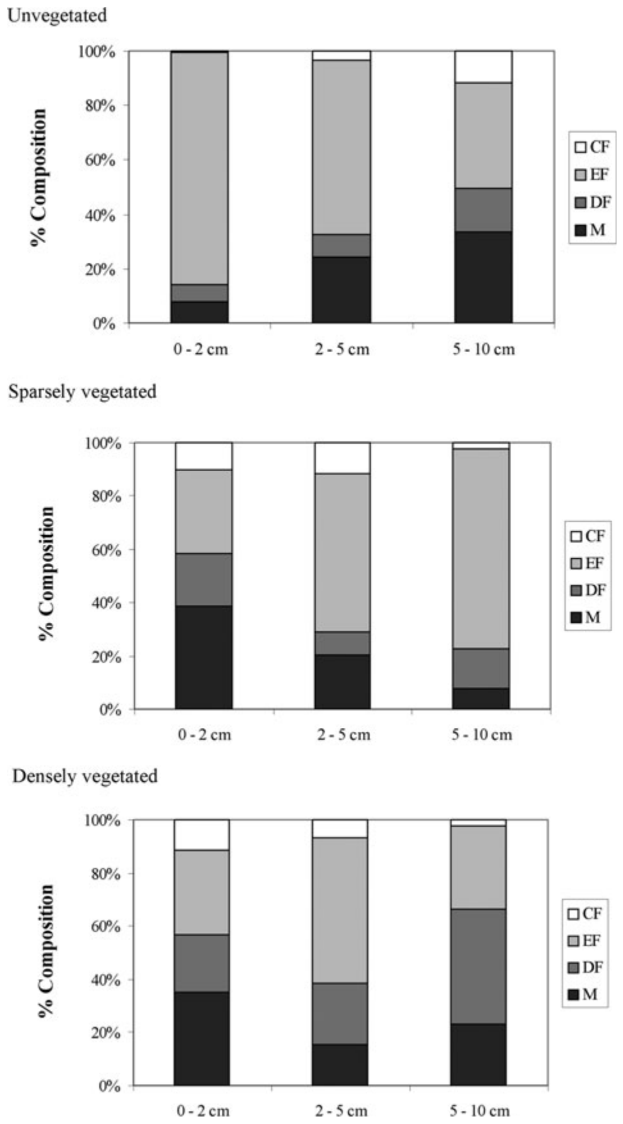

Fig. 3. Composition of nematode feeding groups at the unvegetated, sparsely vegetated, and densely vegetated sites at different sediment depths, January 2006. M, microvores; DF, deposit feeders; EF, epistrate feeders; CF, ciliate feeders.

is required to better understand the mechanisms behind this unexpected pattern.

The mean copepod densities observed in the surface (0–2 cm) layer at the unvegetated site (463–1081 10 cm^{-2}) are in the upper range of values recorded for *Parastenhelia megarostrum* (Hicks, 1984), and amongst the highest reported for harpacticoid copepods (Hicks, 1985). Similar abundances of 1727 and 1283 10 cm^{-2} were reported for *Platychelipus littoralis* on a mudflat in Southampton Water (Barnett 1970, cited in Hicks, 1984) and for *Huntemannia jadensis* on a sandy beach in Puget Sound (Feller, 1980), respectively.

Meiofaunal biomass

Meiofaunal biomass was about 50% greater at the densely vegetated site than at the unvegetated site. This value, however, is relatively small compared to the 4- and 8-fold difference in organic matter and pigment content, respectively, between these sites. This discrepancy suggests that the trophic transfer efficiency between sediment organic matter and meiofauna is lower inside the seagrass bed than outside. Based on the organic carbon content of sediment and meiofauna at the study sites (Leduc *et al.*, 2009), the trophic transfer efficiencies (here calculated as the ratio of meiofauna carbon to sediment organic carbon) at the sparse and unvegetated sites are 3 and 5 times higher than at the dense seagrass site, respectively. The fatty acid profile of sediment organic matter at the densely vegetated site indicates that seagrass detritus (a refractory food source) is a major contributor, whereas benthic microalgae (a labile food source) may be more important at the sparsely vegetated and unvegetated sites (Leduc *et al.*, 2009). These findings are consistent with the suggestion that meiofaunal production in seagrass beds is limited by the amount of labile organic matter available (Danovaro, 1996).

