

# Fish assemblages in seagrass beds are influenced by the proximity of mangrove forests

Jane E. Jelbart · Pauline M. Ross · Rod M. Connolly

Received: 20 March 2006 / Accepted: 15 June 2006 / Published online: 1 August 2006  
© Springer-Verlag 2006

**Abstract** Mangrove forests and seagrass beds frequently occur as adjacent habitats in the temperate waters of southeastern Australia. At low tide when fish cannot occupy mangroves they might utilise adjacent habitats, including seagrass. We first sampled small fish from seagrass beds close to and far from mangroves in the Pittwater estuary, NSW, Australia. Seagrass beds close to mangroves had a greater density of fish species than beds far from mangroves (close: mean 16.0 species net<sup>-1</sup>, SE 1.0; far: 13.2, 1.3;  $P < 0.05$ ). In particular, juvenile fish were in greater densities near to than far from mangroves (close: 5.3, 0.4; far: 3.1, 0.4;  $P < 0.05$ ). We then sampled the mangrove forests during the high tide and seagrass beds during the low tide, in beds along a continuum of distances from mangroves. Multivariate analysis showed that fish assemblages differed with distance from mangroves, and the differences were attributed to the composition of the fish assemblage (i.e. presence/absence of fish

species), not the abundances of individual species. In particular, fish that utilise mangrove forests at high tide were found in greater species densities and species richness in seagrass nearer to mangroves. A negative relationship was found between the density of mangrove-utilising fish species and the distance of the bed from mangroves ( $R^2 = 0.37$ ,  $P < 0.05$ ). This confirms the important connectivity between mangroves and seagrass for fish in temperate Australian waters.

## Introduction

Mangrove forests and seagrass beds frequently occur as adjacent habitats in estuaries of southeastern Australia. The shallow seagrass beds provide important habitat for juvenile fish and small, cryptic adult fish (Connolly 1994a; Jelbart et al. 2006). Coral reef fish in tropical waters can move between different marine habitats in close proximity, including mangroves and seagrasses (e.g. Cocheret de la Morinière et al. 2002), but connectivity between these habitats has not been examined in temperate waters.

Several studies have demonstrated connectivity among estuarine habitats. Irlandi and Crawford (1997) found that pinfish, *Lagodon rhomboides*, were twice as abundant and had greater rates of growth in saltmarsh adjacent to seagrass beds than to unvegetated sediments in North Carolina, USA. A study in the Caribbean found that the species richness of juvenile coral fish was greater in seagrass beds adjacent to mangrove forests than in seagrass beds in bays without mangroves (Nagelkerken et al. 2001). Juveniles of some species of coral reef fish shelter in the mangroves during the day

---

Communicated by G.F. Humphrey, Sydney

---

J. E. Jelbart (✉)  
NSW Department of Environment and Conservation,  
Water and Catchment Science, P.O. Box A290,  
Sydney South, NSW 1232, Australia  
e-mail: jane.jelbart@environment.nsw.gov.au

P. M. Ross  
School of Natural Sciences, University of Western Sydney,  
Locked Bag #1797, Penrith DC, NSW 1797, Australia

R. M. Connolly  
Centre for Aquatic Processes and Pollution,  
and School of Environmental and Applied Sciences,  
Griffith University, PMB 50, Gold Coast Mail Centre,  
Brisbane, QLD 9726, Australia

and forage in the seagrass at night (Cocheret de la Morinière et al. 2002). A further study divided the reef species using mangroves and seagrass into two groups (Nagelkerken and van der Velde 2004a). One group shelter in mangroves during the day and at night feed primarily in the mangroves and use seagrass only as a secondary feeding habitat. The other group feeds and shelters only in seagrass, both day and night (Nagelkerken and van der Velde 2004a).

Whereas recent studies have emphasised the importance of mangroves to juveniles of reef fish species, the contribution of mangroves to fish species strongly associated with seagrass and which do not use reefs when adult, has not been examined. There is no consensus about how mangroves in temperate waters influence fish assemblages associated with seagrass, despite evidence for connectivity between seagrass fauna and other habitats more generally (Ferrell and Bell 1991; Irlandi and Crawford 1997). In the tropics, stable isotope analysis was used to test how juvenile seagrass fishes utilise adjacent mangrove forests as feeding habitats, with 18 of 23 fish species having negligible contributions from mangrove food sources (Nagelkerken and van der Velde 2004b). Other tropical and subtropical studies have sampled adjacent seagrass and mangroves to compare their fish assemblages (e.g. Robertson and Duke 1987; Sheridan 1992). The fish assemblages of these habitats share similarities in species composition, although the mangrove forests typically have greater species richness and/or densities than adjacent seagrass beds at high tide (Laegdsgaard and Johnson 1995). However, most fish must cease using mangroves once they become emergent, moving to alternative habitats at low tide (Sheaves 2005). We therefore expected that seagrass beds close to mangrove forests would have greater fish diversity and possibly abundance than beds further away. Skilleter et al. (2005) demonstrated that the abundances of two penaeid prawns were greater in seagrass beds nearer mangroves, regardless of the density of seagrass shoots within the beds. They found that the influence of habitat connectivity was more important than the effects of structural complexity.

