Vol. 449: 95–108, 2012
doi: 10.3354/meps09547

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 8

Habitat alteration and community-level effects of an invasive ecosystem engineer: a case study along the coast of NSW, Australia

Fabiane Gallucci[1,2,*], Pat Hutchings[2], Paul Gribben[3], Gustavo Fonseca[1,2]

[1]Centro de Biologia Marinha da Universidade de São Paulo, Rodovia Manoel Hypólito do Rego, km 131.5, São Sebastião 11600-000, Brazil

[2]Australian Museum, 6 College Street, Sydney, New South Wales 2010, Australia

[3]Plant Functional Biology and Climate Change Cluster, School of the Environment, University of Technology, Sydney, New South Wales 2007, Australia

ABSTRACT: We investigated the effects of the habitat-modifying green algae *Caulerpa taxifolia* on meiobenthic communities along the coast of New South Wales, Australia. Samples were taken from unvegetated sediments, sediments underneath the native seagrass *Zostera capricorni*, and sediments invaded by *C. taxifolia* at 3 sites along the coast. Meiofaunal responses to invasion varied in type and magnitude depending on the site, ranging from a slight increase to a substantial reduction in meiofauna and nematode abundances and diversity. The multivariate structure of meiofauna communities and nematode assemblages, in particular, differed significantly in sediments invaded by *C. taxifolia* when compared to native habitats, but the magnitude of this dissimilarity differed between the sites. These differential responses of meiofauna to *C. taxifolia* were explained by different sediment redox potentials. Sediments with low redox potential showed significantly lower fauna abundances, lower numbers of meiofaunal taxa and nematode species and more distinct assemblages. The response of meiofauna to *C. taxifolia* also depended on spatial scale. Whereas significant loss of benthic biodiversity was observed locally at one of the sites, at the larger scale *C. taxifolia* promoted an overall increase in nematode species richness by favouring species that were absent from the native environments. Finally, we suggest there might be some time-lags associated with the impacts of *C. taxifolia* and point to the importance of considering the time since invasion when evaluating the impact of invasive species.

KEY WORDS: Ecosystem engineer · Invasive species · Meiofauna · Nematodes · *Caulerpa taxifolia*

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

The concept of 'ecosystem engineering' has been proposed to account for key processes by which some organisms alter the physical state of the environment resulting in the modification, maintenance or creation of habitats (Jones et al. 1994). The so-called habitat-modifying ecosystem engineers can affect not only habitat complexity but also related properties such as environmental chemistry and physical variables (Jones et al. 1994, Crooks 1998, 2002, Chisholm & Moulin 2003, Hastings et al. 2007), all of which have consequences for associated biota. Invasive ecosystem engineers, in particular, create novel environments that differ from what the native biota is adapted to, and as a result, they often have profound effects on native communities (Vitousek 1990, Crooks 1998, 2002, Gribben et al. 2009).

The effects of invasive ecosystem engineers on the resident biota are varied. In marine benthic communities, habitat-modifying invasive species that form aggregations or dense mats often have positive

*Email: fabiane.gallucci@usp.br

© Inter-Research 2012 · www.int-res.com

effects on native biota (see Crooks 2002 for a review). The positive effects of these species are related to added substrate and habitat complexity for recruitment or the provision of a refuge from predation (Crooks 2002, Gribben & Wright 2006, Sellheim et al. 2010). For example, in soft-sediment marine or estuarine systems, invasive seagrass (Posey 1988), macroalgae (Bulleri et al. 2006, Buschbaum et al. 2006, Gribben & Wright 2006) or molluscs (Crooks 1998, Crooks & Khim 1999, Wonham et al. 2005) facilitate greater recruitment, abundance or diversity of native species. However, these positive effects are often described for the epibenthic fauna. On the other hand, effects of habitat-forming invasive species on soft-sediment infaunal communities are often negative (e.g. Crooks 2001, Neira et al. 2005, 2006, McKinnon et al. 2009), although facilitation of infauna has also been described (Posey 1988, Posey et al. 1993, Crooks 1998, Box et al. 2010). The negative effects on native infauna have been linked principally to modification of the abiotic environment, particularly to changes to the sediment quality following invasion (Neira et al. 2005, 2006, Hacker & Dethier 2006, McKinnon et al. 2009, Byers et al. 2010).

Caulerpa taxifolia (Vahl) C. Agardh is a habitat-forming green alga considered to be 1 of the worst 100 invasive species in the world (Lowe et al. 2000). It has invaded several temperate regions worldwide where it covers large areas of soft-sediment habitat (Meinesz et al. 2001, Creese et al. 2004, L. Anderson 2005). The habitat conversion that *C. taxifolia* creates is severe (Byers et al. 2010). It can establish from a single fragment and typically spreads rapidly in invaded regions, forming dense monospecific beds above the sediment (Wright 2005, Wright & Davies 2006). In addition to altering habitat structure, *C. taxifolia* modifies the chemical and physical properties of sediments and water (Chisholm & Moulin 2003, Gribben et al. 2009, McKinnon et al. 2009). For instance, *C. taxifolia* decreases water flow and increases sediment and boundary-layer hypoxia (Gribben et al. 2009, McKinnon et al. 2009). In contrast to other habitat-forming invasive species, *C. taxifolia* can negatively affect many native taxa including algae and seagrasses (de Villèle & Verlaque 1995, Ceccherelli & Cinelli 1997, Ferrer et al. 1997), fish (York et al. 2006), and invertebrates (Wright & Gribben 2008, McKinnon et al. 2009, Byers et al. 2010).

Globally, investigations on the impacts of *Caulerpa taxifolia* and other invasive habitat-forming species on soft-sediment infauna have focused on understanding the response of native macro-invertebrates to invasion (Crooks 1998, Talley & Levin 2001, Neira et al. 2005, 2006, Gribben et al. 2009, McKinnon et al. 2009, Box et al. 2010, Byers et al. 2010). Generally, these studies suggest they are particularly vulnerable to invasion because of changes to sediment properties. Yet, virtually nothing is known about the effects of habitat-modifying invasive species on meiofaunal communities. Since meiofaunal organisms (particularly the nematodes) are the numerically dominant metazoans representative of the benthos of most marine and brackish-water habitats and often exhibit a very high species richness (e.g. finding ca. 50 species in a 10 cm^2 core is common; Heip et al. 1985), investigating the threats posed by *C. taxifolia* and other marine invasive plants on these diverse communities is critical.

To investigate the effects of *Caulerpa taxifolia* on meiobenthic communities, we compared the meiofauna (particularly the nematode assemblages) from sediments invaded by *C. taxifolia* with those from unvegetated sediments and sediments colonized by the native seagrass *Zostera capricorni* at 3 sites along the south-eastern coast of New South Wales (NSW), Australia. Detailed analysis and discussion on the comparison between unvegetated and *Z. capricorni* sediments are given elsewhere (Fonseca et al. 2011a). Specifically, we tested the hypotheses that (1) there are significant differences in sediment properties (median grain size, organic matter content and redox potential) and meiofauna community structure (abundance, total number of meiofaunal taxa, nematode species richness and species composition) between invaded and natural habitats and (2) these differences are site specific.

MATERIALS AND METHODS

Study sites and sampling design

Sampling was conducted in December 2008 at 3 sites along the coast of NSW where *Caulerpa taxifolia* was abundant: (1) Lake Conjola, 35° 15′ S, 150° 29′ E, (2) Port Hacking (Gunnamatta Bay), 34° 03′ S, 151° 08′ E and (3) Pittwater (Little Lovett Bay and Towlers Bay), 33° 35′ S, 151° 16′ E (Fig. 1). *C. taxifolia* was first described in Lake Conjola in 1987, at Port Hacking in 1998 and in Pittwater in 2006 (Grey 2001, NSW Fisheries 2007), and its degree of invasion varies between the 3 estuaries. At the time of this study, in Lake Conjola *C. taxifolia* was the most abundant macrophyte and covered much of the

