

Differences between epiphytic assemblages on introduced *Caulerpa taxifolia* and coexisting eelgrass (*Zostera capricorni*) in Botany Bay (NSW, Australia)

PATRICIA PRADO^{1,2} and THIERRY THIBAUT³

¹ Dauphin Island Sea Laboratory, 101, Bienville Blvd, Dauphin Island, AL 36528, USA. E-mail: pprado@disl.org

² Centre d'Estudis Avançats de Blanes, Accés Cala St. Francesc, 14, E-17300 Blanes, Girona, Spain.

³ EA 4228 ECOMERS, Université de Nice-Sophia Antipolis, Faculté des Sciences, Parc Valrose, 06108 Nice cedex 02, France.

SUMMARY: A preliminary study was conducted to assess the potential effects of introduced *Caulerpa taxifolia* (Caulerpales, Chlorophyta) on the biodiversity and trophic functioning of seagrass systems in New South Wales, Australia. Epiphytic assemblages growing on fronds of *C. taxifolia* were compared to those on eelgrass *Zostera capricorni* (Aschers.) leaves in zones where both species were coexisting. The study was conducted at three shallow sites (ca. 1 m depth) in Botany Bay during austral spring. Assemblages on both *C. taxifolia* and *Z. capricorni* were dominated by epiphytic algae (ca. 65% of the total taxa) but results showed significantly greater numbers on *C. taxifolia* compared to *Z. capricorni* as well as important differences among study sites. n-MDS ordinations and PERMANOVA analyses confirmed the existence of significant differences in the assemblage compositions of *C. taxifolia* and *Z. capricorni* as well as differences between times and sites. SIMPER analysis showed that animal composition made a higher contribution to dissimilarities between habitats compared to epiphytic algae (36% vs. 23% respectively). In particular, filter-feeding organisms, associated with surfaces such as ascidians (5 taxa) and bryozoans (2 taxa) emerged as important contributing taxa. Hence, our results suggest that introduced *C. taxifolia* from Botany Bay is a suitable substratum for settlement of epiphytes, at least during the study period, and that observed patterns are due to differences in habitat structure. Further research is necessary to determine the influence of seasonal processes, such as production of toxic secondary metabolites, in other invaded locations of New South Wales.

Keywords: epiphytic assemblages, *Caulerpa taxifolia*, *Zostera capricorni*, richness of taxa, habitat complexity, New South Wales.

RESUMEN: DIFERENCIAS ENTRE LA COMPOSICIÓN EPIFÍTICA DE *CAULERPA TAXIFOLIA* Y LA DE LA FANERÓGAMA *ZOSTERA CAPRICORNI* EN BOTANY BAY (NSW, AUSTRALIA). – Este trabajo constituye una aproximación preliminar a la evaluación de los posibles efectos que la introducción de *Caulerpa taxifolia* (Caulerpales, Chlorophyta) puede causar en la diversidad y el funcionamiento trófico de los ecosistemas de fanerógamas marinas en New South Wales, Australia. Con este objeto, la composición y el número de taxa sobre los frondes de *C. taxifolia* fue comparada con la del estrato foliar de *Zostera capricorni* (Aschers.) en zonas donde ambas especies ocurren conjuntamente. El estudio se llevó a cabo en tres zonas superficiales (ca. 1 m de profundidad) de Botany Bay (New South Wales, Australia) durante la primavera austral. La composición taxonómica de *C. taxifolia* y *Z. capricorni* estuvo principalmente dominada por epifitos algales (ca. 65% del total), pero los resultados mostraron la presencia de un mayor número de taxa en *C. taxifolia* que en *Z. capricorni*, si bien sujeta a diferencias significativas entre zonas. Análisis multivariantes con n-MDS y PERMANOVA confirmaron la existencia de diferencias en la composición de taxa entre *C. taxifolia* y *Z. capricorni* así como entre tiempos de muestreo y zonas de estudio. Los resultados de los análisis de SIMPER, mostraron que la contribución de la composición animal a las diferencias entre hábitats era mayor que la explicada por los epifitos algales (36% vs. 23%, respectivamente). En particular, organismos filtradores, a menudo vinculados a la disponibilidad de substrato, tales como ascidias (5 taxa) y briozoos (2 taxa) presentaron contribuciones importantes a la disimilaridad. Por lo tanto, los resultados sugieren que *C. taxifolia* en Botany Bay constituye un substrato adecuado para el desarrollo de comunidades epifitas, al menos durante el periodo de estudio y que los patrones observados son debidos a diferencias en la estructura del hábitat. Futuros estudios son necesarios para determinar la influencia de procesos estacionales tales como la producción de metabolitos secundarios, así como la consistencia de los patrones observados en otras localidades de New South Wales.

Palabras clave: comunidad de epifitos, *Caulerpa taxifolia*, *Zostera capricorni*, riqueza taxonómica, complejidad de hábitat, New South Wales.