This study investigated the relationship between seagrass fish assemblages and proximity to mangroves. Two surveys were conducted in the Pittwater estuary of temperate southeastern Australia. Only a few studies have examined fish assemblages in mangroves within temperate Australian waters (e.g. Clynick and Chapman 2002; Hindell and Jenkins 2004), and none have addressed the influence of mangroves on the fish associated with adjacent seagrass habitat. The Pittwater contains numerous *Zostera capricorni* seagrass beds at

varying distances from *Avicennia marina* mangrove forests. We predicted that seagrass beds close to mangroves would have different assemblages and a greater density of fish species than beds further from mangroves. We also predicted that fish species utilising mangroves at high tide would at low tide be found at greater densities in seagrass beds nearer to mangroves.

## Methods

### Study areas

The surveys were done in the Pittwater estuary within Broken Bay, just north of Sydney, NSW, Australia (Fig. 1). The Pittwater is a shallow (mostly < 5-m deep), tide-dominated estuary with a partly urbanised catchment. The first study was in the austral spring (September–November 2000) and the second in the austral autumn (March–April 2002). The tidal range is about 1.8 m, and none of the seagrass beds sampled are exposed on the mean low tide. The Pittwater is an arm of the Hawkesbury River, but receives little freshwater input so there is minimal variation in salinity (mostly between 30 and 35 ppt throughout the year, Bell et al. 1988).

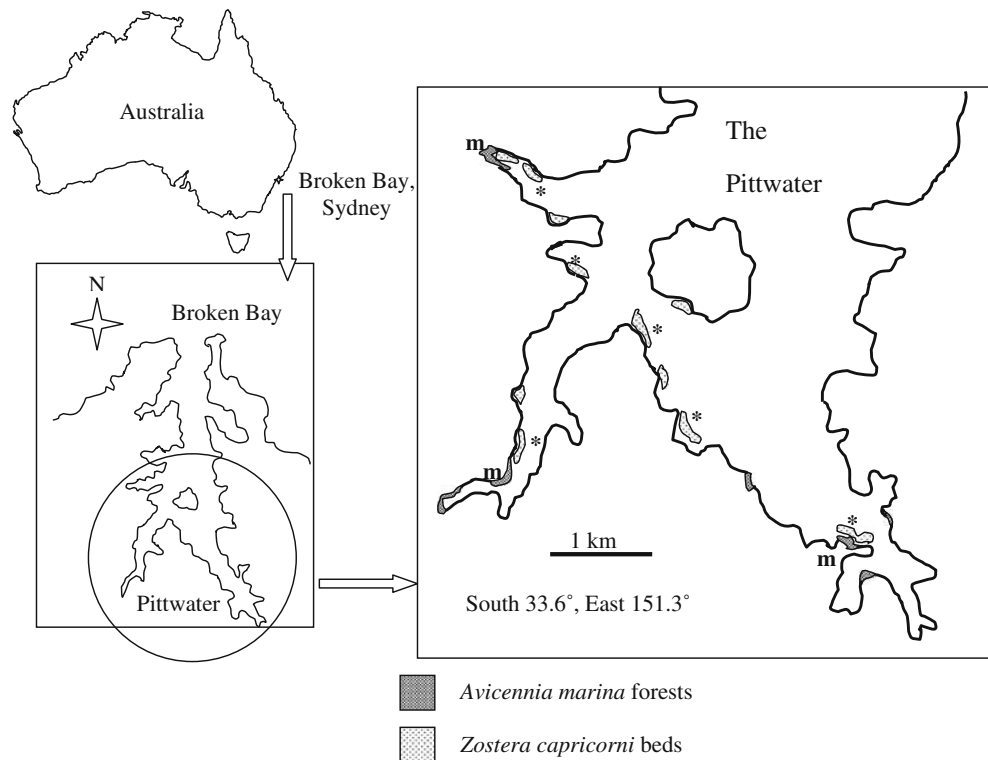
### Study 1 design (spring 2000)

Six beds of *Z. capricorni* were chosen from the upper reaches of the Pittwater, where most of the mangrove forests are located (Fig. 1); three beds were close to mangroves (<200 m from major mangrove forest stands) and three were far from mangrove forests (>500 m from all mangrove forests except isolated trees). The seagrass beds were surrounded by bare sandy substratum with no bed closer than 200 m to another bed (all beds apart from occasionally scattered small patches are shown in Fig. 1). The seagrass shoot density and leaf length in each bed were estimated using eight random quadrats (25 × 25 cm<sup>2</sup>). Each seagrass bed was sampled four times during the day and night (eight times total) to detect any diel patterns. The samples were interspersed both spatially and temporally.