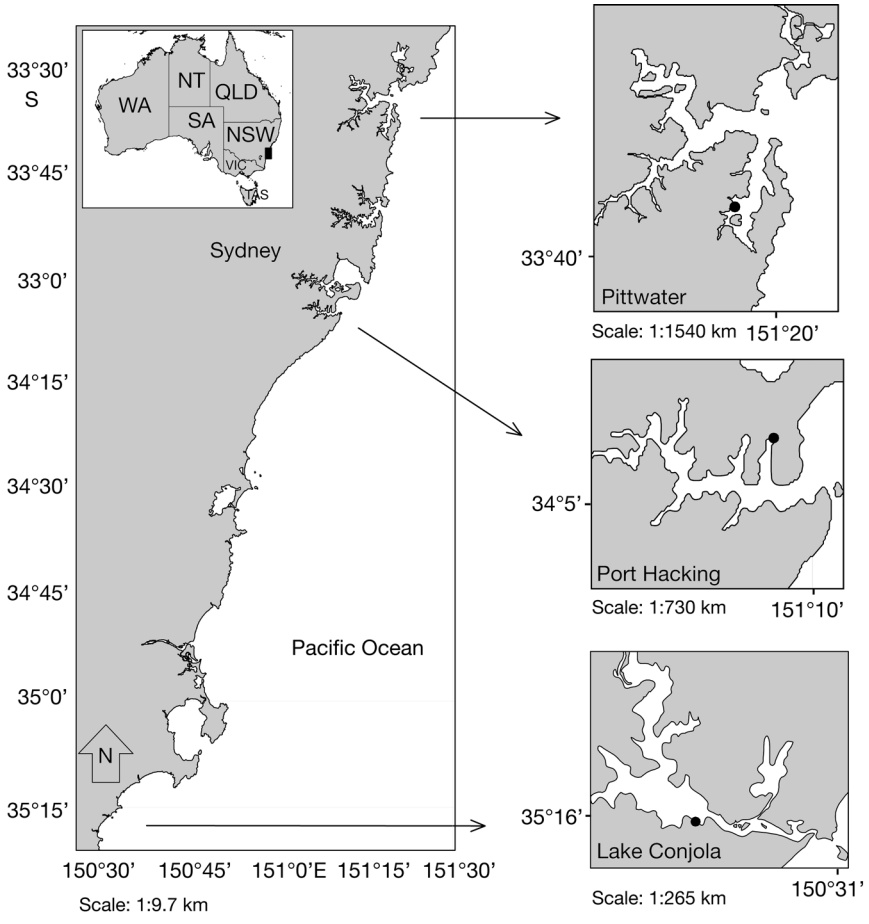

Fig. 1. Study sites along the New South Wales coast, south-eastern Australia. (●) locations where sediment cores were collected

estuary floor outside the main channel at depths <4 m (Wright & Davies 2006). In both Port Hacking and Pittwater, *C. taxifolia* is more patchily distributed and occurs intermingled with uninvaded habitats (mainly *Zostera capricorni*, *Posidonia australis* and unvegetated sediments).

At each site, samples were taken from 3 different habitats: (1) unvegetated sediments, (2) sediments underneath the native seagrass *Zostera capricorni*, and (3) sediments under *Caulerpa taxifolia*. The distance among the different habitats was 10 to 100 m, i.e. all habitats were exposed to the same local environmental conditions (e.g. same water currents, light intensity, etc.). Within each habitat, 4 replicate cores (diameter = 2 cm, depth = 2 cm) were taken at random for (1) meiofauna, (2) sediment redox potential, and (3) organic matter (OM) content, and 2 replicate cores (diameter = 10 cm, depth = 2 cm) were taken for sediment grain size. The first 2 cm were chosen since it is expected to harbour >70% of the meiofauna (Steyaert et al. 2003). Four 0.25 m^2 squares divided into 49 smaller quadrants were designated at random within *C. taxifolia* and *Z. capricorni* habitats to measure vegetation percentage cover. For each square, the number of quadrants occupied by *C. taxifolia* or *Z. capricorni* was counted. Four squares of 25 × 25 cm were sampled within each habitat to estimate the vegetation above-ground biomass. Above-ground biomass was clipped at the surface. All samples were taken at low tide at 0.5 to 1.0 m water depth.

Sample processing

Meiofauna samples were preserved in 4% formalin and stored. In the laboratory, samples were washed through a 45 µm sieve and meiofauna extracted by flotation with Ludox TM50 (Heip et al. 1985). After staining with Rose Bengal, all metazoan meiofaunal organisms were counted and identified to higher taxa. For each sample, 20% of total nematodes were picked (following Vincx 1996), evaporated to anhydrous glycerol and mounted on permanent slides for identification. A maximum limit of 250 nematodes was established (i.e. when the total of nematodes was >1250, only 250 individuals were picked for identification). Nematodes were identified to genus level (Warwick et al. 1998) and further separated into species or putative morphospecies.

Sediment granulometry was determined by sieving dried sediment samples and total organic content by difference in dry weight after combustion for 4 h at 550°C. Redox potential, which is often used to quantify the degree of reduction or oxidation, was measured *in situ* at the sediment surface (~1 cm depth) using a Metrohm AG 9109 Herisau Combined Pt-wire electrode, with an Ag/AgCl reference electrode. The instrument was calibrated using Orion Application Solution ORP Standard 967961, and all redox readings were corrected for EHRef = −210 ± 3 mV, i.e. reported redox potentials are versus that of the hydrogen electrode, EH0 = 0 mV. *Caulerpa taxifolia* and *Zostera capricorni* above-ground biomasses were estimated by dry weight after 24 h at 80°C.

Data analysis

Univariate and multivariate statistical methods were used to test the null hypothesis of no differences in environmental parameters, meiofaunal communities and nematode assemblages between habitats (sediments invaded by *Caulerpa taxifolia*, covered by *Zostera capricorni* or unvegetated) and between sites (Lake Conjola, Port Hacking or Pittwater). Sediment data (grain size distribution, redox potential and organic matter content) were ordinated using a correlation-based principal component analysis (PCA). The similarity matrix was constructed using a normalised Euclidian-distance similarity measure. Parameters that were highly significantly correlated ($p < 0.05$; $r > 0.8$) were not considered for the PCA. Permutational multivariate analysis of variance (PERMANOVA) tests were employed to detect the significance of the differences in the environmental multivariate structure between 'habitat' and 'sites'.

Meiofauna and nematode abundance, number of meiofaunal taxa and number of nematode species were used as univariate descriptors of the fauna. Other diversity indices (e.g. Shannon-Wiener, Pielou's evenness, ES(50) and Taxonomic distinctness) were calculated, but since they yielded the same results as those of species richness they are not reported here. PERMANOVA (Anderson 2001) was applied to assess differences in environmental parameters and fauna univariate measures between habitats and sites with 'habitat' and 'site' as fixed factors. Pairwise *a posteriori* multiple comparisons tests were performed when significant differences were detected ($p < 0.05$). Given the small number of possible permutations, Monte Carlo p-values were calculated for all pairwise comparisons. For differences in vegetation biomass and percentage cover between sites, 1-way PERMANOVA was carried out separately for *Caulerpa taxifolia* and *Zostera capricorni* using 'sites' as fixed factors. All PERMANOVA tests were conducted on Euclidean-distance similarity matrices and the residuals were permutated under a reduced model. PERMANOVA was used instead of the traditional analysis of variance (ANOVA) after testing for the homogeneity of variances (Cochran's test) of all variables and obtaining significant p-values ($p < 0.05$) even after transformation. Although PERMANOVA was designed for multivariate analysis on distance matrices, it can be used for univariate ANOVA, and because it calculates p-values using permutations rather than relying on tabulated p-values, it does not have the traditional ANOVA assumptions (M. Anderson 2005).

PERMANOVA analysis was also used to test for significant 'habitat', 'site' and 'habitat' versus 'site' effects on meiofauna and nematode assemblage structure. Because differences between groups in PERMANOVA may be due to the location of groups as well as their relative dispersion, permutational analysis of multivariate dispersion (PERMDISP) analysis was done to unravel the reasons of eventual differences. The analyses were done on Bray-Curtis distances calculated from $\log(x + 1)$ transformed data. To visualize the multivariate structure of the meiofauna and nematode assemblages, non-metric multi-dimensional scaling ordination (nMDS; Clarke & Ainsworth 1993) was performed based on the same Bray-Curtis similarity matrix. To investigate the potential effects of *Caulerpa taxifolia* invasion on turnover of species between sites and habitats, the same analysis was performed based on Jackard similarity measure. All univariate and multivariate analyses were performed using the PRIMER version 6 computer program (Clarke & Gorley 2006) with the additional add-on package PERMANOVA (Anderson et al. 2008, currently in beta version).

Because anoxia can negatively affect marine infauna (e.g. Van Colen et al. 2009) and sediment redox potential differed among habitats in a reasonably consistent way across sites (see 'Results'), a Spearman rank-correlation analysis was applied to explore relationships between redox potential and all faunal univariate measures. Since different habitats had very different redox values (e.g. unvegetated sediment versus *Zostera capricorni* or *Caulerpa taxifolia,* see 'Results'), correlations were calculated separately for each habitat. In addition, the relationships between the faunistic similarity matrices (meiofauna community and nematode assemblage) and a distance matrix built from the redox data (using Euclidian distance) were determined by a permutation procedure using the Spearman rank-correlation coefficient (*Relate*, Clarke & Warwick 2001).