INTRODUCTION

The introduction of species poses serious threats to native ecosystems and leads to changes in biodiversity, landscape structure and functioning that modify resilience to environmental change and may be economically costly (Vitousek, 1990; Chapin *et al.*, 2000; Pimentel *et al.*, 2000). Ecosystem responses, however, are never simple or direct. Positive, negative or no effects may be detected depending on factors such as habitat type, location, time and/or trophic position of species, among others (Neira *et al.*, 2005).

Strains of the green alga *Caulerpa taxifolia* (Vahl) C. Agardh have successfully invaded distant temperate regions including the Mediterranean, southern California and south-eastern Australia (Jousson *et al.*, 2000; Schaffelke *et al.*, 2002; Thibaut and Meinesz, 2004). In the context of the loss of seagrass habitats, invasive strains of *C. taxifolia* with elevated growth rates and an extremely high three-dimensional occupation of space may result in very efficient plant cover. This leads to leaf shading and therefore severely reduces the vitality of the seagrass (review by Boudouresque, 1997). The competitive success of *C. taxifolia* also excludes native algal communities (Verlaque and Fritayre, 1994; Piazzini *et al.*, 2001), which often leads to further negative impacts on biodiversity (Boudouresque *et al.*, 1995; Bellan-Santini *et al.*, 1996). This occurs due to the strong presence of a high number of bioactive compounds, such as caulerpenyne and taxifolione (Guerriero *et al.*, 1993; Dumay *et al.*, 2002), that may be toxic to seagrasses (Guerriero *et al.*, 1994), reduce or deter grazing by local species of macro-herbivores (Lemée *et al.*, 1996; Boudouresque, 1997) and have antibacterial and cytotoxic properties that prevent the settlement of sessile organisms (Lemée *et al.*, 1993; Galgani *et al.*, 1996). Hence, the functional role that epiphytes provide in marine coastal areas such as seagrass beds may be altered in sites invaded by *C. taxifolia*. For instance, seagrass epiphytic assemblages may exceed the photosynthetic rates of their host by two fold and are therefore important contributors to the ecosystem primary production (Penhale, 1977; Libes *et al.*, 1983; Morgan and Kitting, 1984). Certain macroalgal groups such as epiphytic coralline algae play a determining role in the sediment deposition of CaCO₃ (Walker and Woerkerling, 1988), and the activity of epiphytic blue-green algae contribute to fixing nitrogen in the

system (Goering and Parker, 1972). Seagrass epiphytes are also an important part of the ecosystem biodiversity (Jernakoff *et al.*, 1996), and supply an easily assimilated food source and habitat structure for numerous vagile fauna (Buia *et al.*, 1992; Gambi *et al.*, 1992).

In contrast to other temperate regions affected by introduced strains of *Caulerpa taxifolia*, there are also populations of this species that are indigenous to Australia (Phillips and Price, 2002), and the extent to which invasive populations differ from native populations remains inconclusive. For instance, native Australian populations of *C. taxifolia* feature distinctive demographic and life-history traits that are different to those of invasive strains (Phillips and Price, 2002; Wright, 2005), and may coexist with a number of seagrass species (Thomas, 2003). However, there is reasonable scientific evidence to support the hypothesis that the introduction of *C. taxifolia* in New South Wales was human-mediated from different areas and through distinctive invasion events (Schaffelke *et al.*, 2002). As in other invaded regions, populations form dense, continuous meadows that can overgrow native ecosystems (Grey, 2001) and may potentially cause important alterations to natural communities (review by Thibaut and Meinesz, 2004). Recently, studies at various impacted locations have documented the existence of both positive (Gribben and Wright, 2006) and negative effects (York *et al.*, 2006) on groups of estuarine fauna. Since epiphytes appear to be a central resource of Australian seagrass food-webs (Jernakoff and Nielsen, 1997; Keuskamp, 2004), they could be a good indicator of possible changes at higher trophic levels (see Wardle *et al.*, 1998 for similar evidence of terrestrial systems). *C. taxifolia* chemical defences may decrease settlement and development of sessile organisms in invaded systems. However, marine rhizophytic algae with abundant pinnate branches, such as *Caulerpa* species, offer larger three-dimensional substratum for the settlement of algal propagules and sessile fauna than the native seagrass. This may enhance the abundance and/or species richness of assemblages as has been previously observed for invasive species that provide higher habitat complexity (review by Crooks, 2002). Taking this into consideration, as a preliminary study on the impact of *C. taxifolia* in NSW, we compared epiphyte assemblages growing on fronds of *C. taxifolia* to those on coexisting eelgrass leaves of *Zostera capricorni* and elucidated the possible

consequences for the diversity and working of the ecosystem.

MATERIALS AND METHODS

Study site and experimental design

Three sites with mixed populations of the eelgrass *Zostera capricorni* and the green alga *Caulerpa taxifolia* were selected for sampling at Quibray Bay, Botany Bay, New South Wales. Water temperature in the area ranges between 19 and 21°C and salinity between 23 and 25 ppt (Spring values from Gray, 1991). Site 1 was located on the Kurnell Peninsula (34°00'S, 15°10'E) and was the nearest to the main body of water of Botany Bay. Sites 2 and 3 were sheltered and part of the Towra Point Natural Reserve (34°01'S, 15°10'E), they were about 2 km from Site 1 and 500 m apart from each other (Fig. 1). The sites were shallow (ca. 1 m depth) and were sampled at low tide in both September and October.