### Study 2 design (autumn 2002)

In the second study, the distance of the seagrass beds from mangrove forests was treated as a continuous variable. Eleven seagrass beds were selected from the upper reaches of the Pittwater that ranged from 1 to 1,695 m from mangrove forests (Fig. 1). Each bed was sampled four times during the day because the differ-

**Fig. 1** A map showing the location of Broken Bay and the Pittwater. The map shows the mangroves forests including those sampled (m). The seagrass beds sampled in study 2 are shown and only those beds labelled (\*) were sampled in study 1



ences detected in study 1 were more pronounced during the day. The fish assemblages of three mangrove forests were also sampled at high tide (Fig. 1).

To maintain independence of samples, all seagrass beds were separated by over 200 m of bare sand. The perimeter of each habitat was mapped by taking GPS positions every 2 m. The areas of the seagrass beds and mangrove forests, and the distance of seagrass from mangrove forests, were calculated using the GIS software ARC View<sup>®</sup>. This latter measure was the shortest distance between the nearest edges of the two habitats.

#### Fish survey

For both studies, the seagrass fish were sampled on the low- to mid-tide at similar water depths (30–80 cm). A seine net (8 × 2 m<sup>2</sup>, 1 mm mesh) was used at randomly selected positions, sampling on average 68 m<sup>2</sup> of seagrass at each pass (SE 1.2). Previous research demonstrated that four drags of the net gave an adequate estimation of the fish assemblage (Jelbart 2004), and the net design has previously been demonstrated to be effective at capturing seagrass fish (Connolly 1994b; Guest et al. 2003). Fish were identified, measured and returned to the water.

Fish in the mangrove forest were collected at high tide using two methods. A seine net was deployed between the *A. marina* trees under the forest canopy.

The pneumatophores were bent down by the bottom edge of the net but not broken. Fish traps (56 × 41 × 22 cm, 10-mm mesh) were deployed for 3 h within the forests where the seine net could not be used because of dense trunks and branches.

#### Study 1 univariate data analysis

An analysis of variance (ANOVA) was performed on the densities (number net<sup>-1</sup>) of fish species, fish individuals, juvenile fish species and juvenile fish individuals in seagrass beds. All data were tested using Cochran's C-test and transformed where necessary to ensure homogeneity of variances. The ANOVA was a three-way, mixed model design. The first source of variation was the time (day or night) of sampling (fixed, orthogonal); the second was proximity (close or far) to mangrove forests (fixed, orthogonal) and the third was seagrass beds (random, nested). Single-species analyses on the dominant fish species were also performed using ANOVAs of the same design.

#### Study 2 univariate data analysis

A linear regression was used to test for a relationship between the distance of the seagrass bed to mangrove forests and the density (mean number net<sup>-1</sup>) of: all fish species, mangrove-utilising fish species (those that

were caught in the mangroves), non-mangrove fish species (species not caught in mangroves), juvenile fish species, all fish individuals, mangrove fish individuals, non-mangrove fish individuals and juvenile fish individuals. The species richness (total number of species  $\text{bed}^{-1}$ ) of all fish species, mangrove fish species and non-mangrove fish species were also tested for a relationship with the distance of the seagrass bed to mangrove forests. The densities of some dominant individual fish species were also analysed.

#### Multivariate data analysis

A Bray–Curtis similarity analysis between samples was performed after a square root transformation and used to create a non-metric multi-dimensional scaling (MDS) plot. A second similarity analysis was performed using a presence–absence transformation. The first transformation gave an analysis of the composition and abundance of the fish assemblage whereas the second gave an analysis of the species composition alone. In study 1, each sample from the seine net was used as a variable, while in study 2 the seine net samples from each bed were pooled to create the MDS plot. This allowed the MDS plot created in study 2 to be superimposed with the distances to mangrove for each bed. In study 1, a two-way crossed analysis of similarity (ANOSIM) was also used to test for differences in species composition and abundance between beds close to and far from mangroves and between day and night sampling.

## Results

Overall, 42 fish species and 3,749 individuals were collected from seagrass in the two studies; 36 species and 2,507 individuals from study 1, and 27 species and 1,242 individuals from study 2 (Table 1). Eleven species and 792 individuals were collected from mangrove forests in study 2 (Table 2). The smaller number of species collected from the mangroves possibly reflected the lower sampling effort in mangroves compared with seagrass.

The seagrass varied in average shoot densities (range 514–1,140 shoots  $\text{m}^{-2}$ , mean 830, SE 98) and average blade length (range 7.9–15.8 cm, mean 13.1, SE 1.2). These variables did not differ in beds near to and far from mangroves, and regression analysis demonstrated that neither of the variables was related to densities of fish species nor fish individuals in seagrass beds (all  $P > 0.05$ ). This finding means that any relationship between distance from mangroves and fish assemblages cannot be explained by within-bed seagrass structural characteristics.

#### Study 1 univariate data analysis: abundance and density of fishes

There were significantly greater densities of fish species and juvenile fish species in seagrass beds close to mangrove forests than far away ( $P < 0.05$ ), and in the night than the day ( $P < 0.01$ , Fig. 2, Table 3). No differences were detected in the densities of fish individuals between beds close to and far from mangroves, although there was a trend for greater densities of fish in beds close to mangroves ( $P = 0.080$ , Fig. 2, Table 3). There were, however, significantly greater densities of juvenile fish individuals in beds closer to mangroves ( $P < 0.05$ , Fig. 2, Table 3). A significant bed effect was also detected, where one of the seagrass beds close to mangroves had greater densities of juvenile fish individuals than the other two beds close to mangroves (Table 3).

