Fish assemblages in habitats dominated by *Caulerpa taxifolia* and native seagrasses in south-eastern Australia

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ABSTRACT: Seagrass beds in estuaries are important habitats and nursery grounds for a great variety of fishes, including many economically important species. The introduction of the invasive green alga *Caulerpa taxifolia* could potentially threaten the seagrasses of south-eastern Australia. This study examined the implications of the spread of *C. taxifolia* on ichthyofauna in 2 estuaries in central New South Wales. Fish assemblages were compared among adjacent habitats of *C. taxifolia* and 2 seagrass species (*Posidonia australis* and *Zostera capricorni*). Fish were sampled using a small beam trawl to test for differences among habitats in (1) the species composition of the fish assemblages, (2) total abundance and species richness of fishes, and (3) abundances of major fish families. Fish assemblages separated into 3 significantly distinct groupings based on habitat. Total abundances of fishes were similar among habitats; however, species richness was lower in *C. taxifolia*. The fish assemblages in *C. taxifolia* were largely characterised by high abundances of gobiid fishes, similar to those in *Z. capricorni*, and few or no syngnathid and monacanthid species when compared to seagrass fish assemblages. This suggests that if *C. taxifolia* competitively replaces native seagrass beds in the estuaries of New South Wales, the resulting change in habitat may also cause a change in fish assemblages. This could reduce the abundances of some protected and economically important fish species but may also increase abundances of other opportunistic fishes.

KEY WORDS: *Caulerpa taxifolia* · Fish assemblages · Seagrass · South-eastern Australia

INTRODUCTION

Estuaries have been shown to support a high abundance and diversity of fishes and are important nursery grounds for many species (Claridge et al. 1986, Bell & Pollard 1989, Kennish 1990, Potter & Hyndes 1999). Within estuaries, seagrass beds are the most significant habitat for many of these fish species including a large number with commercial and recreational importance (Pollard 1976, 1984, Bell & Pollard 1989). Studies have shown that areas vegetated by seagrasses have a consistently higher diversity and abundance of fish when compared to adjacent unvegetated areas (Ferrell & Bell 1991, Gray et al. 1996, Jenkins & Wheatley 1998).

Worthington et al. (1992a) demonstrated that total fish abundance was largely a response to the presence of shelter.

The 2 dominant seagrasses in south-eastern Australia are *Posidonia australis* and *Zostera capricorni* (West et al. 1985). Several studies have shown that differences in fish assemblages exist between these seagrass species. A study of small fish sampled in adjacent beds of *Z. capricorni* and *P. australis* by Young (1981) found significant differences in species richness and the relative abundance of species between the 2 habitats in Port Hacking, New South Wales. A more comprehensive study in Botany Bay, New South Wales (Middleton et al. 1984), indicates that the differences

in the fish assemblages are due mainly to temporal and size differences of many species, suggesting that fish recruit first to *Z. capricorni* and then move into *P. australis* when they are older. Recently, Rotherham & West (2002) found significant differences in abundances and lengths of economically important fish species, and also the composition of fish assemblages between seagrass species in Botany Bay and Port Hacking, but not between these habitats in Sussex Inlet (200 km south). They suggest that local recruitment events and differences in the geomorphology of estuaries might also be important in determining the structure of fish assemblages.

Recently, concerns have been raised about seagrass meadows in south-eastern Australia in relation to the spread of the introduced green alga *Caulerpa taxifolia*. This alga was first discovered in estuaries in central New South Wales in 2000 (Schaffelke et al. 2002, Glasby et al. 2005). *C. taxifolia* has reportedly caused problems in the Mediterranean Sea, where it has spread rapidly since its first discovery in 1984 (Meinesz et al. 2001). Studies in the Mediterranean show that *Posidonia oceanica* seagrass beds have a positive effect on the growth of *C. taxifolia* and that sparse beds of the seagrass are particularly vulnerable to invasion (Ceccherelli & Cinelli 1999). Remote sensing and SCUBA surveys in Menton Bay and along 44% of the coast of France suggest, however, that invasion by *C. taxifolia* has not caused a significant reduction in the abundance of *Posidonia oceanica* (Jaubert et al. 1999, 2003). In Australia it is yet to be established whether *C. taxifolia* is having a negative impact on seagrasses; however, it has been observed growing adjacent to and in seagrass beds, as well as in previously unvegetated sediments (Glasby et al. 2005).

Few published studies have compared fish assemblages between native seagrasses and *Caulerpa taxifolia*. One such study on the French coast compared assemblages in areas colonised by *C. taxifolia* with those in native *Posidonia oceanica* beds (Francour et al. 1995). They found similarities in species richness and the composition of fish assemblages, but lower abundance and biomass in the site invaded by *C. taxifolia*. In the Ligurian Sea, Italy, areas colonised by *C. taxifolia* had higher species richness and almost double the abundances of fish compared to the native seagrass *Cymodocea nodosa* (Relini et al. 1998). The results of both these studies should, however, be treated cautiously because they lacked spatial replication, comparing only one site of invasion to one reference site.

The present study compared fish assemblages in 2 native seagrasses, the strapweed *Posidonia australis* and the eelgrass *Zostera capricorni*, with those found in adjacent areas colonised by *Caulerpa taxifolia*, in 2

south-eastern Australian estuaries. The aims of the study were to determine if fish communities in native seagrass beds differed from those in areas colonised by *C. taxifolia* with respect to (1) composition of fish assemblages, (2) total abundance and species richness of fishes and (3) abundances of the families of fishes that were dominant in the assemblages throughout the study.

MATERIALS AND METHODS

Study areas. The study was carried out at 3 sites in south-eastern Australia (Fig. 1). Two sites were sampled within Botany Bay, a large, marine-dominated embayment in the southern suburbs of Sydney (34°00′S, 151°14′E). Much of the land use in the catchment of the bay is urban and industrial. These 2 sites were located at Bona Point and Quibray Bay, on the southern side of the bay within the Towra Point aquatic reserve where all forms of fishing are banned.