RESULTS

Vegetation

Percentage cover of the invasive *Caulerpa taxifolia* varied from 88 to 98% and did not differ between the 3 sites (Pseudo-$F = 3.9$, $p = 0.076$; Fig. 2a). *Zostera capricorni* cover varied from 88 to 100% and was significantly higher at Lake Conjola than at the other 2 sites (Pseudo-$F = 6.8$, $p = 0.008$). Both *C. taxifolia* and *Z. capricorni* had significantly higher above-ground

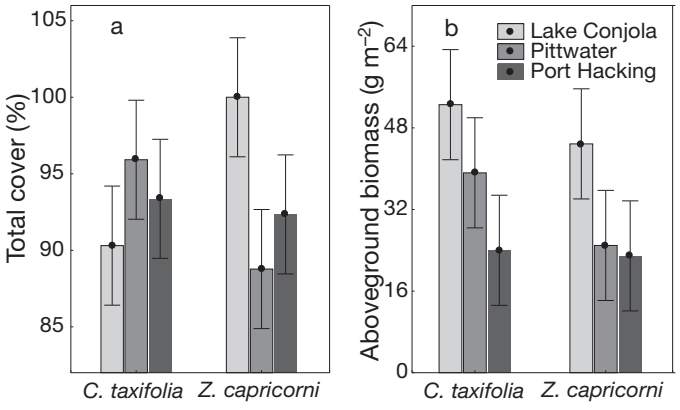

Fig. 2. *Caulerpa taxifolia* and *Zostera capricorni*. (a) Percentage cover and (b) biomass of invasive alga and native seagrass at the 3 study sites. Mean ± 95% CI

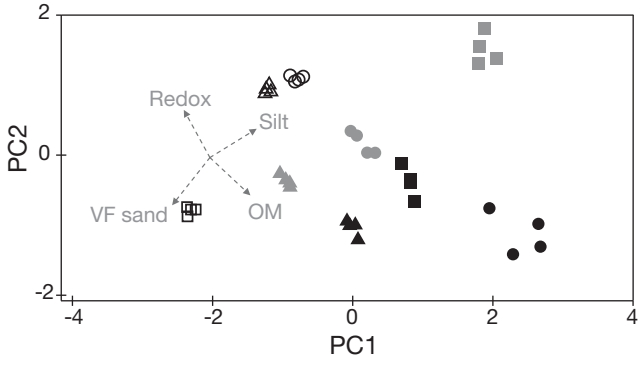

Fig. 3. Ordination of sediment characteristics by a correlation-based principal component analysis. (□) Pittwater, (○) Port Hacking, (△) Lake Conjola. OM: organic matter; VF sand: very fine sand. Symbols: black: *Caulerpa taxifolia*; grey: *Zostera capricorni*; open: unvegetated sediments

biomass at Lake Conjola when compared to Port Hacking (PERMANOVA pairwise test: $p < 0.05$, Fig. 2b). For both plants, above-ground biomass at Pittwater showed values intermediate between those at Lake Conjola and Port Hacking but did not differ from them (PERMANOVA pairwise test: $p > 0.05$, Fig. 2b).

Sedimentary environment

Ordination by a correlation-based principal component analysis (PCA) of the environmental data showed a clear distinction between habitats and did not separate the 3 sites (Fig. 3). Components 1 and 2 explained 75% of the total variability (PC1 52.8%; PC2 22.3%). Distinction between habitats was particularly evident on the first component (PC1), with

Table 1. Results of PERMANOVA for sediment median grain size (MGS), organic matter (OM), redox potential (REDOX) and principal component analysis (PCA) data. Significant values in **bold**

Source	df	MS	Pseudo-*F*	p (perm)
MGS				
Site	2	71457.00	341.97	**0.001**
Habitat	2	24079.00	115.23	**0.001**
Site × Habitat	4	1920.00	9.1885	0.006
Residual	9	208.96		
Total	17			
OM				
Site	2	45.21	131.17	**0.001**
Habitat	2	44.03	127.74	**0.001**
Site × Habitat	4	20.85	60.499	**0.001**
Residual	27	0.34		
Total	35			
REDOX				
Site	2	7606.20	34.649	**0.001**
Habitat	2	1.58E5	719.03	**0.001**
Site × Habitat	4	4728.30	21.539	**0.001**
Residual	27	219.52		
Total	35			
PCA				
Site	2	16.90	187.8	**0.001**
Habitat	2	28.40	315.71	**0.001**
Site × Habitat	4	11.74	130.56	**0.001**
Residual	27	0.09		
Total	35			

Zostera capricorni samples at an intermediate position between unvegetated sediments and *Caulerpa taxifolia* (Fig. 3). Higher positive values (*C. taxifolia* and *Z. capricorni*) were mainly associated with higher OM content and the percentage of silt whereas higher negative values (unvegetated sediments) were due to higher sediment redox potential and the percentage of fine sand. The results of the PERMANOVA pairwise comparisons showed that differences between habitats at each site were significant (Table 1).

The univariate analyses supported the results from the PCA. Sediment properties (i.e. grain size, organic matter and redox potential) in *Caulerpa taxifolia* invaded habitats differed largely compared to adjacent unvegetated sediments and less so compared to *Zostera capricorni* (Tables 1 & 2, Fig. 4). At all sites, sediment median grain size underneath *C. taxifolia* was significantly lower with higher OM content relative to unvegetated habitats (Table 2, Fig. 4a,b). However, with the exception of the significantly higher values of OM in *C. taxifolia* habitat at Port Hacking, both grain size and OM did not differ between *C. taxifolia* and *Z. capricorni* (Table 2, Fig. 4a,b).

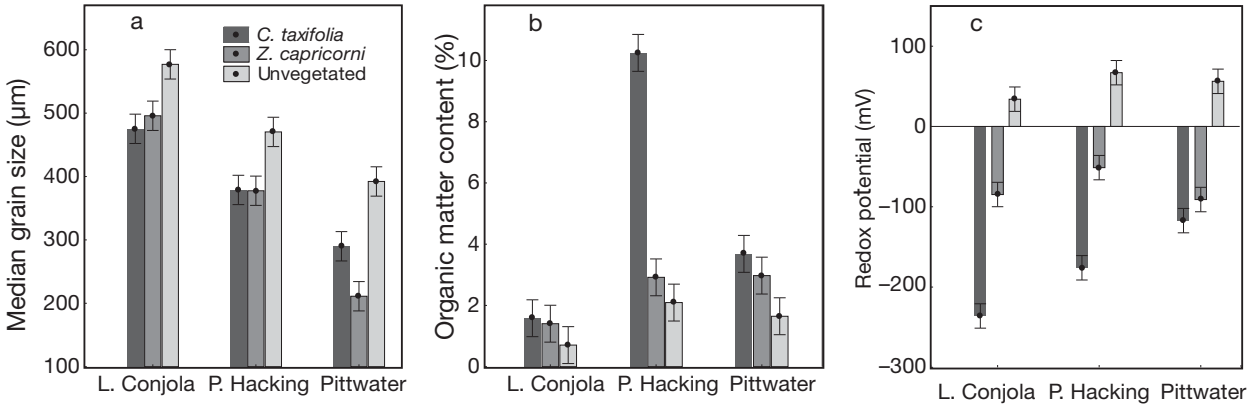

Fig. 4. Mean ± 95% CI (a) sediment median grain size, (b) organic matter content and (c) redox potential in unvegetated sediments and underneath *Zostera capricorni* and *Caulerpa taxifolia* at the study sites. L.: lake; P.: port

Redox potential showed a significant interaction between site and habitat (Table 1). At all sites, sediments underneath *Zostera capricorni* and *Caulerpa taxifolia* exhibited reduced conditions and with the exception of Pittwater, redox values were significantly lower in sediments invaded by *C. taxifolia* (Table 2, Fig. 4c). Unvegetated sediments were more oxygenated and showed redox values significantly higher than *C. taxifolia* and *Z. capricorni* habitats (Table 2, Fig. 4c).

Fauna

The meiofauna was represented by 19 higher taxa with densities ranging from 1101 to 9702 ind. 10 cm^{-2} (Table S1 in the supplement at www.int-res.com/articles/suppl/m449p095_supp.pdf). Nematodes numerically dominated most samples, representing 57 to 91% of the total metazoan meiofauna per sample. Exceptions to this pattern were 2 *Zostera capricorni* samples at Lake Conjola, where copepods, kinorhynchs and polychaetes were particularly abundant. Copepods, polychaetes and kinorhynchs were the following most abundant groups, representing from 2 to 34 (7 to 41% with nauplii), 0 to 27 and 0 to 33% of the total meiofauna per sample. Other taxa each represented <3% of the total number of meiofaunal individuals collected per sample.

Results from PERMANOVA for meiofauna density showed a significant interaction between 'site' and 'habitat', and post-hoc comparisons revealed significant differences between habitats only at Port Hacking (Tables 3 & 4, Fig. 5a). Differences in total number of meiofaunal taxa among habitats depended on site, as shown by the significant interaction between 'site' and 'habitat' (Table 3). Lake Conjola showed a significantly lower number of taxa in sediments invaded by *Caulerpa taxifolia*. At the 2 other sites, meiofauna diversity did not differ significantly between habitats (Table 4, Fig. 5b).

The nMDS of meiofauna data did not show a clear clustering or separation of sites and habitats (Fig. 6a). Considering each site separately, samples from Lake Conjola showed a greater separation between habitats, whereas at Port Hacking and Pittwater samples from the different habitats were more intermingled (Fig. 6a). These patterns were supported by the PERMANOVA analysis (Table 4). A significant interaction between factors indicated that differences between habitats were dependent on site. Post-hoc comparisons showed that while the multivariate structure of meiofauna assemblages differed significantly between the 3 habitats at Lake Conjola, significant differences at Port Hacking were observed only between *Caulerpa taxifolia* and *Zostera capricorni* habitats and at Pittwater differences were not significant (Table 4). PERMDISP analysis showed higher dispersion of samples at Lake Conjola (Table S2 in the supplement).