There were also significant differences in the densities of some individual species. Densities of the goby, *Bathygobius krefftii*, were greater in seagrass beds further from mangroves, and during the night than day, although a significant interaction term (time  $\times$  proximity) revealed this pattern to be attributable to a greater density during the night in seagrass far from mangroves (Table 4). The tarwhine, *Rhabdosargus sarba*, showed greater densities in seagrass close to mangroves (Table 4). However, the density of tarwhine in one of the beds close to mangroves was significantly greater than the other two seagrass beds close to mangroves. The density of the leatherjacket, *Acanthalutere spilomelanurus*, was greater during the day than night, whereas the hardyhead, *Atherinomorus ogilbyi*, was greater during the night than day (Table 4).

#### Study 2 univariate data analysis: abundance and density of fishes

No significant relationship was detected between distance to mangroves and the variables: density of all fish species, juvenile fish species, juvenile fish individuals and the dominant individual species, although there was a trend for the density of all fish individuals to be lower in seagrass beds as the distance from mangroves increased ( $R^2 = 0.29$ ,  $P = 0.090$ ). There was, however, a significant relationship for the density of ‘mangrove’ fish species and the ‘non-mangrove’ fish species with distance of the seagrass bed from mangroves (Fig. 3). The density of ‘mangrove’ fish species and their species richness decreased as the distance of the seagrass to mangroves increased. In contrast, the density of ‘non-mangrove’ species and their species richness increased as the distance of the seagrass from mangroves increased (Fig. 3).

## Multivariate analysis: composition and abundance of fish assemblages

In study 1, a significant difference was found between the fish assemblages in seagrass close to and far from mangroves (Fig. 4). This difference was detected even when the data were transformed to presence–absence, indicating that the composition of the fish assemblage rather than the abundances of fish was contributing to the difference. The SIMPER analysis revealed that the six most discriminating species (*Arenigobius frenatus*, *A. spilomelanurus*, *Girella tricuspidata*, *Pelates sexlineatus*, *R. sarba* and *Urocampus carinirostris*) were

more abundant in seagrass beds close to mangroves (Table 5). Of these species, only two, *A. frenatus* and *R. sarba*, were caught in the mangroves in study 2 (Table 2). There was also a relationship between fish assemblages in seagrass and the distance of the bed from mangroves in study 2 (Fig. 4).

## Discussion

Fish assemblages in seagrass changed with proximity to mangrove forests. Beds near mangroves had different fish assemblages to beds further away, regardless of

**Table 1** The densities of fish (10 m<sup>-2</sup>) in seagrass beds close to and far from mangroves in studies 1 and 2

Family	Species	Study 1		Study 2	
		Close	Far	Close	Far
Atherinidae	<i>Atherinomorus ogilbyi</i>	3.64	1.40	0.06	0
Batrachoididae	<i>Batrachomoeus dubius</i>	0.29	0	0	0
Blennidae	<i>Petroscirtes lupus</i>	0	0.15	0	0.02
Chandidae	<i>Ambassis jacksoniensis</i>	8.75	0.66	0.06	0.01
Clinidae	<i>Cristiceps aurantiacus</i>	0.20	0.29	0	0.01
	<i>Heteroclinus</i> sp 4	0	0.15	0	0
Clupeidae	<i>Hyperlophus translucidus</i>	0.96	0	0	0
	<i>Spratelloides robusta</i>	0	0	0.02	0.01
Diodontidae	<i>Diodon nichthemerus</i>	0.15	0	0	0
Gerreidae	<i>Gerres subfasciatus</i>	0.39	0	0	0
Girellidae	<i>Girella tricuspidata</i>	8.01	0.51	0.01	0
Gobiidae	<i>Arenigobius frenatus</i>	7.30	4.39	0.39	0.30
	<i>Bathygobius kreffti</i>	0.38	1.37	0.02	0.06
	<i>Redigobius macrostoma</i>	1.18	0.15	2.13	0.03
Hemiramphidae	<i>Hyporhamphus australis</i>	0	0.15	0	0
Lethrinidae	<i>Lethrinus laticaudis</i>	0	0	0.01	0
Monacanthidae	<i>Acanthalutere spilomelanurus</i>	4.04	2.89	0.06	0.06
	<i>Acanthaluteres vittiger</i>	0	0	0.05	0.19
	<i>Cantherhinus pardalis</i>	0.29	0	0.10	0.05
	<i>Eubalichthys mosaicus</i>	0	0	0	0.01
	<i>Meuschenia trachylepis</i>	0.29	0	0	0
	<i>Meuschenia venusta</i>	0.22	0.15	0	0
	<i>Monacanthus chinensis</i>	0.20	0.15	0.20	0.54
	<i>Scobinichthys granulatus</i>	0.81	0.44	0	0
Monodactylidae	<i>Monodactylus argenteus</i>	0	0	0.04	0
Mullidae	<i>Upeneus</i> sp.	0.29	0.20	0.01	0.07
	<i>Upeneus tragula</i>	0	0.15	0.02	0.02
Odacidae	<i>Neoodax balteatus</i>	0.15	0.59	0	0
Paralichthyidae	<i>Pseudorhombus jenynsii</i>	0	0.15	0	0
Scorpaenidae	<i>Centropogon australis</i>	0.34	0.63	0	0.05
Sillaginidae	<i>Sillaginodes maculata</i>	0.37	0	0	0
	<i>Sillaginodes punctata</i>	0.15	0.34	0	0
	<i>Sillago flindersi</i>	0.15	0	0	0
Sparidae	<i>Rhabdosargus sarba</i>	6.54	0.81	1.00	1.05
Sphyraenidae	<i>Sphyraena obtusata</i>	0	0	0.01	0
Syngnathidae	<i>Filicampus tigris</i>	0.15	0.15	0	0
	<i>Hippocampus whitei</i>	0.29	0	0	0.02
	<i>Stigmatopora argus</i>	0	0.15	0	0
	<i>Stigmatopora nigra</i>	0.44	0.71	0	0.11
	<i>Urocampus carinirostris</i>	2.60	2.25	0.17	0.37
Terapontidae	<i>Pelates sexlineatus</i>	4.58	1.65	1.17	2.05
Tetraodontidae	<i>Tetractenos hamiltoni</i>	0.15	0.15	0	0.01