Sample collection and processing

At each sampling time, 10 random replicates of both *Zostera capricorni* and *Caulerpa taxifolia* were collected per site, carefully placed into plastic bags and transported in an ice box to the laboratory for further sorting.

The sample size for the study was fixed between 8 to 9 shoots (ca. 250 cm²) of *Z. capricorni*, according to variability in species richness per shoot established for other seagrass species (Ballesteros, 1987). However, since *Z. capricorni* has narrow strip like leaves (ca. 2 mm wide per 30 cm long and up to 5 leaves per shoot) whereas *C. taxifolia* forms pinnate fronds (ca. 5-7 cm long) connected by a rhizomatous stolon, differences in plant architecture required comparable surface areas for settlement of epiphytes to be established. To achieve this, plastic squares of a known surface were oil submerged and the weight difference between before and after the immersion was used to construct a regression line area-oil weight (draining time was fixed at 1 minute). The same procedure was conducted with *C. taxifolia* to determine the relationship between sample weight and the area covered by oil (Mapstone, 1982). This resulted in an equivalence of ca. 9 g of WW of *C. taxifolia* for the previously established sample surface size of *Z. capricorni*. Sub-

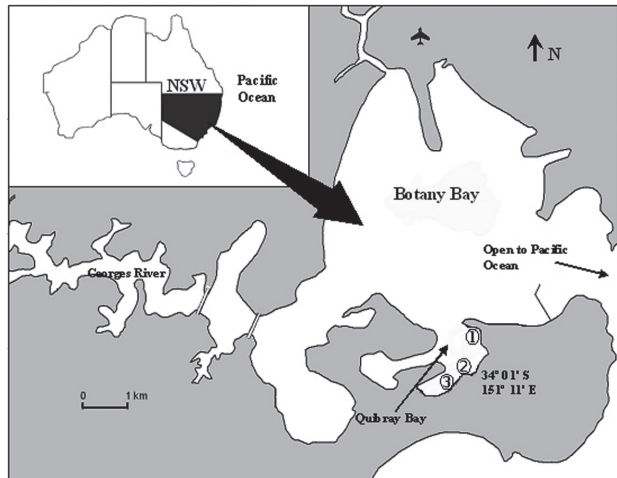


FIG. 1. – Map of Botany Bay, showing the position three sampling sites in Quibray Bay.

samples were then taken from each plastic bag, the plants were weighed until the desired weight was reached, then epiphytes were removed with a razor blade. Epiphytic algae and epifauna from eelgrass leaves and fronds of *Caulerpa taxifolia* were identified under the microscope down to genus level. A taxonomic resolution lower than species level has been successfully used to assess the response of benthic communities to a range of environmental impacts (e.g. Heip *et al.*, 1988; Warwick, 1988a,b; Warwick *et al.*, 1988; Gray *et al.*, 1990). In addition, the existence of a large body of literature that uses functional groups of macroalgae to evaluate food-web interactions and production dynamics (e.g. Littler and Arnold, 1982; Steneck and Dethier, 1994; Benedetti-Cecchi and Cinelli, 1995; Gacia *et al.*, 1999) supports our view that genera which morphologically similar species can still provide an adequate assessment of possible changes in ecosystem function with little or no loss of precision.

Data analyses

Differences in the number of epiphytic taxa between Habitat substrate (fixed factor), Sites (random factor) and sampling Times (random factor) were investigated with 3-way orthogonal ANOVA. Student-Newman-Keuls (SNK) post-hoc comparisons were conducted to examine significant groups of samples. Assumptions of homogeneity of variance and normality were tested with Cochran's test and Kolmogorov-Smirnov distribution-fitting test of the residuals respectively. For all analyses, the critical level of significance was $p < 0.05$.

Patterns of variation in epiphytic assemblages were investigated with the PRIMER 6 software package (Clarke and Warwick, 2001). Data was treated as presence-absence and used to build n-MDS ordinations to assess differences between *Zostera capricorni* and *Caulerpa taxifolia* and among sites at each sampling time. The significance of differences in the assemblage composition between Habitats, Sites and Times was investigated using the PERMANOVA+ $\beta 20$ software package (Anderson and Gorley, 2007), which allows up to nine factors to be tested. Further pair-wise comparisons were conducted for the significant interaction terms.

Similarities in percentage analyses (SIMPER; Clarke, 1993; Clarke and Warwick, 2001) were used to examine the contribution of presence-absence epiphytic taxa to differences between *Caulerpa taxifolia* and *Zostera capricorni* habitats.