The third site was situated in Port Hacking (34°05′S, 151°09′E), about 10 km south of Botany Bay. Port Hacking is a drowned river valley that is bordered on its northern side by residential suburbs and on its southern shore by National Park. It is a relatively pristine waterway, as much of its catchment is situated in national park land, and there is a lack of industry on its foreshores (Anonymous 1997). Port Hacking has been
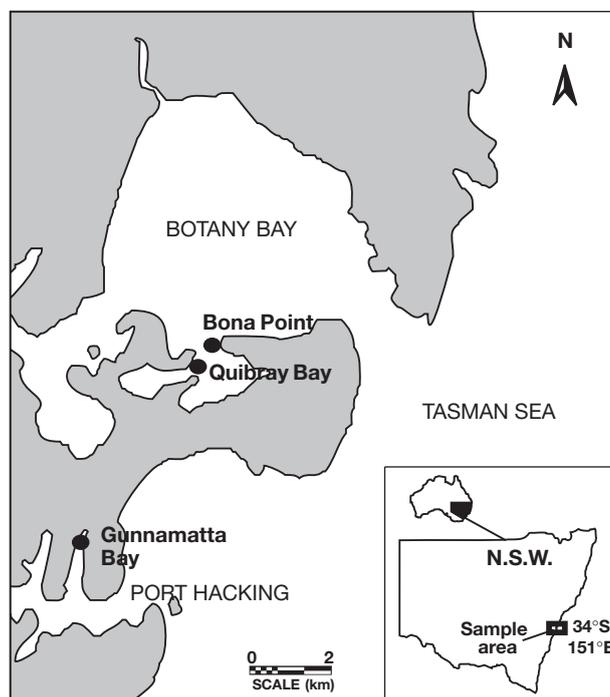

Fig. 1. Location of study sites in south-eastern Australia

closed to commercial fishing since 1886 (Pease & Herbert 2002) but has long been a popular recreational fishing spot in southern Sydney (Henry et al. 1987). This site was located at the head of Gunnamatta Bay. Port Hacking was one of the first estuaries in southeastern Australia where *Caulerpa taxifolia* was discovered (Schaffelke et al. 2002). Due to the differences in vegetation distributions within estuaries, depth varied among habitats at all sites with *Zostera capricorni* at an average depth of 0.5 m, *Posidonia australis* at between 1 and 1.5 m and *C. taxifolia* at around 1.5 m below mean low tide.

Experimental design. In each of the 3 study sites adjacent beds of *Zostera capricorni*, *Posidonia australis* and *Caulerpa taxifolia* were present and separated by no more than 300 m. Individual habitats ranged from ca. 200 m^2 of *Z. Capricorni* at Gunnamatta Bay to greater than 2 ha of *P. australis* in Quibray Bay. Fish assemblages in each benthic habitat were sampled using a small beam trawl, 1 m wide × 0.5 m high, with 3 mm mesh size. Replicate hauls (4 per habitat) of premeasured 25 m lengths were carried out at each site by towing the beam trawl behind a small boat at a speed of 3 to 5 km h^{-1}. Thus the area sampled was 25 m^2 per haul. Beam trawls have been used extensively for catching juvenile fish (Young 1981, Bell et al. 1992, Ferrell et al. 1993). Although seine nets have been found to be more effective than beam trawls for determining the relative proportion of species and estimating densities of fishes in seagrass (Guest et al. 2003), it was not practical to use a seine net in this study as the water was too deep at some of the sites. Sampling was done at roughly monthly intervals from early September 2003 to early February 2004, the main period of recruitment for economically important fish species (McNeill et al. 1992).

Fish caught in the beam trawl were identified, counted and then returned to the water. The vast majority of fish that were released swam away freely and without signs of ill effects. A single specimen of any species that could not be identified in the field was placed in a clove oil solution until death, then kept on ice and taken back to the laboratory for identification to species based on Kuiter (2000) and Gommon et al. (1994).

Previous studies have shown that tidal phase (Kingsford & Suthers 1996), time of day (Griffiths 2001) and moon phase (Smith & Suthers 2000) can affect fish abundances in seagrasses. In this study, sampling was carried out randomly with respect to tidal phase, but shallow water depths prevented sampling of *Zostera capricorni* at low tide. Although samples were collected in daytime only, time of day was randomised and sampling was focused around the full moon where possible to allow for temporal variation in recruitment and abundance of fishes that may be influenced by these factors. Salinity and water temperature were also recorded in each habitat on each sampling day using a multi-probe YSI meter to monitor for temporal and special fluctuations likely to affect the abundances of estuarine fishes.

Data analyses. The similarity of fish communities among sites and habitats for each of the 4 sampling periods was examined using non-parametric multivariate techniques (PRIMER package v5). Total abundances (25 m^{-2}) for each species in each sampling period were square root transformed and a Bray-Curtis similarity matrix was created (Clarke & Warwick 2001). The results were then plotted on a 2D scaling (MDS) plot. Analyses of similarity (ANOSIM) were conducted using a 2-way crossed design with site and habitat as the factors determined *a priori*. Where these groups were significantly different, similarity percentages (SIMPER) were calculated using square root transformed, unstandardised data to determine which species made the largest contribution to the dissimilarities (Clarke & Warwick 2001).

Total abundance was expressed as the number of fish in each 25 m^2 sample. Species richness was estimated for 25 m^2 using the equation:

$$S_{\text{tot}} = S_{\text{obs}} + (a^2/2b)$$

where S_{tot} is the predicted total species richness, S_{obs} is the observed number of species at a given sampling effort, a is the number of species represented by a single individual, and b is the number of species represented by exactly 2 individuals (Chao 1984). This extrapolative technique was found to be the best for limited sampling effort (Foggo et al. 2003). Analysis of variance (ANOVA) tests were applied to the total abundance and species richness indices as well as the abundances of the 3 major families represented in the study (Sygnathidae, Monacanthidae and Gobidae). Homogeneity of variance was not satisfied (Cochran's test), so the data were transformed [ln(x+1)] to fulfil this assumption. A 3-factor ANOVA model was used, with habitat as a fixed variable and site and time as random variables, meaning that an F-test for habitat could not be calculated unless either the Habitat × Site or Habitat × Time interaction could be eliminated. Student-Newman-Keul (SNK) tests were used to compare means when significant differences were detected by ANOVA.