The beds are categorised into close and far for study 2 in this table only for comparison purposes



**Table 2** The total abundance of fish collected from three mangrove forests in study 2 using a seine net and fish traps

Family	Species	Abundance
Atherinidae	<i>Atherinomorus ogilbyi</i>	100
Blenniidae	<i>Omobranchus anolius</i> <sup>a</sup>	1
Chandidae	<i>Ambassis jacksoniensis</i>	422
Gerreidae	<i>Gerres subfasciatus</i>	55
Gobiidae	<i>Arenigobius frenatus</i>	6
	<i>Redigobius macrostoma</i>	6
Monodactylidae	<i>Monodactylus argenteus</i>	12
Mugilidae	<i>Myxus elongatus</i> <sup>a</sup>	14
Sillaginidae	<i>Sillago ciliata</i> <sup>a</sup>	34
Sparidae	<i>Rhabdosargus sarba</i>	130
Tetraodontidae	<i>Tetractenos hamiltoni</i>	12

<sup>a</sup>Not caught in seagrass

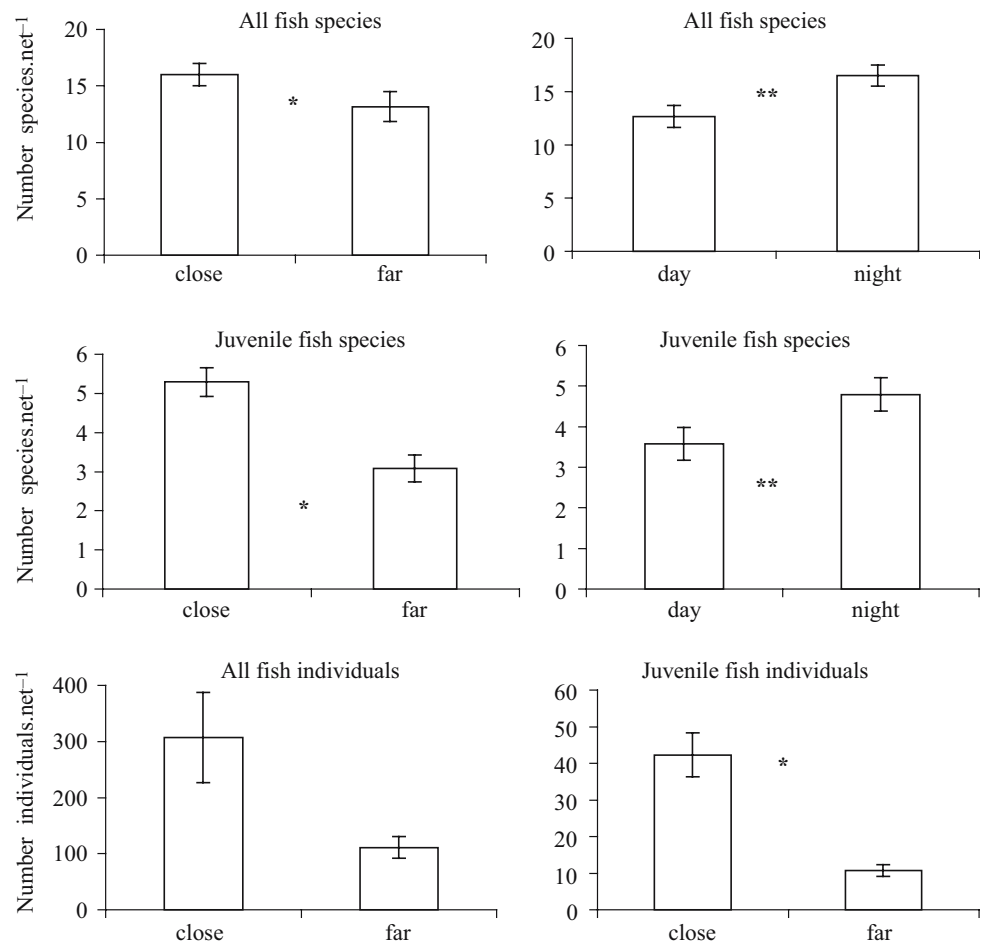
whether we treated distance to mangroves as a discrete or continuous variable. This finding is consistent with results from the tropics, where the combination of adjacent mangroves and seagrass can influence assemblages of juvenile fish (Cocheret de la Morinière et al. 2002; Dorenbosch et al. 2004). Furthermore, in tropical waters, mangroves influence the community