RESULTS

A higher number of taxa was found growing on fronds of *Caulerpa taxifolia* (46 taxa) compared to leaves of *Zostera capricorni* (42 taxa) across the three study sites and the two sampling times (see Appendix 1). These differences were caused by a higher number of algal taxa on *C. taxifolia* compared to *Z. capricorni* (31 vs. 27 taxa respectively) whereas the same number of animal groups was found in both species (15 taxa). In particular, red algae were the most abundant algal group (16 taxa), followed by brown and green algae in equal numbers (6 taxa). Among epifauna, ascidians (6 taxa) and bryozoans (5 taxa) were the most common.

Richness of taxa

ANOVA results evidenced a significantly higher number of taxa on *Caulerpa taxifolia* compared to *Zostera capricorni* (see Table 1). However, the number of taxa on *C. taxifolia* decreased from September to October 2001 whereas it increased on *Z. capricorni* (i.e. a significant Ha x Ti interaction). The number of taxa at Site 1 was also consistently lower than at the other two sites (see Fig. 2) but displayed a slight increase over time in both habitats, whereas the number of taxa at Sites 2 and 3 decreased in *C. taxifolia* but increased in *Z. capricorni* (i.e. Si x Ti and Ha x Si x Ti interactions).

TABLE 1. – Results of 3-way ANOVA (n= 10; untransformed data) testing for differences in the number of taxa between habitats, times and sites. Significant differences are indicated: * p< 0.05, ** p< 0.01, ***p< 0.001.

	SS	d.f.	MS	F	P
Habitat	288.3	1	288.30	48.37	<0.001***
Site	218.6	2	109.31	24.55	<0.001***
Time	0.00	1	0.00	0.00	1.00
Habitat x Site	9.1	2	4.57	1.02	0.361
Habitat x Time	86.7	1	86.70	19.47	<0.001***
Site x Time	46.9	2	23.47	5.27	0.07**
Habitat x Site x Time	64.9	2	32.47	7.29	0.001***
Error		108	4.45		

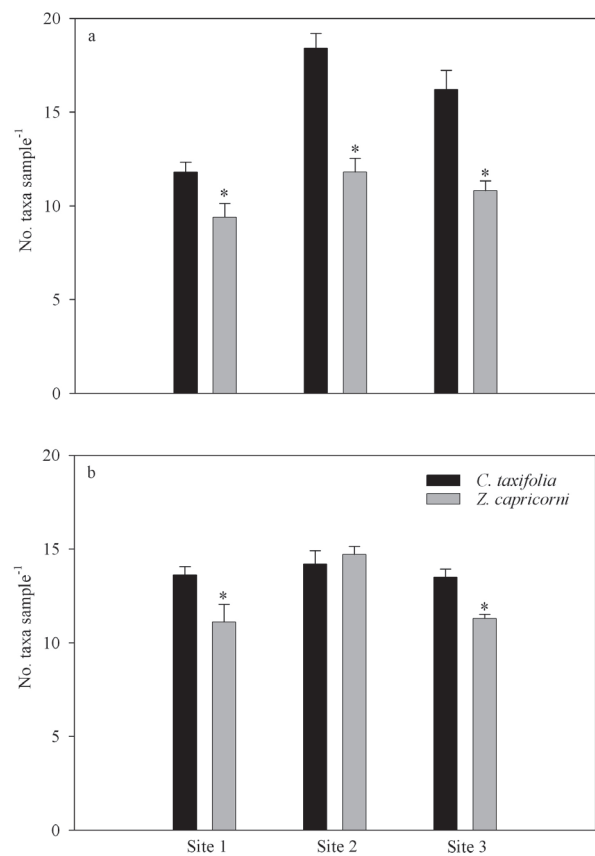


FIG. 2. – Mean No. of taxa recorded on fronds of *Caulerpa taxifolia* and leaves of *Zostera capricorni* at the three study sites in the September (a) and (b) October sampling. In SNK, significant differences among habitats at each site are indicated with asterisks. Error bars are SE.

Epiphytic assemblages

n-MDS ordination of epiphyte assemblages (presence-absence data) displayed two different groupings: one formed by samples from Sites 2 and 3 at the Towra Point Nature Reserve and another formed by samples from Site 1 at Kurnell Peninsula. Further subgroups were caused by differences between samples of *Caulerpa taxifolia* and *Zostera*