Meiofaunal biomass at the vegetated sites was low compared to published values from seagrass beds ($\leq$0.5 versus 2–10 gDW m^{-2}) (Tietjen, 1969; Castel *et al.*, 1989; Danovaro & Gambi, 2002; Danovaro *et al.*, 2002). In addition, meiofaunal biomass represented $<$2% of macrofaunal biomass at the study sites (D. Leduc, unpublished data), which suggests that the contribution of meiofauna to secondary production was low. This is in contrast with studies reporting a substantial contribution of meiofauna to benthic energy flows in seagrass beds (Castel *et al.*, 1989; Danovaro & Gambi, 2002; Danovaro *et al.*, 2002). Meiofauna usually represent about 10% of macrofaunal biomass in shallow littoral sediments (Giere, 2009), but values as low as 1–4%, and up to about 50%, have been reported (Warwick *et al.*, 1979; Witte & Zijlstra, 1984). The ratio of macrofaunal to meiofaunal biomass tends to increase from muddy to sandy sediments (Castel *et al.*, 1989; Giere, 2009). This pattern could be due to a generally lower abundance of nematodes (the dominant meiofaunal taxon) in coarser sediments (Heip *et al.*, 1985), whereas suspension feeding bivalves, which usually represent 30–60% of macrobenthic biomass in coastal sediments (Ricciardi & Bourget, 1999), are usually more common in sandy sediments (Levinton, 1995). The venerid bivalve *Austrovenus Stutchburyi*, in particular, is known to reach very high densities ($>$1000 m^{-2}) in sheltered soft shores of New Zealand (Larcombe, 1971; Dobbinson *et al.*, 1989).

Nematode distribution and community structure

Data on the vertical distribution of nematodes at the study sites show that the positive effect of seagrass on nematode abundance is mostly restricted to the upper 2 cm of sediment. Biotic factors such as the greater silt/clay content and greater amount of organic material available inside than outside the seagrass bed are likely to be important in promoting higher nematode abundance in vegetated areas (Edgar, 1999), but abiotic factors may also be involved. Strong hydrodynamic conditions, for example, may limit the abundance of nematodes in surface sediments of unvegetated, sandy habitats (Steyaert *et al.*, 2003). More pronounced desiccation stress in unvegetated habitats may also induce a downward migration in some meiofaunal taxa (McLachlan *et al.*, 1977). Low nematode abundance in the deepest (5–10 cm) sediment layer of the densely vegetated site relative to the other sites is likely to have been the result of anoxic conditions and high sulphide levels (Hendelberg & Jensen, 1993; Wetzel *et al.*, 1995; Steyaert *et al.*, 2003). This is supported by the observation of a sharp transition between pale and black sediments at a depth of about 2 cm at the dense *Z. muelleri* sites, whereas no such transition was observed at the other two sites.

The surface (0–2 cm) nematode community at the unvegetated site was strongly dominated by *Microlaimus falciferus* and *Metachromadora* sp. (together representing 68% of total nematode abundance) and was characterized by low diversity. Nematode diversity at the vegetated sites, in contrast, was highest in surface sediments. Changes in nematode diversity are associated with a variety of factors such as sediment granulometry (Giere, 2009; Steyaert *et al.*, 1999, 2003), salinity (Soetaert *et al.*, 1995), disturbance (Austen *et al.*, 1998), organic enrichment (Schratzberger & Warwick, 1998) and the nature of organic matter (Danovaro & Gambi, 2002). Higher diversity near the surface of vegetated sites relative to the unvegetated site was probably the result of two main factors: (1) the provision of a sheltered environment by the seagrass blades compared to unvegetated sediments; and (2) the presence of organic particles of various origins and sizes, which would provide more opportunities for niche partitioning based on food and micro-habitat preferences (Edgar, 1999; Danovaro & Gambi, 2002). The low diversity at 0–2 cm depth at the unvegetated site could be explained by strong hydrodynamic and food-stressed conditions present near the surface (as suggested by low organic matter and silt/clay content). Low nematode diversity in surface sediments of an intertidal sandy site of the Westerschelde estuary was also ascribed to strong hydrodynamic conditions and tidal disturbance (Steyaert *et al.*, 2003). The low diversity observed below 2 cm depth at the dense *Z. muelleri* site may be the result of low oxygen concentrations, which would allow only a limited number of physiologically-adapted species to survive.