structure of fish in other adjacent habitats such as coral reefs (Mumby et al. 2004).

The fish assemblages in seagrass also differed between the night and day, with greater densities of fish species during the night than the day. Other studies in southeastern Australia have also detected different fish assemblages in seagrass between the night and day (Gray et al. 1998; Guest et al. 2003). In the present study, this diel influence did not obscure the distinction between assemblages in beds at different distances from mangroves. We also showed that the landscape-scale effects were detectable above any influence of within-bed seagrass structural characteristics, a result consistent with that for penaeid prawns in subtropical Australian waters (Skilleter et al. 2005).

We showed that the density of species (number of species per unit area) in seagrass increased near mangroves. This increase was because of the presence of a higher number of species known to use mangroves. The overall pattern of higher species density near mangroves was evident despite a slight reduction in the number of species of ‘non-mangrove’ fishes near

**Fig. 2** The density (number net<sup>-1</sup>) of all fish species, juvenile fish species, all fish individuals and juvenile fish individuals in seagrass beds close to and far from mangroves in study 1. A comparison of day versus night is given for the density of fish species and juvenile fish species. All comparisons are significantly different from one another except for the density of fish individuals. \* $P < 0.05$ , \*\* $P < 0.01$



**Table 3** Analysis of variance comparing the densities of fish species, fish individuals, juvenile fish species and juvenile fish individuals during different sampling times (day and night); and in beds near and far from mangroves in study 1

Source of variation	Mean squares	df	F
<i>Density of fish species</i>			
Time	108.0	1	75.1**
Proximity	85.3	1	7.6*
Beds (proximity)	11.3	4	2.1
Time × proximity	3.0	1	2.1
Time × bed (proximity)	1.4	4	0.3
Residual	5.3	36	
<i>Density of fish individuals</i>			
Time	336.0	1	0.2
Proximity	28,178.5	1	2.7
Beds (proximity)	10,299.4	4	13.7***
Time × proximity	1,530.0	1	1.0
Time × bed (proximity)	1,591.6	4	2.1
Residual	754.6	36	
<i>Density of juvenile fish species</i> ( $\sqrt{(x+1)}$ )			
Time	0.96	1	19.2**
Proximity	3.10	1	9.7*
Beds (proximity)	0.32	4	2.2
Time × proximity	0.16	1	3.2
Time × bed (proximity)	0.05	4	0.3
Residual	0.15	36	
<i>Density of juvenile fish individuals</i> ( $\sqrt{(x+1)}$ )			
Time	0.74	1	1.4
Proximity	101.50	1	8.1*
Beds (proximity)	12.51	4	3.9**
Time × proximity	0.68	1	1.3
Time × bed (proximity)	0.54	4	0.2
Residual	3.23	36	

No transformation of data was required for the first two variables

\**P* < 0.05

\*\**P* < 0.01

\*\*\**P* < 0.001

mangroves. In study 1, seagrass beds close to mangroves had greater abundances of *R. sarba*, *G. tricuspidata*, *A. ogilbyi*, *Ambassis jacksoniensis*, *A. frenatus*, *Redigobius macrostoma* and *P. sexlineatus*, although not all of these results were statistically significant. These species have been recorded in mangroves in eastern Australia (Bell et al. 1984; Laegdsgaard and Johnson 1995). In our study, *R. sarba*, *A. jacksoniensis* and *A. ogilbyi* were abundant in the mangroves. However, when patterns in abundances of individual