RESULTS

The abundance of each species and their percentage contribution to the total catch in each habitat is summarised in Table 1. During the study 2744 individuals

Table 1. List of fish species caught during the study showing their abundance (1.2 km^2 area) and percentage contribution among the 3 habitats. Total abundance (N) of each fish species during the study (3.6 km^2 area) and their percentage contribution within the study are also shown. Z: *Zostera capricorni*, P: *Posidonia australis*, C: *Caulerpa taxifolia*

Family and species	Common name	Abundance/habitat			% contribution			Total	
		Z	P	C	Z	P	C	N	%
Syngnathidae	**Pipefishes and Seahorses**	425	93	11	32.3	14.5	1.4	529	19.3
Hippocampus whitei	White's seahorse	1	3	1	0.1	0.5	0.1	5	0.2
Stigmatapora argus	Spotted pipefish	32	69	0	2.4	10.8	0	101	3.7
Stigmatapora nigra	Wide-bodied pipefish	87	3	0	6.6	0.5	0	90	3.3
Urocampus carinirostris	Hairy pipefish	303	10	8	23.0	1.6	1.0	321	11.7
Vanacampus margaritifer	Mother-of-pearl pipefish	2	8	2	0.2	1.2	0.3	12	0.4
Scorpaenidae	**Scorpionfishes**								
Centropogon australis	Common fortescue	76	88	90	5.8	3.7	1.5	254	9.3
Ambassidae	**Glassfishes**								
Ambassis jacksoniensis	Port Jackson perchlet	7	20	54	0.5	3.1	6.9	81	3.0
Terapontidae	**Grunters**								
Pelates sexlineatus	Six-lined trumpeter	25	23	7	1.9	3.6	0.9	55	2.0
Apogonidae	**Cardinalfishes**								
Siphamia cephalotes	Wood's siphonfish	1	74	71	0.1	11.5	9.0	146	5.3
Gerreidae	**Silver bellies**								
Gerres subfasciatus	Common silver belly	0	1	0	0	0.2	0	1	0.1
Sparidae	**Snapper and Bream**	37	0	0	2.8	0	0	37	1.3
Acanthopagrus australis	Yellow-fin bream	2	0	0	0.2	0	0	2	0.1
Rhabdosargus sarba	Tarwhine	35	0	0	2.7	0	0	35	1.3
Girellidae	**Blackfishes**								
Girella tricuspidata	Luderick	23	1	0	1.8	0.2	0	24	0.9
Enoplosidae	**Oldwives**								
Enoplosus armatus	Old wife	2	2	0	0.2	0.3	0	4	0.1
Labridae	**Wrasses**								
Achoerodus viridis	Eastern blue groper	9	5	0	0.7	0.8	0	14	0.5
Odacidae	**Weed-whitings**								
Neoodax balteatus	Little rock-whiting	1	46	11	0.1	7.2	1.4	58	2.1
Scaridae	**Parrotfishes**								
Leptoscarus vaigiensis	Seagrass parrotfish	1	0	0	0.1	0	0	1	0.1
Blennidae	**Blennies**								
Petroscirtes lupus	Sabre-toothed blenny	0	0	1	0	0	0.1	1	0.1
Clinidae	**Weedfishes**								
Cristiceps australis	Crested weedfish	11	42	12	0.8	6.6	1.5	65	2.4
Gobiidae	**Gobies**	600	67	518	45.6	10.3	65.9	1184	43.2
Arenigobius bifrenatus	Bridled goby	1	0	5	0.1	0	0.6	6	0.2
Arenigobius frenatus	Half-bridled goby	177	21	138	13.4	3.3	17.6	336	12.2
Bathygobius kreffti	Frayed-fin goby	52	22	65	4.0	3.4	8.3	139	5.1
Cristagobius gobioides	Oyster goby	0	0	2	0	0	0.3	2	0.1
Favonigobius exquisitus	Exquisite sand-goby	24	4	48	1.8	0.6	6.1	76	2.8
Favonigobius lateralis	Long-finned goby	184	8	39	14.0	1.3	5.0	231	8.4
Gobiopterus semivestita	Glass goby	2	0	0	0.2	0	0	2	0.1
Redigobius macrostoma	Large-mouthed goby	160	11	221	12.2	1.7	28.1	392	14.3
Bothidae	**Flounders**								
Pseudorhombus jenynsii		0	1	1	0	0.2	0.1	2	0.1
Monacanthidae	**Leatherjackets**	97	177	8	7.4	27.6	1.3	284	10.4
Acanthaluteres spilomelanurus	Bridled leatherjacket	15	51	3	1.1	8.0	0.4	69	2.5
Brachaluteres jacksonianus	Pygmy leatherjacket	0	8	0	0	1.3	0	8	0.3
Meuschenia freycineti	Six-spined leatherjacket	62	77	3	4.7	12.0	0.4	142	5.2
Meuschenia trachylepis	Yellow-finned leatherjacket	10	16	0	0.8	2.5	0	26	1.0
Monacanthus chinensis	Fan-belly leatherjacket	9	11	4	0.7	1.7	0.5	24	0.9
Nelusetta ayraudi	Chinaman leatherjacket	1	6	0	0.1	0.9	0	7	0.3
Scobinichthys granulatus	Rough leatherjacket	0	8	0	0	1.3	0	8	0.3
Tetradontidae	**Toadfishes**								
Tetractenos glaber	Smooth toadfish	2	1	0	0.2	0.2	0	3	0.1
Diodontidae	**Porcupinefishes**								
Dicotylichthys punctulatus	Three-bar porcupinefish	0	1	0	0	0.2	0	1	0.1