Several common species that were most abundant in vegetated habitats, such as *Aponema subtile*, *Sabatieria annulata*, *Desmolaimus courti*, and *Diplolaimella* sp., belong to taxa that are often found in sediments rich in organic matter and/or low in oxygen (e.g. Villano & Warwick, 1995; Schratzberger *et al.*, 2006; Steyaert *et al.*, 2007; Portnova, 2009). Species restricted to unvegetated sediment, such as *Dasynemoides* sp., *Metadasynemoides* sp., and, to a lesser extent, *Microlaimus falciferus*, *Campylaimus* sp., and *Morlaixia* sp., are characterized by ornamented cuticles. Species with thick and/or ornamented cuticles are common in sandy sediments (Heip *et al.*, 1985), probably because elaborate cuticular ornamentation aids locomotion and helps prevent mechanical damage in coarse, unstable sediments (Ward, 1975). In addition, *M. falciferus*, which dominated surface nematode assemblages in unvegetated sediments, possesses numerous mucus-producing glands which may help anchor the animal to sediment particles and reduce desiccation stress at low tide (Turpeenniemi & Hyvarinen, 1996; Leduc & Wharton, 2008). Overall, nematodes in vegetated sediments show a tendency for adaption to high organic matter input and low oxygen concentration whereas nematodes living in nearby unvegetated sediments are better adapted to live in strongly hydrodynamic conditions.

Nematode feeding groups

The strong dominance of epistrate feeders in the top 2 cm of unvegetated sediments suggests that benthic microlagae were the most important food source at that site. Microvores were the dominant feeding group in the top 2 cm of vegetated sediments, but epistrate feeders, deposit feeders, and ciliate feeders were also common, suggesting a greater diversity of available food resources than in unvegetated sediments. Macrophyte detritus and benthic microalgae are both potential food sources at the vegetated sites. These results are consistent with the findings of a biomarker study carried out at the same sites in January 2006, which indicated that benthic microalgae and macrophyte detritus were the most likely food sources for nematodes at the unvegetated and vegetated sites, respectively (Leduc *et al.*, 2009). Isotopic and fatty acid biomarkers of copepods (which dominated meiofaunal production at the unvegetated site) and nematodes from the unvegetated site were also consistent with benthic microalgae as the main carbon source (Leduc, 2009; Leduc *et al.*, 2009).

The relative abundance of epistrate feeders at the unvegetated site declined gradually with depth, whilst microvores, ciliate feeders, and deposit feeders increased. This shift in the composition of trophic groups suggests that the contribution of benthic microalgae to the diet of nematodes declined in deeper sediment layers whereas other food sources, such as bacteria and protists, became more important. The greater dominance of epistrate feeders (mostly *Chromaspirinia* spp.) in deeper (2–10 cm) sediment layers of the vegetated sites was somewhat unexpected. Microalgae growing along macrofaunal burrows (as evidenced by an orange coloration of burrow linings, D. Leduc personal observation) may be an important food source for nematodes, which could explain subsurface maxima in the distribution of this trophic group. Both *Chromaspirinia* spp. have a slender shape (length to maximum width ratio >60), a common characteristic of nematode species living in thiobiotic environments (Giere, 2009). It is therefore possible that these species live in close association with the seagrass roots in the thin oxygenated layer surrounding the rhizosphere. Some uncertainty remains with the classification of nematode feeding types, and *Chromaspirinia* spp. may rely on other food sources such as bacteria (Moens & Vincx, 1997; Koller *et al.*, 2006), or even dissolved organic matter exuded by seagrass roots. The deepest sediment layer at the dense seagrass site was dominated by *Desmolaimus courti*, a deposit feeder. Species of this family have been found to be abundant in the oxic zone surrounding polychaete burrows (Wetzel *et al.*, 1995). This habitat preference could explain the high variability in the abundance of this species (0–70 per core) in the deepest (5–10 cm) sediment layer of the dense *Z. muelleri* site.

The near absence of predators and facultative predators in this study contrasts with previous studies reporting high numbers of these feeding groups in seagrass beds (Hopper & Meyers, 1967) and unvegetated sand (Steyaert *et al.*, 2003). It is possible that the sediment characteristics at the study sites are unfavourable to predators. For example, mean grain size below 180 μm, as reported in this study (125–164 μm), led to severely reduced predation by *Enoploides longispiculosus* (Gallucci *et al.*, 2005).

CONCLUSIONS

This study confirmed some of the trends often observed in studies of seagrass-associated benthic communities, i.e. that faunal biomass is greater inside than outside seagrass beds, that macrophyte detritus and associated microbiota are important food sources for invertebrates and that secondary production inside seagrass meadows is limited by the amount of labile organic matter available.