A total of 153 nematode species belonging to 107 genera and 33 families were recorded. Densities ranged from 321 to 8830 ind. 10 cm^{-2} (Table S3 in the supplement). PERMANOVA analysis for nematode densities and diversity showed similar results to those for meiofauna. For nematode densities, there was a significant interaction between 'site' and 'habitat' with significantly lower values in sediments invaded by *Caulerpa taxifolia* when compared to unvegetated sediments and *Zostera capricorni* beds at Port Hacking (Table 4, Fig. 5c). For total number of

nematode species, there was again a significant interaction between 'site' and 'habitat' (Table 3). Post-hoc comparisons showed that nematode species richness was significantly lower in sediments invaded by *C. taxifolia* at Lake Conjola while at Pittwater it was significantly higher (Table 4, Fig. 5d). Nematode species richness at Port Hacking did not differ significantly between habitats (Table 4, Fig. 5d).

The nMDS on abundances of nematode species showed a clear separation of the 3 different sites, with Pittwater and Port Hacking clustered together and Lake Conjola well separated (Fig. 6b). Within each site, there was also a separation of samples between habitats, with samples from *Zostera capricorni* assuming an intermediate position between unvegetated sediments and *Caulerpa taxifolia* ones. The PERMANOVA analysis supported these results with a significant interaction effect (Table 4). As indicated by the nMDS plot, post-hoc comparisons for the interaction term 'Site' × 'Habitat' revealed significant differences between unvegetated sediments, *Z. capricorni* and *C. taxifolia* samples within each site and significant differences between sites for each habitat

Table 2. Monte-Carlo (MC) post-hoc results for sediment median grain size (MGS), organic matter (OM), redox potential (REDOX) and principal components analysis (PCA) data within habitats without vegetation and underneath *Zostera capricorni* or *Caulerpa taxifolia* and within sites. LC: Lake Conjola; PW: Pittwater; PH: Port Hacking. Significant values in **bold** ($p < 0.05$)

Source	Within habitats					
	Unvegetated		*Z. capricorni*		*C. taxifolia*	
	t	p (MC)	*t*	p (MC)	*t*	p (MC)
MGS						
LC × PW	**19.05**	**0.006**	**46.41**	**0.001**	**10.24**	**0.008**
LC × PH	**9.08**	**0.013**	**14.80**	**0.003**	**4.59**	**0.050**
PW × PH	**7.60**	**0.018**	**17.26**	**0.007**	3.69	0.069
OM						
LC × PW	**6.03**	**0.001**	**5.66**	**0.001**	**8.77**	**0.001**
LC × PH	**4.82**	**0.005**	**7.21**	**0.001**	**12.17**	**0.001**
PW × PH	1.52	0.180	0.17	0.884	**8.82**	**0.001**
REDOX						
LC × PW	**5.90**	**0.002**	0.59	0.597	**11.65**	**0.001**
LC × PH	**23.34**	**0.002**	**3.51**	**0.018**	**3.69**	**0.008**
PW × PH	**2.96**	**0.020**	**3.60**	**0.014**	**3.61**	**0.011**
PCA						
LC × PW	**28.40**	**0.001**	**20.00**	**0.001**	**11.02**	**0.001**
LC × PH	**6.72**	**0.001**	**9.71**	**0.001**	**11.19**	**0.001**
PW × PH	**21.58**	**0.001**	**10.50**	**0.001**	**7.55**	**0.001**

Source	Within sites					
	Lake Conjola		Port Hacking		Pittwater	
	t	p (MC)	*t*	p (MC)	*t*	p (MC)
MGS						
C. taxifolia × Unvegetated	8.10	**0.015**	4.45	**0.041**	6.29	**0.028**
C. taxifolia × *Z. capricorni*	2.07	0.186	0.06	0.959	4.83	**0.042**
Unvegetated × *Z. capricorni*	9.88	**0.012**	8.01	**0.019**	22.56	**0.002**
OM						
C. taxifolia × Unvegetated	7.02	**0.002**	10.76	**0.001**	7.91	**0.003**
C. taxifolia × *Z. capricorni*	2.08	0.084	9.94	**0.001**	1.99	0.094
Unvegetated × *Z. capricorni*	6.31	**0.001**	2.43	0.052	4.45	0.006
REDOX						
C. taxifolia × Unvegetated	36.97	**0.001**	16.66	**0.001**	21.56	**0.001**
C. taxifolia × *Z. capricorni*	15.69	**0.001**	7.71	**0.001**	2.35	0.064
Unvegetated × *Z. capricorni*	18.20	**0.001**	16.66	**0.001**	15.98	**0.001**
PCA						
C. taxifolia × Unvegetated	27.65	**0.001**	12.41	**0.001**	16.40	**0.001**
C. taxifolia × *Z. capricorni*	14.36	**0.001**	8.59	**0.001**	8.97	**0.001**
Unvegetated × *Z. capricorni*	17.02	**0.001**	8.70	**0.001**	26.81	**0.001**

Table 3. Results of permutational multivariate analysis of variance (PERMANOVA) for abundance (N), number of taxa (*S*), and multivariate structure (*M*) of meiofauna and nematode assemblages. Significant values in **bold**

Source	df	N			*S*			*M*		
		MS	Pseudo-*F*	p (perm)	MS	Pseudo-*F*	p (perm)	MS	Pseudo-*F*	p (perm)
Meiofauna										
Site	2	4.83E6	26.251	**0.001**	2.11	0.65517	0.534	1299.70	6.0905	**0.001**
Habitat	2	2.89E5	1.5687	0.205	2.69	0.83621	0.444	1296.50	6.0752	**0.001**
Site × Habitat	4	1.30E6	7.0939	**0.002**	10.90	3.3836	**0.028**	739.32	3.4645	**0.001**
Residual	27	1.84E5			3.22			213.40		
Total	35									
Nematodes										
Site	2	4.26	22.459	**0.001**	1088.40	66.981	**0.001**	14326.00	18.216	**0.001**
Habitat	2	0.03	0.17765	0.839	38.53	2.3709	0.109	10166.00	12.926	**0.001**
Site × Habitat	4	1.74	9.1761	**0.001**	176.74	10.876	**0.001**	5849.90	7.4384	**0.001**
Residual	27	0.19			16.25			786.45		
Total	35									

Table 4. Monte-Carlo (MC) post-hoc results for meiofauna abundance (N_{meio}), number of meiofaunal taxa (S_{meio}), nematode abundance (N_{nema}), number of nematode species (S_{nema}), multivariate structure of meiofauna (M_{meio}) and multivariate structure of nematode assemblages (M_{nema}) within unvegetated sediments and those underneath *Zostera capricorni* or *Caulerpa taxifolia* and within sites. LC: Lake Conjola; PW: Pittwater; PH: Port Hacking. Significant values in **bold** ($p < 0.05$)