were caught, representing 37 species and 19 families. *Zostera capricorni* had the highest abundance with 1317 individuals belonging to 30 species and 15 families, followed by *Caulerpa*, with 786 individuals from 21 species and 11 families, and *Posidonia australis* with 641 individuals belonging to 30 species from 16 families. The most abundant species were from Family Gobiidae (gobies) and included *Redigobius macrostoma*, *Arenigobius frenatus*, *Favonigobius lateralis* and *Bathygobius kreffti*, which were distributed across all habitats. Family Syngnathidae (pipefishes and seahorses) comprised a large portion of the catch with *Urocampus carinirostris* and *Stigmatapora nigra* mainly inhabiting *Z. capricorni* beds and *Stigmatapora argus* mainly in *P. australis* beds. Monacanthidae (leatherjackets) such as *Meuschenia freycineti* and *Acanthaluteres spilomelanurus* were also relatively abundant in the seagrass habitats. Other fish caught in relatively large numbers were 2 pelagic schooling species *Siphamia cephalotes* and *Ambassis jacksoniensis*

as well as the benthic species *Centropogon australis*, *Neoodax balteatus* and *Cristiceps australis*. Recruits of economically important species *Rhabdosargus sarba*, *Acanthopagrus australis* and *Girella tricuspidata* were found infrequently and in low numbers during the study, but when caught they were almost exclusively in *Z. capricorni* beds.

Fish assemblages in the 3 habitats showed reasonably consistent patterns during all 4 sampling periods based on the MDS plots (Fig. 2). The samples grouped together based on habitat and were partially separated from one another. Overall, *Caulerpa taxifolia* and *Posidonia australis* appear to be the most distant in terms of assemblages with *Zostera capricorni* assemblages lying between the two. Samples within *C. taxifolia* in October and January and *Z. capricorni* in November/December and January showed greater spread in relation to each other indicating greater variation within these habitats than the other months. The stress values for the 4 different multidimensional scaling plots ranged between
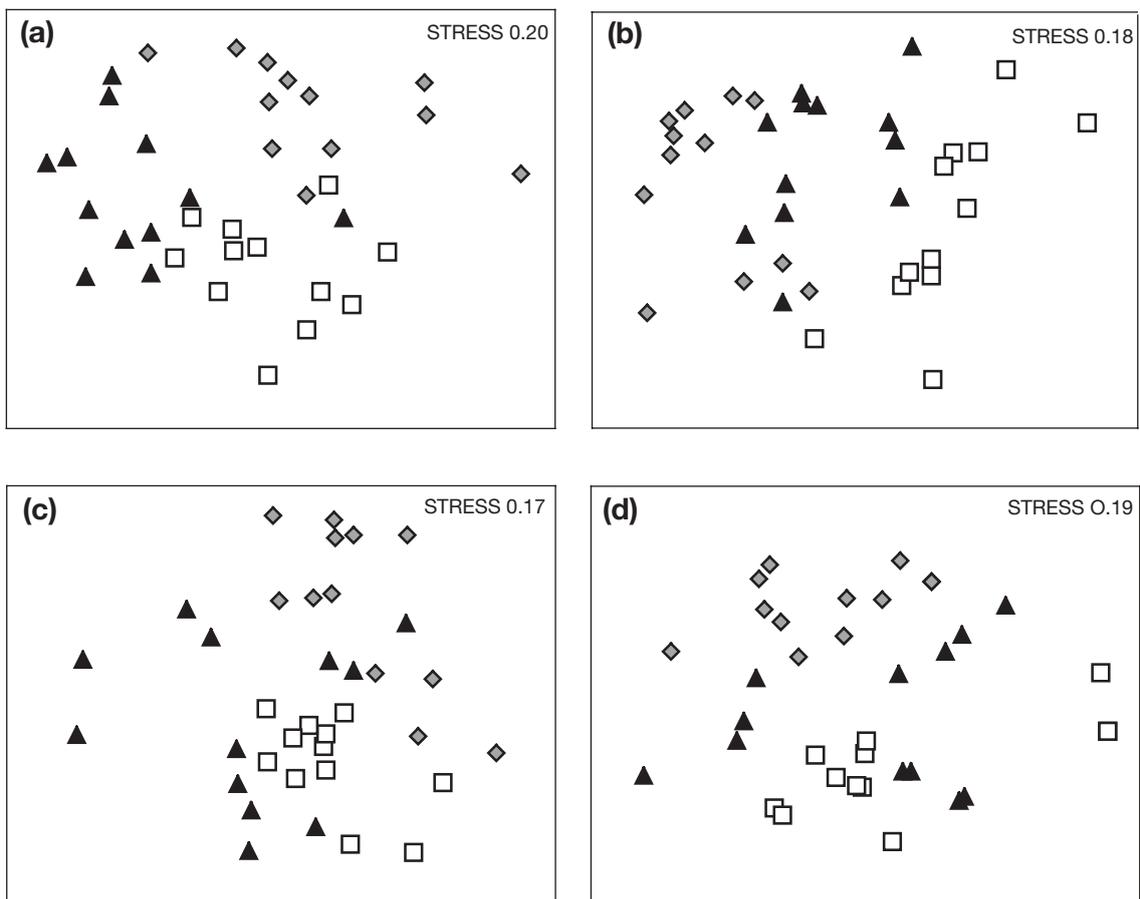

Fig. 2. Multidimensional scaling plots based on square root transformed abundance data for the 4 sampling periods: (a) September 2003, (b) October 2003, (c) November/December 2003, (d) January 2004. ▲: *Zostera capricorni*, ◆: *Posidonia australis*, □: *Caulerpa taxifolia*

Table 2. ANOSIM using a 2-factor crossed design (habitat and site differences) at each of the 4 sampling periods (S = September 2003, O = October 2003, N/D = November/December 2003, J = January 2004). Global R values calculated after 5000 random permutations. All values significant at p < 0.01

	S	O	N/D	J
Habitat	0.686	0.664	0.601	0.736
Site	0.471	0.573	0.431	0.572

Table 3. Pairwise comparisons of differences between habitats (ANOSIM) at each of the 4 sampling periods (see Table 2). Global R values and significance levels were calculated after 5000 random permutations. *Significant results at p < 0.05

	Z. capricorni vs. *P. australis*		*Z. capricorni* vs. *C. taxifolia*		*P. australis* vs. *C. taxifolia*	
	Global R	p	Global R	p	Global R	p
S	0.809	>0.01*	0.609	>0.01*	0.764	>0.01*
O	0.910	>0.01*	0.712	>0.01*	0.549	>0.01*
N/D	0.764	0.01*	0.635	>0.01*	0.684	>0.01*
J	0.705	>0.01*	0.767	>0.01*	0.868	>0.01*

0.17 and 0.2, which are high but acceptable for display on a 2D plot (Clarke 1993).