Other findings, however, appear to contradict some generally accepted tenets of seagrass community ecology. Meiofaunal biomass inside the *Zostera muelleri* meadow, for example, was low, indicating that the contribution of meiofauna to secondary productivity was limited. In addition, harpacticoid copepod abundance was highest in unvegetated sediments, which also contrasts with findings from previous studies. We did not observe trends in (depth-integrated) nematode diversity between vegetated and unvegetated habitats, although contrasting vertical diversity patterns were observed between vegetated and unvegetated sites. The near absence of predators at all study sites, as well as the high abundance of epistrate feeders in subsurface sediment inside the seagrass bed, is also intriguing. These discrepancies may indicate that the nature of seagrass–invertebrate interactions depends on habitat characteristics (e.g. intertidal versus subtidal, hydrodynamic conditions, sediment granulometry) and the identity and ecology of species considered. Nevertheless, our results show that the presence of *Zostera muelleri* creates complex 3-dimensional habitats characterized by markedly different invertebrate assemblages from surrounding unvegetated sediments, resulting in altered structure and function of sheltered soft-shore communities.

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APPENDIX

Nematode species found at the unvegetated, sparsely vegetated and densely vegetated sites, Papanui Inlet, January 2006. Species abundance is expressed as % of total nematode abundance. Species representing ≥5% of abundance are in bold. CF, ciliate feeder; DF, deposit feeder; EF, epistrate feeder; FP, facultative predator; M, microvore; P, predator.

	Family	Feeding type	Unvegetated	Sparsely vegetated	Densely vegetated
Anoplostoma sp.	Anoplostomatidae	DF	0.0	0.0	0.7
Aponema subtile	Microlaimidae	M	0.5	**7.5**	**9.0**
Atrochromadora sp.	Chromadoridae	EF	0.9	0.1	0.4
Axonolaimus sp. 1	Axonolaimidae	CF	0.0	0.5	0.7
Axonolaimus sp. 2	Axonolaimidae	CF	0.0	0.1	0.0
Bathylaimus australis	Trypiloididae	CF	0.0	0.1	0.1
Camacolaimus sp.	Leptolaimidae	EF	0.0	0.1	0.2
Campylaimus sp.	Diplopeltidae	M	2.7	0.3	0.9
Cervonema sp.	Comesomatidae	M	0.2	0.0	0.0
Chaetonema sp.	Anoplostomatidae	CF	0.0	0.1	0.1
Chromadora nudicapitata	Chromadoridae	EF	0.5	0.1	0.7
Chromadora sp. 1	Chromadoridae	EF	0.0	0.1	2.6
Chromadora sp. 2	Chromadoridae	EF	0.0	0.4	0.0
Chromadorita sp.	Chromadoridae	EF	1.2	2.6	0.2
***Chromaspirinia* sp. 1**	Desmodoridae	EF	1.2	**19.1**	**11.0**
***Chromaspirinia* sp. 2**	Desmodoridae	EF	2.6	**13.2**	**8.2**
Cobbia sp. 1	Xyalidae	EF	0.3	0.0	0.2
Cobbia sp. 2	Xyalidae	EF	0.2	2.3	0.5
Cobbia sp. 3	Xyalidae	EF	0.0	0.2	1.8
Comesa sp.	Comesomatidae	DF	0.2	0.6	0.1
Comesoma sp.	Comesomatidae	DF	1.0	0.6	0.0
Comesomatidae sp. 1	Comesomatidae	DF	0.0	0.0	0.1
Comesomatidae sp. 2	Comesomatidae	DF	0.0	0.1	0.0
Daptonema sp. 1	Xyalidae	DF	0.0	0.2	0.2
***Daptonema* sp. 2**	Xyalidae	EF	2.4	**5.1**	0.1
Daptonema sp. 3	Xyalidae	DF	0.2	0.4	0.2
Daptonema sp. 4	Xyalidae	DF	0.2	0.1	0.0
Daptonema sp. 5	Xyalidae	DF	0.8	0.1	0.4
Dasynemoides sp. 1	Ceramonematidae	M	2.2	0.1	0.0
Dasynemoides sp. 2	Ceramonematidae	M	1.3	0.0	0.0
Desmodora sp.	Desmodoridae	EF	0.0	0.0	0.5
Desmolaimus courti	Linhomoeidae	DF	0.0	4.4	**15.1**
Dichromadora sp.	Chromadoridae	EF	0.3	0.0	0.0
***Diplolaimella* sp.**	Monhysteridae	M	0.0	0.1	**8.7**
Enoplid sp.		P	0.0	0.0	0.2
Enoploides sp.	Thoracostomopsidae	P	0.0	0.3	0.0
Epacanthion sp.	Thoracostomopsidae	P	1.6	0.1	0.0
Eubostrichus sp.	Stilbonematidae	M	3.5	1.7	0.2
Gonionchus sp.	Xyalidae	DF	1.9	0.1	0.0
Halalaimus sp. 1	Oxystominidae	M	0.2	0.0	0.0
Halalaimus sp. 2	Oxystominidae	M	0.3	0.0	0.0
Leptolaimus sp.	Leptolaimidae	M	0.0	0.0	0.2
***Metachromadora* sp.**	Desmodoridae	EF	**20.9**	0.5	0.5
Metadasynemoides sp.	Ceramonematidae	M	3.8	0.0	0.1
Metadesmolaimus sp.	Xyalidae	DF	0.0	0.0	0.1
Metalinhomoeus sp.	Linhomoeidae	M	0.0	1.4	0.1
Microlaimus falciferus	Microlaimidae	EF	**15.4**	0.1	0.1
***Microlaimus* sp. 1**	Microlaimidae	EF	**12.7**	**8.9**	0.2
Microlaimus sp. 3	Microlaimidae	EF	0.0	3.7	0.7
Microlaimus sp. 2	Microlaimidae	EF	0.0	0.2	1.5
Morlaixia sp.	Diplopeltidae	M	2.1	0.0	0.0
Nannolaimoides sp.	Cyatholaimidae	EF	2.0	0.6	0.4
Neochromadora sp.	Chromadoridae	EF	0.0	0.1	0.0
Noffsingeria sp.	Meyliidae	M	0.8	0.1	0.0
Nudora sp.	Monoposthiidae	EF	0.1	0.4	0.1
***Odontophora* sp.**	Axonolaimidae	CF	**5.0**	**7.3**	**5.9**
***Paracanthonchus* sp.**	Cyatholaimidae	EF	0.0	0.4	**9.9**
Paracyatholaimus sp.	Cyatholaimidae	EF	1.8	0.7	0.0