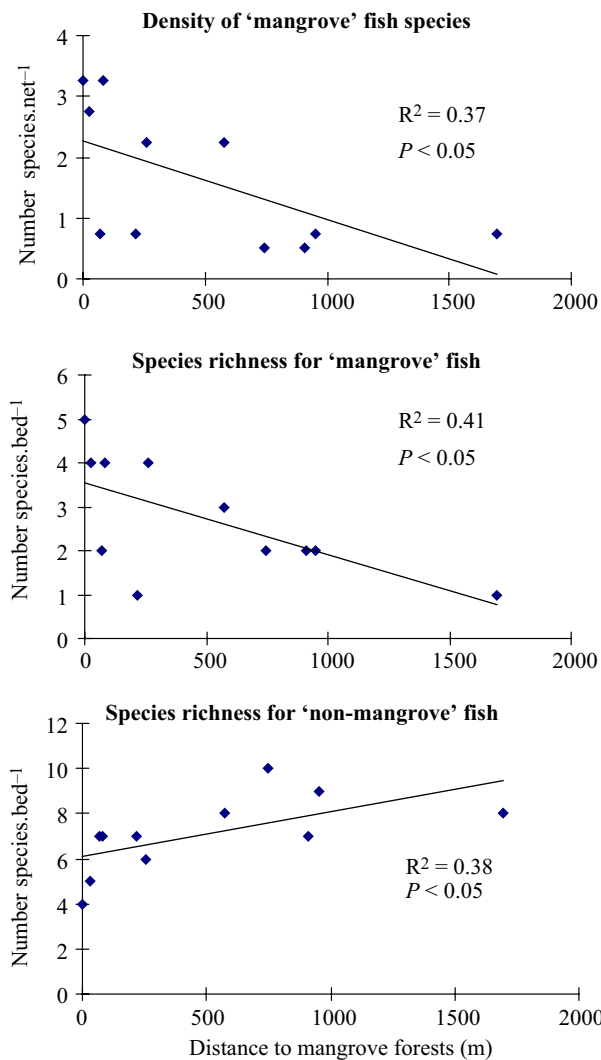
species were examined using regressions in study 2, no significant relationships with distance were detected for these three species. Rather it was the presence of a suite of ‘mangrove’-utilising fishes, and not abundances of individual species, which increased as distance to mangroves decreased.

Mangroves are considered important habitats for juvenile fish (Robertson and Duke 1987; Laegdsgaard and Johnson 1995). Juvenile fish are attracted to the structural complexity of the roots and the shade pro-

**Table 4** The summary of analyses of variances comparing individual fish species collected during different times (day and night) and from seagrass beds near and far from mangrove in study 1

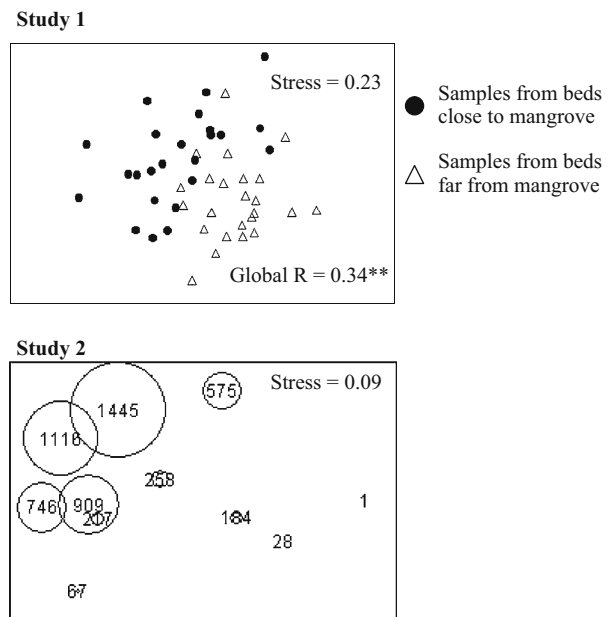
Species	Time <i>df</i> =1	Proximity to mangrove <i>df</i> = 1	Beds (proximity) <i>df</i> = 4	Time × proximity <i>df</i> = 1	Time × bed (proximity) <i>df</i> = 4
<i>Acanthalutere spilomelanurus</i>	15.95*	0.25	1.63	0	0.17
<i>Arenigobius frenatus</i>	0.77	2.94	1.88	0.33	1.93
<i>Atherinomorus ogilbyi</i>	54.13**	2.92	0.89	1.52	0.60
<i>Bathygobius krefftii</i>	21.85**	9.61*	1.12	8.03*	0.79
<i>Centropogon australis</i>	2.17	2.32	0.75	4.99	1.47
<i>Girella subfasciata</i>	0.46	6.71	10.70***	0.01	0.54
<i>Pelates sexlineatus</i>	2.59	3.65	3.27*	0.29	1.82
<i>Rhabdosargus sarba</i>	0.47	8.41*	3.03*	0.14	0.92
<i>Urocampus carinirostris</i>	0.03	0.16	1.04	0.77	1.95

The *F* values are shown with the *P* values (\**P* < 0.05, \*\**P* < 0.01, \*\*\* *P* < 0.001). Residual *df* = 36, Total *df* = 47



**Fig. 3** The relationships between; the densities of mangrove utilising fish, the species richness of mangrove fish, the species richness of non-mangrove fish with the distance of each seagrass bed ( $n = 11$ ) from the mangrove forests in study 2

vided by the canopy (Cocheret de la Morinière et al. 2004). Seagrass beds are also considered important for juvenile fish. This suggests that the proximity of the two habitats might influence fish assemblages. Our study suggests that mangrove forests may elevate the



**Fig. 4** Two-dimensional configurations for multi-dimensional scaling (MDS) ordinations of the composition and abundance of fish in seagrass beds in studies 1 and 2. The analysis of similarity (ANOSIM) results (Global  $R$ ) are given for study 1 (\*\* $P < 0.01$ ). The MDS for study 2 shows the distance of the seagrass bed from the mangrove forest (in metres) which is also represented by increasing circles for increasing distance

carrying capacity of adjacent seagrass beds, because there were greater densities of juvenile fish in seagrass beds close to mangroves. This result is similar to that for juveniles of coral reef fish in tropical waters (Nagelkerken et al. 2001).