The analysis of similarity (ANOSIM) for each sampling period (Table 2) showed that there were significant differences in the fish assemblages at all times among all habitats and sites. In all cases these differences were stronger between habitats than they were between sites, as shown by the global R values that ranged from 0.601 to 0.736 for habitats compared to 0.572 to 0.431 for sites. Pairwise comparisons (Table 3) showed significant differences between all habitats at every sampling period.

The application of SIMPER analysis (Table 4) showed that differences between the 2 seagrass habitats were due largely to greater abundances of *Urocampus carinirostris*, *Arenigobius frenatus* and *Favonigobius lateralis* in *Zostera capricorni* beds and a larger contribution of *Stigmatapora argus*, *Siphamia cephalotes* and *Meuschenia freycineti* in *Posidonia australis* beds. Assemblages in *Caulerpa taxifolia* differed from those in *Z. capricorni* due to the high abundance of *U. carinirostris* in *Z. capricorni* and its absence in *C. taxifolia* as well as the greater abundances of *Redigobius*

Table 4. SIMPER analysis showing the percentage contribution (% C) of the 5 most important fish species to the dissimilarity of samples between different habitats (pairwise comparisons) for the 4 sampling periods. Also shown are the average abundances (#) 25 m^{-2} for these species in each habitat. Z = *Zostera capricorni*, P = *Posidonia australis*, C = *Caulerpa taxifolia*. See Table 1 for full species names. AD = average dissimilarity

Z. capricorni vs. *P. australis*	# Z	# P	% C	*Z. capricorni* vs. *C. taxifolia*	# Z	# C	% C	*P. australis* vs. *C. taxifolia*	# P	# C	% C
September 2003											
AD = 82.71				**AD = 75.70**				**AD = 82.92**			
F. lateralis	4.4	0.4	10.0	*R. macrostoma*	1.08	8.42	15.2	*R. macrostoma*	0.2	8.4	13.1
U. carinirostris	4.3	0.3	9.2	*A. frenatus*	4.42	2.75	12.5	*A. spilomelanurus*	3.2	0.3	9.9
A. spilomelanurus	0.5	3.2	7.9	*U. carinirostris*	4.25	0.50	12.3	*A. frenatus*	0.6	2.8	8.6
A. frenatus	4.4	0.6	7.6	*F. lateralis*	4.42	1.17	11.1	*S. cephalotes*	1.9	0.0	8.0
S. cephalotes	0.0	1.9	7.2	*S. nigra*	2.33	0.00	8.3	*S. argus*	2.1	0.0	6.6
October 2003											
AD = 71.45				**AD = 75.08**				**AD = 81.67**			
F. lateralis	8.6	0.2	12.6	*U. carinirostris*	6.33	0.08	13.1	*M. freycineti*	2.7	0.1	11.4
U. carinirostris	6.3	0.3	10.6	*F. lateralis*	8.58	0.75	12.9	*A. frenatus*	0.3	2.9	10.3
A. frenatus	3.7	0.3	7.2	*M. freycineti*	3.67	0.08	10.2	*R. macrostoma*	0.3	3.1	9.5
M. freycineti	3.7	2.7	6.5	*R. macrostoma*	1.25	3.08	8.6	*S. cephalotes*	1.9	0.0	7.7
S. cephalotes	0.0	1.9	6.2	*A. frenatus*	3.67	2.92	8.6	*C. australis*	1.2	1.9	7.1
November/December 2003											
AD = 79.67				**AD = 70.20**				**AD = 77.49**			
A. frenatus	3.8	0.4	10.1	*A. frenatus*	3.75	3.67	11.7	*A. frenatus*	0.4	3.7	14.6
U. carinirostris	6.8	0.1	9.8	*R. macrostoma*	3.75	2.00	11.5	*S. argus*	1.6	0.0	10.0
S. argus	0.2	1.6	8.5	*U. carinirostris*	6.83	0.00	10.6	*R. macrostoma*	0.1	2.0	9.8
F. lateralis	1.7	0.1	7.9	*B. kreffti*	0.67	2.25	8.9	*B. kreffti*	1.0	2.3	8.9
S. nigra	3.2	0.0	7.6	*F. lateralis*	1.67	1.17	8.7	*S. cephalotes*	0.7	5.8	8.9
January 2004											
AD = 74.88				**AD =73.66**				**AD = 76.63**			
U. carinirostris	7.8	0.1	12.1	*U. carinirostris*	7.83	0.08	13.3	*M. freycineti*	2.3	0.1	11.5
C. australis	2.7	4.0	9.9	*R. macrostoma*	7.25	4.92	12.5	*C. australis*	4.0	2.8	11.3
R. macrostoma	7.3	0.3	8.7	*C. australis*	2.67	2.83	10.3	*F. exquisites*	0.2	2.8	10.5
A. frenatus	2.9	0.5	7.6	*F. exquisites*	1.67	2.75	10.0	*R. macrostoma*	0.3	4.9	9.9
M. freycineti	0.6	2.3	7.5	*A. frenatus*	2.92	2.17	8.8	*S. cephalotes*	1.7	0.1	8.4

macrostoma and *A. frenatus* in *C. taxifolia.* Fish assemblages in *P. australis* differed from those in *C. taxifolia* due to much higher abundances of *S. argus*, *M. freycineti* and *S. cephalotes* and lower abundances of *R. macrostoma* and *A. frenatus* in the seagrass.