Continued

Continued

	Family	Feeding type	Unvegetated	Sparsely vegetated	Densely vegetated
Paramonohystera sp. 1	Xyalidae	M	0.5	0.4	0.0
***Paramonohystera* sp. 2**	Xyalidae	M	3.4	**10.8**	**5.6**
Paramonohystera sp. 3	Xyalidae	DF	0.0	0.0	0.2
Prochromadorella sp.	Chromadoridae	EF	0.0	0.4	0.1
Promonhystera sp.	Xyalidae	DF	0.2	0.1	0.3
Pseudochromadora reathae	Desmodoridae	EF	0.4	0.0	0.0
Pseudochromadora sp. 1	Desmodoridae	EF	1.8	0.1	0.4
Pterygonema sp.	Ceramonematidae	M	0.0	0.1	0.0
Rhabdocoma sp.	Trefusiidae	M	0.0	0.0	0.3
Rhips sp.	Chromadoridae	EF	0.0	0.0	0.1
Rhynchonema sp.	Xyalidae	M	0.2	0.1	0.0
Sabatieria annulata	Comesomatidae	DF	0.0	0.5	3.4
Setoplectus sp.	Haliplectidae	M	0.2	0.0	0.0
Setosabatieria australis	Comesomatidae	DF	0.0	0.0	0.2
Sphaerolaimus sp.	Sphaerolaimidae	P	0.0	0.0	0.1
Steineria sp.	Xyalidae	DF	0.0	0.0	0.2
Stephanolaimus sp.	Leptolaimidae	M	0.0	0.3	0.5
Thalassomonhystera sp.	Monhysteridae	DF	0.0	0.0	0.1
Theristus cf. *denticulatus*	Xyalidae	DF	1.5	0.7	0.7
Theristus sp. 1	Xyalidae	DF	0.0	0.4	4.8
Theristus sp. 2	Xyalidae	DF	0.0	0.3	0.0
Theristus sp. 3	Xyalidae	DF	0.6	0.0	0.0
Thrichotheristus sp.	Xyalidae	DF	0.0	0.1	0.0
Viscosia sp.	Oncholaimidae	FP	0.2	0.4	0.4
Xyalidae sp. 1	Xyalidae	DF	0.0	0.2	0.1
Xyalidae sp. 2	Xyalidae	DF	0.4	0.0	0.0