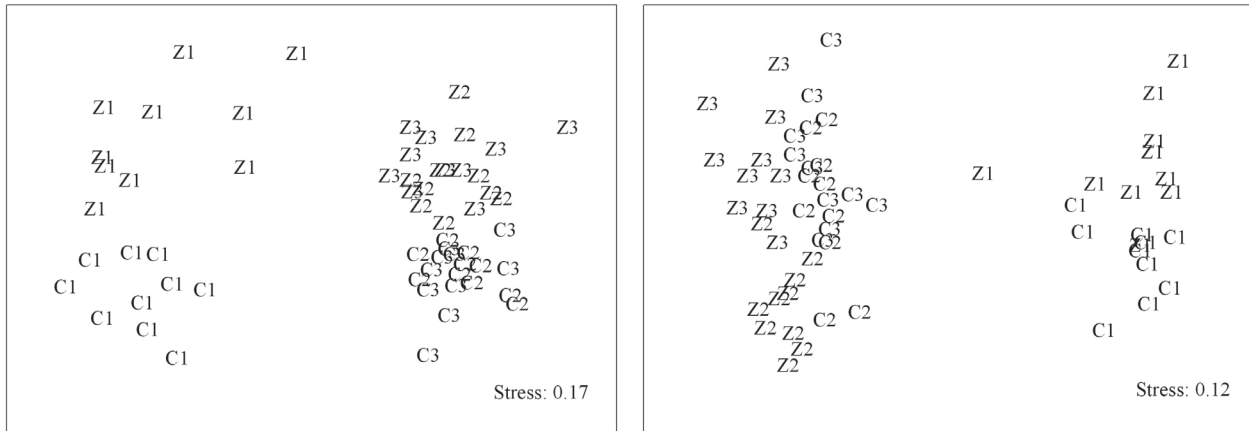


FIG. 3. – n-MDS ordination showing differences found between epiphyte assemblages growing on *Caulerpa taxifolia* (C) and *Zostera capricorni* (Z) at the three study sites in (a) September and (b) October sampling.

capricorni, particularly at Site 1 (see Fig. 3). Differences between habitats were, however, more evident at the first sampling site in early September than in October. PERMANOVA results for assemblage compositions were consistent with those from

ANOVA (i.e. significant Ha, Si, Ha x Si, Si x Ti and Ha x Si x Ti interactions; see above) but there were also significant differences between times ($p < 0.01$; see Table 2a). Pair-wise comparisons for the Ha x Ti interaction indicated that differences between C.

TABLE 2.– Results of (a) 3-factor PERMANOVA testing for differences in epiphyte composition, and (b) pair-wise comparisons test for the significant terms. Significant differences are indicated: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

(a) Treatments	SS	d.f.	MS	pseudo-F	P
Habitat	16060	1	16060	1.96	0.01*
Site	81256	2	40628	4.48	0.001**
Time	21021	1	21021	2.15	0.006**
Habitat x Site	8278.3	2	4139.1	1.41	0.149
Habitat x Time	5544.6	2	5544.6	1.89	0.044*
Site x Time	11146	2	5573.2	1.90	0.029*
Habitat x Site x Time	5853.4	2	2926.7	2.33	0.001**
Residual	1.35E5	108			

(b) Pair-wise comparisons							
Habitat x Time	t	P	Habitat x Site x Time	t	P		
<i>Caulerpa</i> vs. <i>Zostera</i>	Time1	1.96	<i>Caulerpa</i> vs. <i>Zostera</i>	Site1 x Time1	2.19	0.001**	
	Time2	1.38		Site2 x Time1	2.72	0.001**	
Time1 vs. Time2	<i>Caulerpa</i>	1.69	Site3 x Time1	2.68	0.001**		
	<i>Zostera</i>	1.85	Site1 x Time2	2.07	0.01*		
Site x Time			Site2 x Time2	1.73	0.001**		
	Site1 vs. Site2	Time1	2.48	Site3 x Time2	1.62	0.002**	
		Time2	3.15	Time1 vs. Time2	<i>Caulerpa</i> x Site1	2.33	0.001**
Site1 vs. Site3	Time1	2.43	<i>Caulerpa</i> x Site2	2.48	0.001**		
	Time2	3.36	<i>Caulerpa</i> x Site3	2.86	0.001**		
Site2 vs. Site3	Time1	1.26	<i>Zostera</i> x Site1	2.22	0.001**		
	Time2	1.45	<i>Zostera</i> x Site2	2.05	0.001**		
Time1 vs. Time2	Site1	2.04	<i>Zostera</i> x Site3	2.54	0.001**		
	Site2	1.29	Site1 vs. Site2	<i>Caulerpa</i> x Time1	4.22	0.001**	
	Site3	1.78	<i>Caulerpa</i> x Time2	3.85	0.001**		
			<i>Zostera</i> x Time1	3.17	0.001**		
			<i>Zostera</i> x Time2	3.42	0.001**		
			Site1 vs. Site3	<i>Caulerpa</i> x Time1	3.85	0.001**	
			<i>Caulerpa</i> x Time2	4.86	0.001**		
			<i>Zostera</i> x Time1	3.23	0.001**		
			<i>Zostera</i> x Time2	4.23	0.001**		
			Site2 vs. Site3	<i>Caulerpa</i> x Time1	1.81	0.001**	
			<i>Caulerpa</i> x Time2	1.48	0.007**		
			<i>Zostera</i> x Time1	1.41	0.02*		
			<i>Zostera</i> x Time2	1.98	0.001**		

TABLE 3. – SIMPER analysis of presence/ absence data showing the contribution (% cumulative=90%) of each taxa to average dissimilarities (Jaccard Index) between *Caulerpa taxifolia* and *Zostera capricorni* habitats.