ANOVA determined interactions between site and habitat were significant for both total abundance of fishes and species richness (Table 5). Total abundance was similar among habitats at Gunnamatta Bay and Bona Point, but there were significantly more fishes in *Zostera capricorni* beds in Quibray Bay (SNK test; Fig. 3a). This was the cause of the significant Site × Habitat interaction, although there was a similar, but non-significant, trend in Gunnamatta Bay. Similarly, species richness differed among habitats at 2 sites (Fig. 3b). *Caulerpa taxifolia* habitats had significantly fewer species than the seagrass habitats in Gunnamatta Bay and Quibray Bay (SNK test). In contrast, for Bona Point, *Posidonia australis* beds had significantly more species than *C. taxifolia* or *Z. capricorni* beds.

Patterns of abundance of fishes from Family Syngnathidae among habitats differed at each site (Table 5c). *Zostera capricorni* had significantly higher abundances of syngnathids compared to *Posidonia australis* at both Gunnamatta Bay and Quibray Bay, but there were similar abundances in the 2 seagrass habitats at Bona Point (SNK test, Fig. 4a). Abundances of syngnathids in *Caulerpa taxifolia* were significantly less than in either seagrass habitat at all 3 sites (Fig. 4a).

Abundance of Monacanthidae also differed among habitats and sites (Table 5d). In Gunnamatta Bay and at Bona Point, significantly more monacanthids were caught in seagrass habitats than in *Caulerpa taxifolia*, whilst in Quibray Bay this significant difference occurred only between *Zostera capricorni* and *C. taxifolia* (SNK test; Fig. 4b). Moreover, in the 2 sites in Botany Bay (Bona Point and Quibray Bay), *Posidonia australis* contained significantly higher numbers of syngnathid fishes than did *Z. capricorni.* Interestingly, there was an opposite trend in Gunnamatta Bay (Fig. 4b).

For Gobiidae, there was a significant interaction among site, habitat and time (Table 5e). Abundances of species from this family were consistently, and often significantly, lowest in *Posidonia australis* (SNK test; Fig. 4c). Although the magnitude of differences in abundances of gobies among habitats differed among times and sites, there was a consistent trend for gobies to be most abundant in *Zostera capricorni* and *Caulerpa taxifolia* (Fig. 4c).

Water temperature ranged from 12.7°C in September to 26.8°C in January, with an overall trend of rising temperatures between each successive sampling period. At no time, however, was there a difference greater than 2°C between the 3 habitats on any sampling day.

Table 5. Results of 3-factor ANOVA for total abundance, species richness and abundance of major families. Data were $\ln(x + 1)$ transformed to reduce heterogeneity of variance. Significant differences at *p = 0.05 and **p = 0.01. N/A: not applicable

Source	df	MS	*F*-value	p
(a) Total abundance				
Site (S)	2	7.6115	8.10	
Habitat (H)	2	3.6989	No test	N/A
Time (T)	3	0.0996	0.11	
S × H	4	2.5511	5.08	*
S × T	6	0.9397	3.18	**
H × T	6	0.8107	1.62	
S × H × T	12	0.5019	1.70	
Residual	108	0.2956		
(b) Estimated species richness				
Site (S)	2	0.5601	1.41	
Habitat (H)	2	3.4384	No test	N/A
Time (T)	3	0.7135	1.80	
S × H	4	0.8036	4.71	*
S × T	6	0.3969	1.68	
H × T	6	0.2547	1.49	
S × H × T	12	0.1706	0.72	
Residual	108	0.2359		
(c) Abundance, Syngnathidae				
Site (S)	2	4.2853	12.68	**
Habitat (H)	2	20.0503	No test	N/A
Time (T)	3	0.2971	0.88	
S × H	4	1.1441	5.20	*
S × T	6	0.3381	1.65	
H × T	6	0.1528	0.69	
S × H × T	12	0.2200	1.08	
Residual	108	0.2046		
(d) Abundance, Monacanthidae				
Site (S)	2	0.3831	0.69	
Habitat (H)	2	13.4537	No test	N/A
Time (T)	3	0.9715	1.75	
S × H	4	1.7407	7.82	**
S × T	6	0.5567	2.94	*
H × T	6	0.4315	1.94	
S × H × T	12	0.2227	1.18	
Residual	108	0.1894		
(e) Abundance, Gobiidae				
Site (S)	2	2.1680	1338	**
Habitat (H)	2	12.6460	No test	N/A
Time (T)	3	0.1449	0.89	
S × H	4	1.8996	5.34	*
S × T	6	0.1621	1.26	
H × T	6	0.1482	0.42	
S × H × T	12	0.3557	2.77	**
Residual	108	0.1286		