Source	Within habitats						Source	Within sites					
	Unvegetated		*Z. capricorni*		*C. taxifolia*			Lake Conjola		Port Hacking		Pittwater	
	t	p (MC)	*t*	p (MC)	*t*	p (MC)		*t*	p (MC)	*t*	p (MC)	*t*	p (MC)
$\mathbf{N_{meio}}$							$\mathbf{N_{meio}}$						
LC × PW	0.88	0.421	9.72	**0.001**	8.11	**0.001**	*C. taxifolia* × Unvegetated	1.61	0.135	2.22	0.057	2.42	0.057
LC × PH	2.26	0.071	8.20	**0.001**	1.15	0.298	*C. taxifolia* × *Z. capricorni*	0.38	0.720	4.64	**0.001**	1.35	0.243
PW × PH	0.86	0.407	0.05	0.952	4.84	**0.002**	Unvegetated. × *Z.capricorni*	1.68	0.134	1.13	0.293	1.98	0.090
$\mathbf{S_{meio}}$							$\mathbf{S_{meio}}$						
LC × PW	1.30	0.240	1.10	0.311	2.96	**0.027**	*C. taxifolia* × Unvegetated	2.75	**0.028**	0.177	0.859	1.67	0.148
LC × PH	1.63	0.130	1.26	0.281	1.28	**0.243**	*C. taxifolia* × *Z. capricorni*	2.92	**0.035**	0.37	0.729	1.34	0.235
PW × PH	<0.01	1.000	0.25	0.805	1.57	0.180	Unvegetated × *Z. capricorni*	0.28	0.788	0.65	0.544	0.74	0.495
$\mathbf{N_{nema}}$							$\mathbf{N_{nema}}$						
LC × PW	0.48	0.640	11.18	**0.001**	6.45	**0.002**	*C. taxifolia* × Unvegetated	1.22	0.255	2.60	**0.046**	2.97	**0.023**
LC × PH	1.94	0.111	9.21	**0.001**	0.40	0.695	*C. taxifolia* × *Z. capricorni*	1.42	0.190	7.36	**0.001**	1.35	0.216
PW × PH	1.11	0.339	0.34	0.771	6.11	0.003	Unvegetated × *Z. capricorni*	2.32	0.057	0.99	0.380	2.58	**0.044**
$\mathbf{S_{nema}}$							$\mathbf{S_{nema}}$						
LC × PW	11.89	**0.001**	2.82	**0.026**	22.94	**0.001**	*C. taxifolia* × Unvegetated	18.33	**0.001**	0.24	0.814	5.78	**0.006**
LC × PH	1.73	0.143	3.24	**0.024**	6.79	**0.001**	*C. taxifolia* × *Z. capricorni*	5.65	**0.002**	1.69	0.143	2.36	0.069
PW × PH	1.80	0.130	1.02	0.385	5.30	**0.004**	Unvegetated × *Z. capricorni*	0.29	0.788	1.12	0.326	0.31	0.789
$\mathbf{M_{meio}}$							$\mathbf{M_{meio}}$						
LC × PW	2.42	**0.008**	2.29	**0.013**	2.33	**0.006**	*C. taxifolia* × Unvegetated	2.32	**0.004**	1.67	0.077	1.34	0.166
LC × PH	1.84	**0.034**	2.72	**0.008**	1.67	0.057	*C. taxifolia* × *Z. capricorni*	2.58	**0.005**	2.00	**0.027**	1.05	0.364
PW × PH	2.05	**0.027**	1.05	0.357	1.84	**0.037**	Unvegetated × *Z. capricorni*	2.95	**0.007**	1.77	0.057	1.39	0.116
$\mathbf{M_{nema}}$							$\mathbf{M_{nema}}$						
LC × PW	3.21	**0.003**	3.12	**0.002**	4.52	**0.001**	*C. taxifolia* × Unvegetated	6.06	**0.001**	2.87	**0.004**	2.59	**0.003**
LC × PH	3.65	**0.003**	3.17	**0.002**	4.07	**0.001**	*C. taxifolia* x *Z. capricorni*	2.93	**0.004**	2.55	**0.005**	1.50	0.085
PW × PH	2.62	0.003	2.67	**0.002**	2.93	**0.003**	Unvegetated × *Z. capricorni*	3.56	**0.002**	2.95	**0.002**	2.58	**0.007**

(Table 4). The exception to this was Pittwater, which showed no differences between nematode assemblages from sediments underneath *Z. capricorni* and *C. taxifolia* (Table 4). Results from PERMDISP analysis did not follow this pattern (Table S3 in the supplement), indicating that differences revealed by PERMANOVA were mainly due to differences in the location of samples rather than differences in the dispersion of samples between the groups. Values of average similarity between groups indicated a greater difference in community structure between habitats at Lake Conjola and higher similarity at Pittwater. PERMANOVA analysis based on Jackard similarity measure showed the same results described above, suggesting that the observed differences are largely due to the turnover of species. As such, species turnover between habitats was largest in Lake Conjola and larger between bare sediment and *C. taxifolia* than with *Z. capricorni*. Each habitat and each site had as many restricted species as they had shared species. For instance, *C. taxifolia*, *Z. capricorni* and unvegetated sediments had 18, 19 and 27 species respectively restricted to each. Distance-based redundancy analysis showed 2 different groups, separating those taxa that occurred typically in unvegetated sediments from those that were present in vegetated sites (Fig. 7). Vegetated samples from Lake Conjola were further separated due to the ubiquitous presence of the nematode *Spirinia* sp. 1 in sediments colonized by *Z. capricorni* and *Metoncholaimus* sp. 1 and *Comesa* sp. 1 in sediments invaded by *C. taxifolia*.

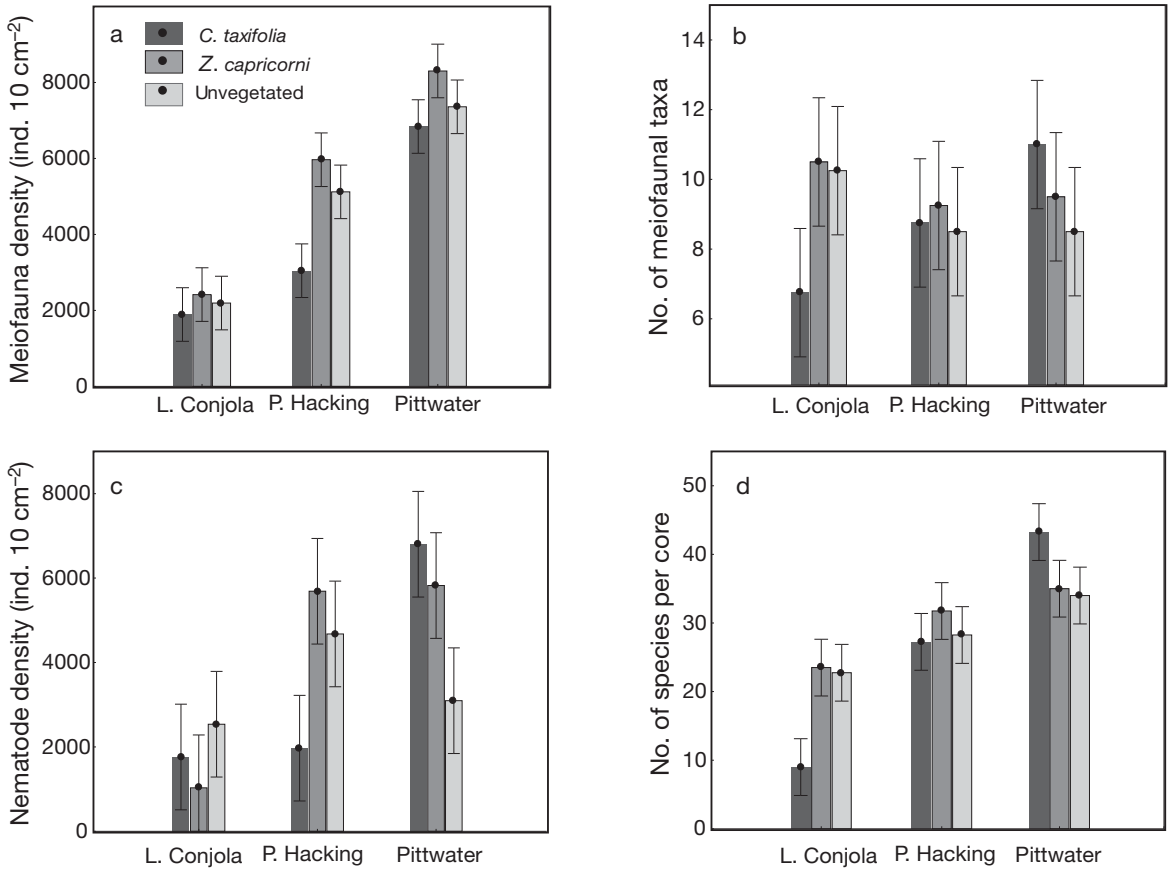

Fig. 5. Mean ± 95% CI for (a) meiofauna densities, (b) number of meiofaunal taxa, (c) nematode densities and (d) number of nematode species in unvegetated sediments and underneath *Zostera capricorni* and *Caulerpa taxifolia* at the 3 study sites. L: lake; P: port

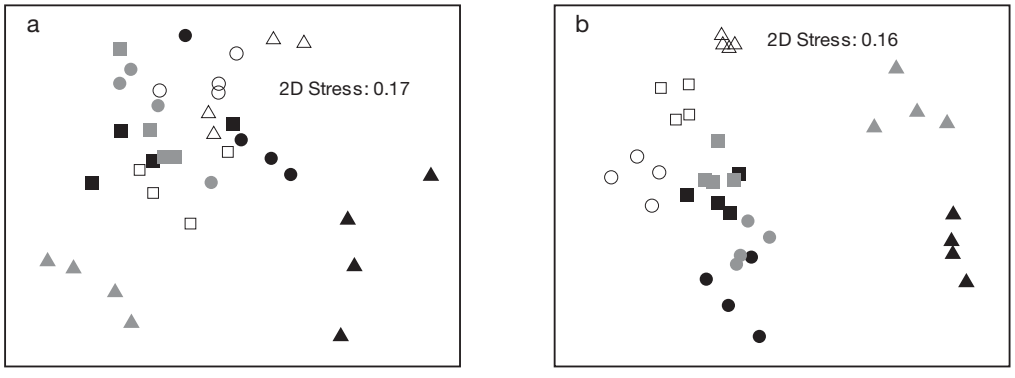

Fig. 6. Non-metric multi-dimensional scaling (nMDS) ordination from log(x + 1) transformed abundances of (a) meiofauna taxa and (b) nematode species. (□) Pittwater, (○) Port Hacking, (△) Lake Conjola. Symbols: black: *Caulerpa taxifolia*; grey: *Zostera capricorni*; open: unvegetated sediments

Relationships between environmental data and fauna

Relationships between sediment redox potential and univariate measures of meiofauna and nematode assemblages were significant only in *Caulerpa taxifolia* samples. In this habitat, redox potential was positively correlated with meiofauna and nematode densities as well as with the number of meiofauna taxa and number of nematode species (Table 5).