Taxa	<i>C. taxifolia</i> <i>Z. capricorni</i>		Av. Diss.	Contrib.%	Cum.%
	Av. Abund.	Av. Abund.			
<i>Asciidiella</i> juv	2.00	0.00	4.41	12.21	12.21
<i>Scrupocellaria</i> sp.	0.00	2.67	4.41	12.21	24.41
<i>Ciona</i> sp.	0.33	1.33	3.10	8.59	33.00
Trochidae juv.	0.00	1.00	2.90	8.04	41.04
<i>Watersipora</i> sp.	0.00	0.67	2.83	7.84	48.88
Botrylloides sp.	2.00	0.00	2.78	7.71	56.59
Ampharetidae	1.00	0.00	2.78	7.71	64.30
<i>Clytia</i> sp.	6.33	6.00	2.42	6.72	71.01
<i>Botryllus</i> sp.	3.67	0.67	2.03	5.63	76.64
<i>Pyura</i> sp.	1.67	4.00	2.00	5.53	82.17
<i>Elphidium</i> sp.	2.67	2.00	1.97	5.47	87.64
<i>Barentsia</i> sp.	1.00	0.67	1.83	5.08	92.72

taxifolia and *Z. capricorni* were only significant at time 1 (i.e. September) whereas both habitats experienced significant changes over time. Pair-wise tests for the term Si x Ti, showed significant differences between Site 1 and Sites 2 and 3 at both study times, whereas differences between Sites 2 and 3 were not significant in September or October. Sites 1 and 3 also changed over time whereas Site 2 remained unchanged. Finally, pair-wise results for the Ha x Si x Ti interaction showed the existence of significant differences for all pairs of levels of each factor (for details see Table 2b).

The SIMPER analysis results indicated that, at the taxonomic level evaluated, epifauna made a higher contribution to average dissimilarities between habitats (36.10%) compared to epiphytic algae (23.11%) and the entire community (27.35%). Twelve epifauna taxa including ascidians (5), bryozoans (2), gastropods (1), polychaeta (1), hydrozoans (1), foraminifera (1) and kamptozoa (1), with contributions ranging from 12.21 to 5.08% (see Table 3) accounted for the entire 36.10% dissimilarity between *Caulerpa taxifolia* and *Zostera capricorni* during the study period.

DISCUSSION

This study evidences the presence of slightly higher numbers of taxa growing on fronds of the introduced green algae *Caulerpa taxifolia* compared to the native eelgrass *Zostera capricorni*, which suggests that the former is a favourable substratum for epiphytic settlement and development. Multivariate analyses also showed the existence of significant dif-

ferences in epiphyte composition between habitats, particularly animals, though taxa consisted mainly of epiphytic algae and were generally found on both plants. Further variability was also evidenced between the site at Kurnell Peninsula and the Towra Point Nature Reserve sites, which was possibly due to higher exposure to the saltwater influx and/ or variable hydrodynamic conditions (e.g. Kendrick *et al.*, 1988; Kendrick and Burt, 1997). Our results are in agreement with previous research in the Mediterranean that reports the existence of significant differences in the animal composition between *C. taxifolia* and control locations (Relini *et al.*, 1998; Travizi and Zavodnik, 2004), and with seasonal variability in the abundance of epiphytic algae (Verlaque and Fritayre, 1994).

Epiphytic biomass and species turnover are known to be tightly controlled by the seasonal variables of the host plant such as leaf growth (e.g. Mazzella *et al.*, 1981; Wittmann *et al.*, 1981; Alcoverro *et al.*, 1997). In tropical regions, natural populations of *Caulerpa taxifolia* have a development cycle with maximum growth rates in spring (Garrigue, 1994), whereas in the Mediterranean strain maximum growth occurs in summer (Komatsu *et al.*, 1994; Meinesz *et al.*, 1995). Laboratory experiments have also evidenced faster growth and lower mortality for New South Wales strains at usual summer temperatures ranging between 20 and 25°C (West and West, 2007). *Zostera capricorni* populations in Botany Bay start producing new shoots in early spring (i.e. September-October) and undergo high rates of leaf elongation throughout summer (Larkum *et al.*, 1984). Therefore, low standing biomass of *Z. capricorni* during the spring period concurs with the resting stage of *C. taxifolia* (see Boudouresque, 1997). In fact, temporal trends between sampling times during the study showed a decrease in the number of taxa on *C. Taxifolia*, whereas the number on *Z. capricorni* increased (see Fig. 2), combined with the loss of significant differences in taxa composition between habitats (Table 2b). As in other invaded regions, reduced growth of *C. taxifolia* in September (i.e. early austral spring) may be connected with lower production of toxic compounds (e.g. Amade *et al.*, 1996; Dumay *et al.*, 2002), but there are no available data on any New South Wales populations to compare them with. Hence, the greater structural complexity of pinnate *C. taxifolia* compared to the strip-like leaves of *Z. capricorni* may account for the overall higher richness of taxa during the study. In fact, there is a large body