There was also no systematic ranking of habitat with respect to water temperature, and differences were most likely due to the time of day that sampling was undertaken. Salinity was relatively stable throughout the study period, ranging from 34.1 to 36.1 psu across all sites, habitats and times. It is therefore considered unlikely that salinity or water temperature had any influence on the distribution of fishes.
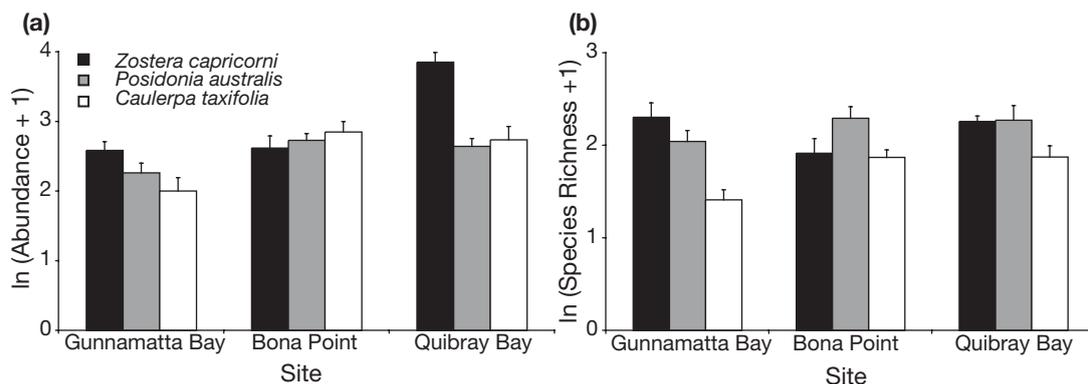
Fig. 3. Mean numbers (±SE) 25 m^{-2} sample for (a) total abundance of fishes and (b) estimated species richness at each site for the different habitats studied. Data have been ln(x + 1) transformed to reduce heterogeneity of variance
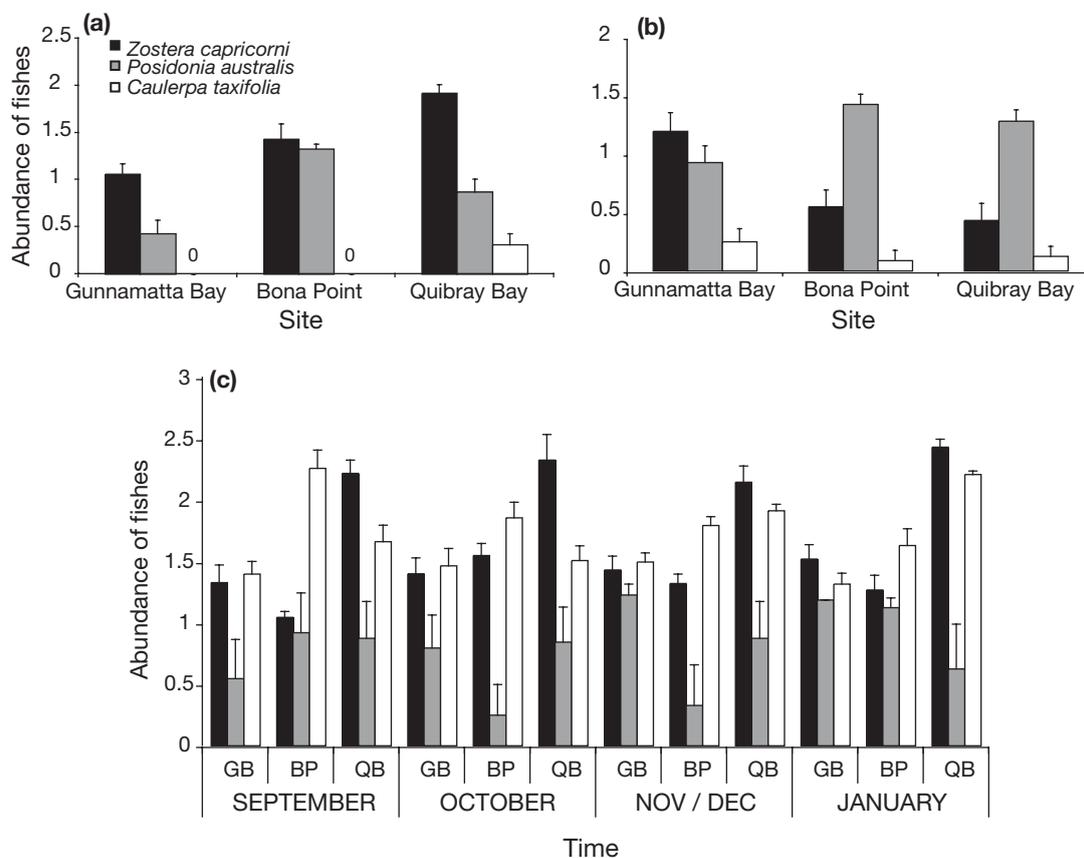

Fig. 4. Mean numbers (±SE) of fishes 25 m^{-2} sample for (a) family Syngnathidae, (b) family Monacanthidae (site and habitat) and (c) family Gobiidae (site, habitat and time). Data have been ln(x + 1) transformed to reduce heterogeneity of variance

DISCUSSION

This study identified significant differences in fish assemblages among habitats dominated by *Zostera capricorni*, *Posidonia australis* or *Caulerpa taxifolia*. At 2 sites, the species richness of fishes and at 1 site the total abundance of fishes in *C. taxifolia* was signifi-

cantly less than in the 2 seagrass habitats. Specifically, syngnathids and monacanthids were rare or absent in *C. taxifolia* compared to seagrasses. These results run counter to the situation in the Mediterranean, where species richness of fish assemblages is similar, though abundances of fishes are less in *C. taxifolia* compared to *Posidonia oceanica* (Francour et al. 1995), or both

total abundance and species richness are greater in *C. taxifolia* compared to *Cymodocea nodosa* (Relini et al. 1998). It is possible that the results of these Mediterranean studies were confused because spatially confounded sampling designs were used, or patterns in the Mediterranean are opposite to those in New South Wales. Seagrass habitats in this study comprised similar fish assemblages to those found in previous ones in *Z. capricorni* and *P. australis* in south-eastern Australia (Young 1981, Middleton et al. 1984, Rotherham & West 2002).

One possible reason for the differences in fish assemblages may be variation in structural complexity among the 3 habitats. Habitat complexity in seagrasses and other aquatic vegetation is a function of many morphological features of the plant such as leaf density and blade height, width and shape (Rooker et al. 1998). It has been demonstrated that more complex habitats are capable of supporting much greater abundances of fish because the shelter they provide is an effective aid in the avoidance of predators (Heck & Orth 1980, Stoner & Lewis 1985, Savino & Stein 1993, Rooker et al. 1998). Relini et al. (2001) compared *Posidonia oceania*, *Cymodocea nodosa* and sparse and dense *Caulerpa taxifolia*, and found that structural complexity was important in determining the species composition of fish assemblages among habitats. Levi & Francour (2004) also found that increases in habitat complexity due to the colonisation of previously unvegetated areas by *C. taxifolia* in the Mediterranean Sea reduced the abundances of *Mullus surmuletus*, a fish species usually found over bare substrate.