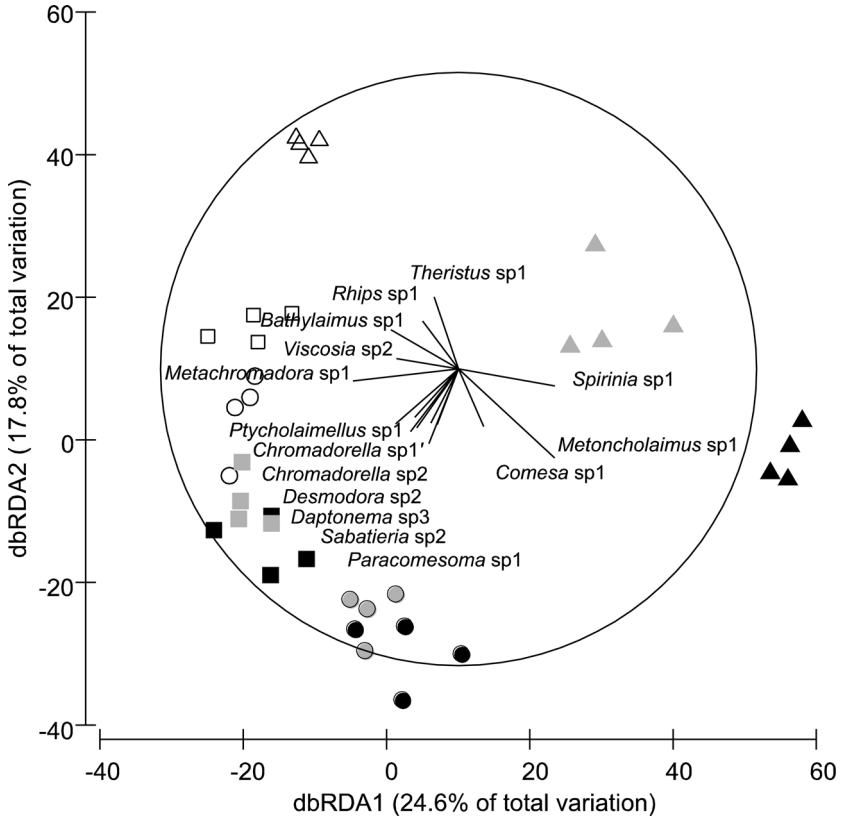

Fig. 7. Distance-based redundancy analysis (dbRDA) for nematode assemblages showing all taxa which were significantly correlated with the dbRDA coordinates (r > 0.2). Vector length corresponds to the correlation values. (□) Pittwater, (○) Port Hacking, (△) Lake Conjola. Symbols: black: *Caulerpa taxifolia*; grey: *Zostera capricorni*; open: unvegetated sediments

Similar to the univariate measures, the correlation between the meiofauna similarity matrix and the distance matrix built from the redox data was significant only for sediments invaded by *Caulerpa taxifolia* (R = 0.65, p = 0.002). On the other hand, the similarity matrix derived from nematode species abundances was positively correlated with the matrix derived from the redox data in all habitats. The highest correlation, nevertheless, was found in samples from sediments invaded by *C. taxifolia* (R = 0.8, p = 0.001 for *C. taxifolia;* R = 0.55, p = 0.002 for unvegetated sediments; R = 0.53, p = 0.01 for *Zostera capricorni*).

DISCUSSION

The present study showed that the invasion of *Caulerpa taxifolia* clearly changes the sedimentary environment. At all sites, the presence of *C. taxifolia* increased deposition of finer sediments and associated organic matter, creating a physical environment more similar to that of sediments colonized by the native seagrass *Zostera capricorni* when compared to unvegetated habitats. As for seagrass meadows, *C. taxifolia* affects sedimentary dynamics by modifying the energy regime of their environment (Hendriks et al. 2010). Generally, water flowing through the vegetation is blocked by the leafy canopy, and thus reduced in energy, promoting deposition as well as preventing resuspension (Molinier & Picard 1952, Patriquin 1975, Clarke & Kirkman 1989). Although *C. taxifolia* leaves are much smaller than those of *Z. capricorni* and other seagrasses, it concentrates its biomass close to the sediment surface and forms a thick mat (with biomass comparable to the larger *Z. capricorni*; Fig. 2), increasing bottom roughness at the sediment–water interface (Fonseca 1989) and therefore causing an effect similar to that of larger species of seagrass.

The lower water flow velocity caused by the leafy canopy is also associated with a decrease in oxygen concentration in the bottom water (Vichkovitten & Holmer 2005, Matheson & Schwarz 2007, Gribben et al. 2009). This, together with an enhanced oxygen demand of more organically rich sediments, characterizes a sedimentary environment more depleted in oxygen than compared to habitats lacking vegetation. However, although anoxia or hypoxia is a natural phenomenon of vegetated estuarine areas, the redox potential values underneath *Caulerpa taxifolia* were significantly lower than those underneath the native seagrass *Zostera capricorni*. The same has been observed for *C. taxifolia* when compared to other seagrass species (McKinnon

Table 5. Spearman rank correlation coefficients between redox potential and meiofauna univariate measures for samples underneath *Caulerpa taxifolia*. All coefficients are significant at p < 0.05

	Redox potential	
	Abundance	No. of taxa
Meiofauna	+0.70	0.60
Nematodes	+0.70	0.88

et al. 2009). The negative redox values observed in sediments underneath *Z. capricorni* are probably an effect of the physical habitat modification caused by the seagrass (Vichkovitten & Holmer 2005). Yet, the much lower redox values in sediments invaded by *C. taxifolia* are not only a result of physical habitat modification but also an indirect consequence of higher sulphate reduction stimulated by *Caulerpa* spp. rhizoids which enhance N_2 fixation (Chisholm et al. 1996). The rhizoids have an associated sulfate-reducing bacterial community that converts sulphates to sulphides, which in turn is oxidized by chemoautotrophic bacteria (Howarth 1984). In addition, the thick mat formed by *C. taxifolia* just above the sediment–water interface probably precludes exchange between the pore-water and the overlying oxygenated waters.

Although changes in the sedimentary environment caused by *Caulerpa taxifolia* were consistent across the 3 studied sites, it was not uniformly reflected by the meiofauna. Meiofaunal responses to *C. taxifolia* invasion varied in type and magnitude, ranging from a slight increase in meiofauna and nematode densities and diversity (Pittwater) to a substantial reduction in their abundance (Port Hacking) and diversity (Lake Conjola) in surface sediments. Likewise, the multivariate structure of meiofauna communities and nematode assemblages differed significantly in sediments invaded by *C. taxifolia* when compared to the native habitats, but the magnitude of this dissimilarity differed between the sites. Differences in the composition and structure of assemblages between habitats, as well as species turnover, were smallest in Pittwater, intermediate at Port Hacking and greatest in Lake Conjola.

Among all environmental parameters investigated, variability of both univariate measures and multivariate structure of the fauna were best explained by sediment redox potential. Particularly at the invaded sites, sediments with lower redox potential showed significantly lower fauna abundances, lower numbers of meiofaunal taxa and nematode species and more distinct meiofauna and nematode assemblages (Table 5), indicating that the fauna is indeed largely responding to the reduced environment created by *Caulerpa taxifolia.* Oxygen availability has a well-known direct effect on the meiofauna (Steyaert et al. 2007). Generally, meiofauna species are adversely affected by anoxia, and most of the taxa are restricted to the upper oxic zone (Hendelberg & Jensen 1993, Steyaert et al. 2007). Yet, the reduced environment created by anoxia can also affect the fauna indirectly. For instance, sulfides (which are toxic to many marine invertebrates; Bagarinao 1992) may accumulate due to increased activity of sulphate-reducing bacteria, aggravating the negative effects of anoxia. Indeed, our data also indicate that the differential effects of *C. taxifolia* invasion on the fauna are probably due to different degrees of chemical reduction in invaded sediments at the different sites, which in turn cause other geochemical differences, for instance as in sulphide concentrations. When redox values from sediments invaded by *C. taxifolia* and those colonized by *Zostera capricorni* were similar, as was the case in Pittwater, the fauna from invaded sediments was abundant and diverse and fauna composition from these 2 habitats were also similar. Several taxa typical of seagrass beds (e.g. larvae of insects and polychaetes, nematodes from the genera *Microlaimus, Ptycholaimellus* and *Chromadorella*) and the nematodes, in particular, flourished in sediments invaded by *C. taxifolia* at Pittwater. These taxa are probably adapted to natural low levels of oxygen (as those observed in seagrass beds; Fonseca et al. 2011a) and took advantage of the organically rich and physically stable habitat created by *C. taxifolia*. However, when invaded sediments reached redox values much lower than those observed underneath *Z. capricorni*, as was the case at Port Hacking and Lake Conjola, many organisms disappeared. Particularly at Lake Conjola, where the decrease in redox was more dramatic, there was a significant reduction in the number of meiofaunal taxa and an even more conspicuous decrease in number of nematode species. At this redox level, the environment becomes toxic for the fauna so that only a few tolerant taxa survive (Levin et al. 2009).