of evidence to show that enhanced structural complexity may exert a large influence on the abundance, richness and diversity of marine assemblages (e.g. Roberts and Ormond, 1987; Hull 1997; Gratwicke and Speight, 2005; Hereu *et al.*, 2005), including invasive habitat forming species (reviewed by Crooks, 2002). In the Mediterranean, invasive strains of *C. taxifolia* have been shown to host greater numbers of epiphytic fauna than the native seagrass *Cymodocea nodosa* (Relini *et al.*, 1998) and to provide shelter to larger proportions of juvenile fish (Francour *et al.*, 1995; Harmelin-Vivien *et al.*, 1996) and meiofauna assemblages than control sites (Travizi and Zavodnik, 2004). In Quibray Bay, epifauna composition during the study period accounted for more of the dissimilarities between *C. taxifolia* and *Z. capricorni* than epiphytic algae (36.1% vs. 23.1% respectively), but the total numbers of taxa were not affected. Twelve taxa, out of a total of eighteen, fully explained the observed differences in animal composition between habitats. In particular, three taxa (2 ascidians and 1 polychaeta), were exclusive to *C. taxifolia*, and another three taxa (2 bryozoans and 1 gastropod) were found only on *Z. capricorni* (see Table 3). Many of these taxa were filter-feeding, often associated with surfaces, and may have been influenced by structural differences between the two habitats. In contrast, only one epiphytic algae, *Acrosorium* sp., was commonly found in *C. taxifolia* and was absent in *Z. capricorni* (see Appendix 1) despite taxa richness (Fig. 2). Biomass (authors' person. observ.) was higher in the *C. taxifolia* habitat. Our results suggest that epifaunal assemblages (particularly Ascidians and bryozoans; see also Relini *et al.*, 1998) could be a good indicator of ecosystem change in invaded areas, at least during the study period with potentially low metabolite production. At the ecosystem level, the relevance of these changes may be largely dependent on keystone predator effects, exploitative competition and control of primary productivity (Paine, 1980; Bologna and Heck, 1999). Further investigations are needed to assess the local relevance of these processes more fully.

The extent of the impact may be intensified by the magnitude of direct seagrass consumption because many macroherbivores often avoid feeding directly on *C. taxifolia* during most of the year (Lemée *et al.*, 1993; Lemée *et al.*, 1996; Boudouresque *et al.*, 1996). This may be particularly true for the Mediterranean, where the impact of macroherbivores on shallow meadows may reach ca. 57% of the annual

leaf production of *Posidonia oceanica* (Prado *et al.*, 2007) but may have a lesser influence on temperate meadows of *Z. capricorni* where leaf herbivory is comparatively less important (Conacher *et al.*, 1979; Larkum and West, 1990). Secondary metabolites of *C. taxifolia* are also known to be toxic to *P. oceanica* (Guerriero *et al.*, 1994) whereas *Z. capricorni* has not shown significant effects on neither growth nor photosynthetic parameters in response to experimental assays at various concentrations of caulerpenyne (Thomas, 2003). The interaction between the seasonal growth dynamics of *C. taxifolia* and that of the seagrass may produce different outcomes in systems with distinctive rates of productivity. For instance, enhanced growth of *C. taxifolia* and accumulation of reserves in seagrass rhizomes during the summer period causes loss of *P. oceanica* due to increased shading (Boudouresque, 1997). Equally, shading has been shown to decrease growth in *Z. capricorni* (Kirkman, 1978); however, comparatively higher rates of leaf productivity (ca. 7 leaves per yr; Duarte, 1991) may account for the rapid recovery and colonization of previously disturbed sites in Botany Bay (Larkum and West, 1990).

To conclude, epiphytic assemblages do not suggest that the introduced *Caulerpa taxifolia* in Botany Bay has a negative influence, at least during the study period. There were, however, significant differences between the two study habitats, particularly in terms of epifaunal composition, which could be used as indicators of ecosystem change in invaded systems. Further research is necessary to determine the influence of seasonal processes such as production of secondary metabolites on the observed patterns and on other invaded locations of New South Wales. Given the number of anthropogenic impacts and alien species documented for Botany Bay (e.g. McGuinness, 1988; Larkum and West, 1990; Davis *et al.*, 1997) it is also apparent that long-term monitoring and development of policy options are needed to preserve local seagrass ecosystems.

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APPENDIX 1. – No. of times that each taxa was observed on *Caulerpa taxifolia* and *Zostera capricorni* habitats at each Site and Time (n= 10).