Diets of fishes and the availability of food in each habitat is another possible reason that may explain the differences in fish assemblages among habitats. Fish in seagrasses are known to have a variety of diets. Herbivorous and omnivorous fishes are well represented in the seagrass beds of south-eastern Australia, especially monacanthids and *Girella tricuspidata* (Bell & Pollard 1989). Herbivory may be the disadvantaged in *Caulerpa taxifolia* habitat due to the lack of epiphytic algae growing on fronds and the toxic metabolites produced by the alga when wounded (Amade & Lemee 1998), and indeed monacanthids and *G. tricuspidata* were largely absent in this habitat. Other fishes in seagrasses feed on planktonic and epifaunal crustaceans such as copepods and amphipods (Burchmore et al. 1984). Carnivorous fishes may find a reduction in food such as epifaunal and benthic invertebrates in *C. taxifolia*, as is the case in the Mediterranean (Boudouresque et al. 1992, Bellan-Santini et al. 1996). This may partially explain the low numbers of syngnathids in *C. taxifolia*; however, gobies, which are mainly carnivorous, were common in this habitat.

It is also possible that differences in fish assemblages may be due to differences in water depth between habitats. Although there were slight differences in low tide water depth, particularly between *Caulerpa taxifolia* and *Zostera capricorni*, the fact that the fish assemblages in *C. taxifolia* beds were more similar to those in *Z. capricorni* than those in *Posidonia australis* indicates this is an unlikely explanation. Another possible reason for differences in fish assemblages may be an artefact of the sampling method used. The beam trawl used in the present study was biased towards smaller and slower fish (<500 mm) (Guest et al. 2003). Middleton et al. (1984) found that *P. australis* supports predominately the same species as *Z. capricorni*, although of larger body sizes, using a variety of sampling methods to target different size classes of fish. Gray & Bell (1986) also showed that daytime sampling with a beam trawl catches slightly fewer species (30%) and dramatically fewer individual fishes (up to 85%) than other techniques such as night trawling and poisoning. Daytime trawling was the only feasible option available and was used consistently across all sites and habitats; however, we concede that this method does not describe the entire fish assemblage living within the sampled habitats. Several other reasons for differences in fish assemblages need to be explored further including differences in hydrodynamic factors and predation intensity among habitats.

Of the major families represented in the study, syngnathids were found to be far more abundant in seagrasses than *Caulerpa taxifolia* habitat. The syngnathids caught in this study were closely associated with seagrasses in previous studies in south-eastern Australia (Middleton et al. 1984, Steffe et al. 1989, Rotherham & West 2002). It appears that these species of pipefishes are specially adapted to seagrass habitat with their colour and shape mimicking those of the seagrass blades in which they are found (Jenkins & Wheatley 1998). Pipefish feeding behaviour, which involves them grasping the leaf blade with their tail and consuming passing copepods and amphipods, also appears to be suited to seagrass habitat (Howard & Koehn 1985).

Monacanthids were also more abundant in seagrass beds, in particular *Posidonia australis* compared to *Caulerpa taxifolia*. Monacanthids are known to be omnivorous, with many species feeding on a diet of epiphytic algae growing on seagrass blades, invertebrates and possibly seagrass itself (Bell et al. 1978, Conacher et al. 1979, Robertson & White 1986). Epiphytic algae were not seen growing on *C. taxifolia* either when it was hauled in with the net or when inspected under SCUBA. In addition, better shelter may be available to these fishes in seagrasses. Many other studies have found high abundances of mona-

canthids in seagrass meadows and particularly among the larger leaf blades of *P. australis* (Burchmore et al. 1984, Middleton et al. 1984, Ferrell et al. 1993, Rotherham & West 2002).

Gobies were commonly found in all 3 habitats. Previous studies show that the suite of gobiid species in this study inhabit not only seagrass but also bare sand and rocky reefs (Middleton et al. 1984, Gray et al. 1996, Jenkins & Wheatley 1998). In this study gobies were more prevalent overall in *Caulerpa taxifolia* beds at both Botany Bay sites and in *Zostera capricorni* beds at Quibray Bay. These 2 habitats were most similar in terms of habitat complexity (leaf density, leaf height and width, but not leaf shape or colour, unpubl. data). Perhaps the adaptability of gobies to different habitats allowed them to settle in *C. taxifolia* and exploit the niche that is available due to the unsuitability of this habitat to other fish species (Townsend et al. 2000).

Recruits of economically important fish such as *Acanthopagrus australis*, *Rhabdosargus sarba* and *Girella tricuspidata* were only caught in very low numbers and predominately in *Zostera capricorni* in Quibray Bay. This was an unexpected result as the study coincided with the main recruitment season of juvenile fish in Botany Bay, i.e. spring and summer (Bell et al. 1988, McNeill et al. 1992, Worthington et al. 1992b, Smith & Suthers 2000). Fish abundances in seagrasses vary both spatially and temporally (Ferrell et al. 1993), and the present study appeared to be conducted in a particularly poor year for recruitment. Given such low abundances and no definite trend between sites, it is difficult to draw strong conclusions regarding the distribution of these species between habitats. Previously, juvenile recruits of these species have been predominately distributed in *Z. capricorni* beds (Middleton et al. 1984, Rotherham & West 2002). Mediterranean studies have found that sparids readily recruited to *C. taxifolia* (Francour et al. 1995, Relini et al. 1998).

CONCLUSION

The main finding of this study was that there were significant differences in fish assemblages among the 3 habitats of *Zostera capricorni*, *Posidonia australis* and *Caulerpa taxifolia*. The main differences between the assemblages of *C. taxifolia* and the 2 seagrasses were due to lower species richness in *C. taxifolia* due largely to an absence or rarity of fishes from the syngnathid and monacanthid families. Some of the possible reasons for these differences in fish assemblages could be differences in habitat complexity or the availability of food among the 3 habitats. Manipulative laboratory or field experiments would be useful in determining these and other likely causes of these differences. If *C. taxifolia* were to replace seagrass in New South Wales, it is possible that some fish species would decline in numbers or possibly disappear altogether. Another possibility is that once the seagrass was replaced, fish favouring this habitat would successfully switch to *C. taxifolia* beds. Further study is required to determine what the most likely outcome may be.

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