Although the mechanisms that allow certain nematode species to tolerate anoxia are still unknown, the present study suggests physiological and behavioural adaptations to survive or even thrive in reduced environments. Among the tolerant taxa observed, the majority were nematode species belonging to the genera *Methoncholaimus*, *Paracomesoma*, *Spirinia* and some members of the family Linhomoidae (*Metalinhomoeus*, *Paralinhomoeus* and *Terschellingia*). Apparently the species belonging to these groups have different mechanisms to live under anoxic conditions. For instance, granules of elemental sulfur accumulated in the epidermis were observed in several specimens of *Methoncholaimus* sp. 1, the most abundant species encountered in sediments invaded by *Caulerpa taxifolia*. Granules of sulfur were already reported for the co-familial species *Oncholaimus campylocercoides* (Thiermann et al. 2000). The strategy of sulfur inclusion in the epi-

dermis temporally reduces the concentrations and toxic effect of H_2S and at the same time provides an energetic deposit for later oxidation under oxic conditions (Thiermann et al. 2000). The other taxonomic groups did not present an evident adaptation to survive under anoxic conditions, but they share the common characteristic of being long and slender. One possible strategy is that their body shape allows them to make short excursions from the oxic zone (epistrate) to the anoxic sub-layers, as suggested for other species commonly found in deeper sediment layers (Soetaert et al. 2002, Fonseca et al. 2007, Gallucci et al. 2008). In addition, their slender body shape increases the body surface area per body volume, which facilitates the absorption of oxygen (Jensen 1986).

As discussed above, it is very likely that the differential effects of *Caulerpa taxifolia* invasion on the fauna are probably due to different degrees of reduction in invaded sediments at the different sites. There are at least 2 possible explanations to such variation only at invaded sites. The variable effects of *C. taxifolia* on sediment redox potential might be due to differences in (1) the magnitude of invasion (i.e. differential algae biomass and coverage) and/or (2) time since invasion. The first possibility is unlikely since redox potential was neither correlated with above-ground biomass and coverage of the algae or with total organic matter. On the other hand, although studies evaluating the impacts of *C. taxifolia* have so far neglected the temporal context of invasion, we expect habitat modification associated with *C. taxifolia* to increase with time, so that stronger effects might be expected in older patches (Crooks 2005). In this case, sediments recently colonized by the algae would be less anoxic and with less H_2S than sediments colonized for longer periods. Assuming this hypothesis is true, the different responses of the fauna at each site are possibly a consequence of different successional stages after invasion. Sediments recently invaded by *C. taxifolia* would have an assemblage more similar to those of native sediments. However, as long as *C. taxifolia* remains, the changes in the sedimentary environment (particularly the reduced conditions) would accumulate and the effects on the fauna would be magnified. Although the current sampling design involving 3 sites each with a different time since invasion does not allow a replicated test of age influence on *C. taxifolia* effects, our data suggest there might be some time dependence. *C. taxifolia* first invaded Lake Conjola (between 1987 and 1995) and then Port Hacking (during 1998 or earlier) (Grey 2001) and only recently has it invaded the sampled site in Pittwater (which was considered free of *C. taxifolia* until 2006, NSW Fisheries 2007). In agreement, differences in meiofauna and nematode assemblages between habitats were greater in Lake Conjola, intermediate at Port Hacking and smaller in Pittwater. Particularly in Pittwater, meiofauna community structure did not differ between habitats and nematode assemblages from sediments under *C. taxifolia* were very similar to those of sediments colonized by *Z. capricorni* (Fig. 6). These results show a greater effect of *C. taxifolia* at the longer colonized sites suggesting it might have a long-term cumulative effect on the benthic environment and fauna, as already reported for other invasive ecosystem engineers (Posey 1988, Talley & Levin 2001, Neira et al. 2005). Unfortunately, given the limitations of our sampling design, time dependence for the impacts of *C. taxifolia* on the benthic environment and the native meiofauna remains to be confirmed.

The present study illustrates the heterogeneous effects of an invasive plant on estuarine benthos. First of all, the effects of *Caulerpa taxifolia* on habitat and native fauna were clearly site dependent. At one of the sites, habitat modification caused by *C. taxifolia* invasion seemed to facilitate some infaunal organisms slightly increasing local diversity, while at another site it strongly degraded sediment conditions causing a significant loss of benthic biodiversity. *C. taxifolia* effects on the native fauna also depended on scale. Whereas at the local scale *C. taxifolia* have reduced species richness at 1 of the sites, at the larger scale it caused an apparent increase in species richness by favouring species that were seemingly absent from the native environments. As suggested by previous studies (Gallucci et al. 2008, Fonseca et al. 2011b) these species are probably rare in the surrounding environments (particularly in the superficial layers, i.e. 0 to 2 cm) and take advantage of the 'unfavourable' conditions created by *C. taxifolia* and the consequent lack of competition to prosper. While some of these species might have migrated from other anoxic patches, others may have migrated vertically from deeper anoxic layers of the sediment, where they might occur in greater abundances (Franco et al. 2008). Finally, our results suggest there might be some time-lags associated with the impacts of *C. taxifolia*. Future studies considering the timescales of invasion or time-series studies on benthic communities after invasion are needed to predict how the ecological effects of *C. taxifolia* change over time.

Acknowledgements. We are grateful to the 'marine inverts' from the Australian Museum for their support during this study. Special thanks are due to A. Murray for endless help at the laboratory. We thank T. Glasby from the Aquatic Ecosystems Unit of New South Wales Department of Primary Industries for information on *C. taxifolia* and advice on sampling sites. We also thank G. Skilbeck from the University of Technology of Sydney for help with grain size analysis. F.G. and G.F. are currently sponsored by Fundação de Amparo à Pesquisa do Estado de São Paulo (2010/12232-5 and 200/05472-0, respectively). F.G. acknowledges the Australian Government for a postdoc Endeavour Research Fellowship during the 2009 calendar year.

LITERATURE CITED

Anderson LWJ (2005) California's reaction to *Caulerpa taxifolia*: a model for invasive species rapid response. Biol Invasions 7:1003–1006

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Anderson MJ (2005) PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland, Auckland

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth

Bagarinao T (1992) Sulfide as an environmental factor and toxicant: tolerance and adaptations in aquatic organism. Aquat Toxicol 24:21–62

Box A, Martin D, Deudero S (2010) Changes in seagrass polychaete assemblages after invasion by *Caulerpa racemosa* var. *cylindracea* (Chlorophyta: Caulerpales): community structure, trophic guilds and taxonomic distinctness. Sci Mar 74:317–329

Bulleri F, Airoldi L, Branca GM, Abbiati M (2006) Positive effects of the introduced green alga, *Codium fragile* ssp. *tomentosoides*, on recruitment and survival of mussels. Mar Biol 148:1213–1220

Buschbaum C, Chapman AS, Saier B (2006) How an introduced seaweed can affect epibiota diversity in different coastal systems. Mar Biol 148:743–754

Byers JE, Wright JT, Gribben PE (2010) Variable direct and indirect effects of a habitat-modifying invasive species on mortality of native fauna. Ecology 91:1787–1798

Ceccherelli G, Cinelli F (1997) Short-term effects of nutrient enrichment of the sediment and interactions between the seagrasses *Cymodocea nodosa* and the introduced green alga *Caulerpa taxifolia* in a Mediterranean bay. J Exp Mar Biol Ecol 217:165–177

Chisholm JRM, Moulin P (2003) Stimulation of nitrogen fixation in refractory organic sediments by *Caulerpa taxifolia* (Chlorophyta). Limnol Oceanogr 48:787–794

Chisholm JRM, Dauga G, Ageron E, Grimont PAD, Jaubert JM (1996) 'Roots' in mixotrophic algae. Nature 381:382

Clarke KR, Ainsworth M (1993) A method of linking multivariate community structure to environmental variables. Mar Ecol Prog Ser 92:205–219

Clarke KR, Gorley RN (2006) Primer v6: user manual/tutorial. PRIMER-E, Plymouth

Clarke KR, Warwick RM (2001) Changes in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth

Clarke SM, Kirkman H (1989) Seagrass dynamics. In: Larkum AWD, McComb AJ, Shepherd SA (eds) Biology of seagrasses. Aquatic plant studies, Vol 2. Elsevier, New York, NY, p 304–345

Creese RG, Davis AR, Glasby TM (2004) Eradicating and preventing the spread of the invasive alga *Caulerpa taxifolia* in NSW. NSW Fisheries Final Report Series. NSW Fisheries, Cronulla

Crooks JA (1998) Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia.* Mar Ecol Prog Ser 162:137–152

Crooks JA (2001) Assessing invader roles within changing ecosystems: historical and experimental perspectives on an exotic mussel in an urbanized lagoon. Biol Invasions 3:23–36