		<i>C. taxifolia</i>						<i>Z. capricorni</i>					
		S1		S2		S3		S1		S2		S3	
		t 1	t 2	t 1	t 2	t 1	t 2	t 1	t 2	t 1	t 2	t 1	t 2
Bacillariophyceae	Tube dwelling diatoms	1	0	10	10	10	9	1	0	9	4	8	9
Cyanophyceae	<i>Lyngbya</i> spp.	0	0	1	0	0	0	0	0	0	0	0	0
	<i>Microcoleus</i> sp.	0	0	5	6	3	7	1	0	4	4	1	7
	<i>Hydrocoleum</i> sp.	0	0	2	2	2	1	0	0	3	0	2	3
Rodophyceae	<i>Acrosorium</i> sp.	5	8	0	0	0	0	0	0	0	0	0	0
	<i>Anotrichium</i> sp.	0	8	0	0	0	3	0	4	1	1	0	0
	<i>Ceramium</i> spp.	2	8	1	3	7	3	3	5	0	2	1	0
	<i>Centroceras</i> sp.	2	9	1	3	3	2	2	9	0	7	0	2
	<i>Champia</i> sp.	10	10	2	6	1	2	5	10	0	1	2	0
	<i>Chondria</i> spp.	3	2	9	9	9	10	2	3	9	9	10	9
	<i>Crouania</i> sp.	9	10	0	0	0	0	2	9	0	0	0	0
	<i>Dasya</i> spp.	2	9	0	1	0	6	1	7	0	0	0	0
	<i>Herposiphonia</i> sp.	0	1	0	0	0	0	0	0	0	0	0	0
	<i>Hypnea</i> sp.	6	9	1	0	0	1	2	5	0	0	0	0
	Encrusting Corallinaceae	9	10	6	10	10	10	10	10	10	10	10	9
	<i>Laurencia</i> spp.	2	0	8	1	9	2	3	0	4	7	9	4
	<i>Polysiphonia</i> spp.	2	0	10	7	9	8	2	0	10	10	10	10
	<i>Scinia</i> sp.	1	0	0	0	0	1	2	0	0	0	2	0
	<i>Spyridia</i> spp.	0	0	0	0	0	3	0	0	0	0	0	1
	<i>Stylonema</i> sp.	6	2	10	10	9	9	1	2	8	10	5	6
Phaeophyceae	<i>Asperococcus</i> sp.	0	0	10	4	7	1	0	0	3	0	2	0
	<i>Colpomenia</i> sp.	1	0	9	1	10	1	0	0	2	2	2	0
	<i>Dictyopteria</i> sp.	0	0	0	0	0	0	0	0	0	1	0	2
	Ectocarpaceae	0	0	9	2	3	0	0	1	3	3	0	2
	Ralfsiaceae	0	0	0	1	0	0	0	0	0	0	0	0
	<i>Sphaecelaria</i> sp.	0	0	1	0	0	0	0	0	0	0	0	0
Chlorophyceae	<i>Chaetomorpha</i> sp.	0	0	0	0	3	0	0	0	3	0	0	0
	<i>Cladophora</i> spp.	0	0	10	9	8	10	0	2	9	10	10	9
	<i>Enteromorpha</i> sp.	0	0	8	6	5	6	0	1	4	9	2	3
	<i>Microdictyon</i> sp.	6	0	0	1	0	0	5	0	0	0	0	0
	<i>Valonia</i> sp.	0	0	6	0	6	0	1	0	3	2	5	0
	<i>Ulvea</i> sp.	0	0	2	6	1	9	0	1	1	3	1	3
Ascidians	<i>Ascidiella</i> sp.	0	1	2	0	3	0	0	0	0	0	0	0
	<i>Botryllus</i> sp.	0	1	7	3	0	0	1	0	0	1	0	0
	<i>Ciona</i> sp.	0	1	0	0	0	0	0	1	0	2	0	1
	<i>Didemnum</i> sp.	0	0	1	0	1	1	1	0	2	3	0	2
	<i>Botrylloides</i> sp.	0	4	0	2	0	0	0	0	0	0	0	0
	<i>Pyura</i> sp.	4	0	0	0	0	1	5	6	0	1	0	0
Bryozoans	<i>Bowerbankia</i> sp.	1	1	6	2	3	0	6	0	9	7	8	1
	<i>Bugula</i> sp.	3	1	9	4	6	0	1	1	1	2	1	0
	<i>Electra</i> sp.	3	2	6	0	3	0	8	3	3	0	4	0
	<i>Scrupocellaria</i> sp.	0	0	0	0	0	0	0	1	0	6	0	1
	<i>Watersipora</i> sp.	0	0	0	0	0	0	0	1	1	0	0	0
Foraminifera	<i>Elphidium</i> sp.	2	1	0	0	0	5	0	1	0	0	1	4
Gastropods	<i>Trochidae</i> juv.	0	0	0	0	0	0	1	0	0	0	2	0
Hydrozoans	<i>Clytia</i> sp.	8	10	1	0	0	0	9	9	0	0	0	0
Kamptozoans	<i>Barentsia</i> sp.	3	0	0	0	0	0	2	0	0	0	0	0
Polichaeta	Spirorbidae	10	8	8	10	7	6	10	8	10	10	8	10
	Ampharetidae	1	0	1	1	0	0	0	0	0	0	0	0
Sponges	<i>Clathrina</i> sp.	0	1	5	3	8	1	0	0	0	1	1	0