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166

Crooks JA (2005) Lag times and exotic species: the ecology and management of biological invasions in slow-motion. Ecoscience 12:316–329

Crooks JA, Khim HS (1999) Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia.* J Exp Mar Biol Ecol 240:53–75

de Villèle X, Verlaque M (1995) Changes and degradation in a *Posidonia oceanica* bed invaded by the introduced tropical alga *Caulerpa taxifolia* in the north western Mediterranean. Bot Mar 38:79–87

Ferrer E, Gómez Garreta A, Ribera MA (1997) Effect of *Caulerpa taxifolia* on the productivity of two Mediterranean macrophytes. Mar Ecol Prog Ser 149:279–287

Fonseca G, Muthumbi AW, Vanreusel A (2007) Species richness of the genus *Molgolaimus* (Nematoda) from local to ocean scale along continental slopes. Mar Ecol 28:446–459

Fonseca G, Hutchings P, Gallucci F (2011a) Meiobenthic communities of seagrass beds (*Zostera capricorni*) and unvegetated sediments along the coast of New South Wales, Australia. Estuar Coast Shelf Sci 91:69–77

Fonseca G, Hutchings P, Vieira DC, Gallucci F (2011b) Meiobenthic community underneath the carcass of a stingray: a snapshot after natural death. Aquat Biol 13:27–33

Fonseca MS (1989) Sediment stabilization by *Halophila decipiens* in comparison to other seagrasses. Estuar Coast Shelf Sci 29:501–507

Franco MA, Steyaert M, Cabral HN, Tenreiro R and others (2008) Impact of discards of beam trawl fishing on the nematode community from the Tagus estuary (Portugal). Mar Pol Bull 56:1728–1736

Gallucci F, Moens T, Vanreusel A, Fonseca G (2008) Active colonisation of disturbed sediments by deep-sea nematodes: evidence for the patch mosaic model. Mar Ecol Prog Ser 367:173–183

Grey D (2001) *Caulerpa taxifolia*: invasive weed prompts response actions. Fisheries NSW Magazine 4:4–5

Gribben PE, Wright JT (2006) Invasive seaweed enhances recruitment of a native bivalve: roles of refuge from predation and the habitat choice of recruits. Mar Ecol Prog Ser 318:177–185

Gribben PE, Wright JT, O'Connor WA, Doblin MA, Eyre B, Steinberg PD (2009) Reduced performance of native infauna following recruitment to a habitat-forming invasive marine alga. Oecologia 158:733–745

Hacker SD, Dethier MN (2006) Community modification by a grass invader has differing impacts for marine habitats. Oikos 113:279–286

Hastings A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JG, Talley TS, Wilson WG (2007) Ecosystem engineering in space and time. Ecol Lett 10:153–164

Heip C, Vincx M, Vranken G (1985) The ecology of marine nematodes. Oceanogr Mar Biol Annu Rev 23:399–489

Hendelberg M, Jensen P (1993) Vertical distribution of the nematode fauna in a coastal sediment influenced by seasonal hypoxia in the bottom water. Ophelia 37:83–94

Hendriks IE, Bouma TJ, Morris EP, Duarte CM (2010) Effects of seagrasses and algae of the *Caulerpa* family on hydrodynamics and particle-trapping rates. Mar Biol 157:473–481

Howarth RW (1984) The ecological significance of sulfur in the energy dynamics of salt marsh and coastal marine sediments. Biogeochemistry 1:5–27

Jensen P (1986) Nematode fauna in the sulphide-rich brine seep and adjacent bottoms of the East Flower Garden, NW Gulf of Mexico. IV. Ecological aspects. Mar Biol 92: 489–503

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Levin LA, Ekau W, Gooday AJ, Jorissen F and others (2009) Effects of natural and human-induced hypoxia on coastal benthos. Biogeosciences 6:2063–2098

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species. Invasive Species Specialist Group, Species Survival Commission, International Union for the Conservation of Nature and Natural Resources, Gland

Matheson FE, Schwarz AM (2007) Growth responses of *Zostera capricorni* to estuarine sediment conditions. Aquat Bot 87:299–306

McKinnon JG, Gribben PE, Davis AR, Jolley DF, Wright JT (2009) Differences in soft-sediment macrobenthic assemblages invaded by *Caulerpa taxifolia* compared to uninvaded habitats. Mar Ecol Prog Ser 380:59–71

Meinesz A, Belsher T, Thibaut T, Antolic B and others (2001) The introduced green alga *Caulerpa taxifolia* continues to spread in the Mediterranean. Biol Invasions 3:201–210

Molinier R, Picard J (1952) Recherches sur les herbiers de phanérogames marines du littoral Méditerraneén français. Ann Inst Oceanogr 27:157–234

Neira C, Levin LA, Grosholz ED (2005) Benthic macrofaunal communities of three sites in San Francisco Bay invaded by hybrid *Spartina*, with comparison to uninvaded habitats. Mar Ecol Prog Ser 292:111–126

Neira C, Grosholz ED, Levin LA, Blake R (2006) Mechanisms generating modification of benthos following tidal flat invasion by a *Spartina* hybrid. Ecol Appl 16: 1391–1404

NSW Fisheries (2007) Caulerpa (*Caulerpa taxifolia*). Department of Primary Industries of NSW, Australia. www.dpi.nsw.gov.au/fisheries/pests-diseases/marine-pests/nsw/caulerpa-taxifolia. Accessed on 18/11/2010

Patriquin DG (1975) 'Migration' of blowouts in seagrass beds at Barbados and Carriacou, West Indies, and its ecological and geological implications. Aquat Bot 1: 163–189

Posey MH (1988) Community changes associated with the spread of an introduced seagrass, *Zostera japonica.* Ecology 69:974–983

Posey MH, Wigand C, Stevenson JC (1993) Effects of an introduced aquatic plant, *Hydrilla verticillata*, on benthic communities in the Upper Chesapeake Bay. Estuar Coast Shelf Sci 37:539–555

Sellheim K, Stachowicz JJ, Coates RC (2010) Effects of a nonnative habitat-forming species on mobile and sessile epifaunal communities. Mar Ecol Prog Ser 398: 69–80

Soetaert K, Muthumbi A, Heip C (2002) Size and shape of ocean margin nematodes: morphological diversity and depth-related patterns. Mar Ecol Prog Ser 242:179–193

Steyaert M, Vanaverbeke J, Vanreusel A, Barranguet C, Lucas M, Vincx M (2003) The importance of fine-scale, vertical profiles in characterising nematode community structure. Estuar Coast Shelf Sci 58:353–366

Steyaert M, Moodley L, Nadong T, Moens T, Soetaert K, Vincx M (2007) Responses of intertidal nematodes to short-term anoxic events. J Exp Mar Biol Ecol 345: 175–184

Talley TS, Levin LA (2001) Modification of sediments and macrofauna by an invasive marsh plant. Biol Invasions 3: 51–68

Thiermann F, Vismann B, Giere O (2000) Sulphide tolerance of the marine nematode *Oncholaimus campylocercoides*—a result of internal sulphur formation? Mar Ecol Prog Ser 193:251–259

Van Colen C, Montserrat F, Verbist K, Vincx M and others (2009) Tidal flat nematode responses to hypoxia and subsequent macrofauna-mediated alterations of sediment properties. Mar Ecol Prog Ser 381:189–197

Vichkovitten T, Holmer M (2005) Dissolved and particulate organic matter in contrasting *Zostera marina* (eelgrass) sediments. J Exp Mar Biol Ecol 316:183–201

Vincx M (1996) Meiofauna in marine and freshwater sediments. In: Hall GS (ed) Methods for the examination of organismal diversity in soils and sediments. CAB International, Wallingford, p 187–195

Vitousek PM (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57:7–13

Warwick RM, Platt HM, Somerfield PJ (1998) Free-living marine nematodes. Part III Monhysterids. Synopsis of the British fauna (new series). Cambridge University Press, Cambridge

Wonham MJ, O'Connor M, Harley CDG (2005) Positive effects of a dominant invader on introduced and native mudflat species. Mar Ecol Prog Ser 289:109–116

Wright JT (2005) Differences between native and invasive *Caulerpa taxifolia*: a link between asexual fragmentation and abundance in invasive populations. Mar Biol 147: 559–569

Wright JT, Davis AR (2006) Demographic feedback between clonal growth and fragmentation in an invasive seaweed. Ecology 87:1744–1754

Wright JT, Gribben PE (2008) Predicting the impact of an invasive seaweed on the fitness of native fauna. J Appl Ecol 45:1540–1549

York PH, Booth DJ, Glasby TM, Pease BC (2006) Fish assemblages in habitats dominated by *Caulerpa taxifolia* and native seagrasses in south-eastern Australia. Mar Ecol Prog Ser 312:223–234

Editorial responsibility: Hans Heinrich Janssen, Oldendorf/Luhe, Germany

Submitted: June 8, 2011; Accepted: December 7, 2011
Proofs received from author(s): February 29, 2012