In the Caribbean, stable isotope analysis was used to test if seagrass fishes utilise adjacent mangrove forests as a feeding habitat (Nagelkerken and van der Velde 2004b). Only 5 of 23 seagrass fish species had contributions from the adjacent mangrove food sources, and this low proportion was attributed to the high food availability in tropical seagrass and low tidal differences in the study region (Nagelkerken and van der Velde 2004b). The possibility that seagrass fish use the mangroves as alternative habitat for other reasons, such as protection from predators, should not yet be

**Table 5** The SIMPER results for study 1, showing the most discriminating species

Species name	Average abundance in beds close	Average abundance in beds far	Ratio Dissim./SD	Contribution (%)
<i>Arenigobius frenatus</i>	12.4	7.5	1.12	15.4
<i>Urocampus carinirostris</i>	4.4	3.8	1.07	6.6
<i>Acanthalutere spilomelanurus</i>	6.5	4.9	1.01	9.8
<i>Girella tricuspidata</i>	13.6	0.3	0.99	13.9
<i>Rhabdosargus sarba</i>	11.1	0.9	0.90	12.3
<i>Pelates sexlineatus</i>	7.8	2.3	0.90	11.3



excluded (Sheaves 2005). Nagelkerken et al. (2001) have previously suggested that the enhancement of the seagrass fish assemblage by the presence of mangrove forests could be mutual (i.e. seagrass enhancing the fish assemblage of mangrove forests). Evidence is emerging that the proximity of seagrass may influence the fish assemblages within mangroves in temperate Australian waters (Hindell et al. 2004).

Comparisons of fish assemblages in mangroves and seagrass made using high-tide collections show higher abundances of fish or fish species in mangroves than seagrass (Laegdsgaard and Johnson 1995). In these same systems, however, it is expected that at low tide, when mangrove forests are emergent, fish would move to adjacent seagrass beds. Few fish can use mangroves exclusively as habitat for either feeding or refuge, and most are forced to use alternative nearby habitats, establishing an interconnected habitat mosaic (Sheaves 2005). Results from our sampling of seagrass at low tide support this connectivity. Differences in assemblages near to and far from mangroves were attributable to species commonly found in mangroves that presumably move to seagrass at low tide. Our results support the model that fish move among estuarine habitats on a tidal basis. In Florida, the abundance and biomass of decapod crustaceans and fish in adjacent intertidal seagrass, mangroves and open water habitats were compared and the mangroves were found to be the lowest (Sheridan 1992). The flooded mangroves, however, had at times similar densities of both resident and transient fish and crabs to those in seagrass and open water, confirming the movement of fish among the habitats.

Caribbean studies confirm the importance of tidal movements of fish among habitats, including from unvegetated mudflats to a mangrove/seagrass complex (Nagelkerken et al. 2001). Other work there shows movements between seagrass and mangroves at different times of the day (Cocheret de la Morinière et al. 2002). Over longer periods, grey snapper (*Lutjanus griseus*) show ontogenetic shifts in habitat utilisation, foraging in the prop root fringe of mangroves as juveniles and in adjacent habitats including seagrass as adults (Thayer et al. 1987).

One of the few other studies to examine fish assemblages at different distances from mangroves in temperate Australian waters found no relationship with distance (Clynick and Chapman 2002). Assemblages of fish caught over mudflats adjacent to mangroves (within 50 m) in Sydney Harbour were not measurably different to those of mudflats further from mangroves (~200 m). The lack of influence of distance from mangroves in the study by Clynick and Chapman (2002) may reflect a lack of interaction between fish of

mudflats and adjacent mangroves. Their survey was done in winter, however, when juvenile fish are in low abundances in the harbour, and the lack of influence of mangroves might also have resulted from the timing of sampling. Our results are more similar to those from tropical waters, but more temperate studies are required before general conclusions can be made about the influence of mangroves on fish in adjacent habitats in tropical and temperate waters.

**Acknowledgments** The support of the School of Natural Sciences at the University of Western Sydney made this study possible. Special thanks to V. Rao for field assistance. This research was conducted within institutional, national and international guidelines concerning the use of animals in research.

## References

- Bell JD, Steffe AS, Westoby M (1988) Location of seagrass beds in estuaries: affects on associated fish and decapods. *J Exp Mar Biol Ecol* 122:127–146
- Bell JD, Pollard DA, Burchmore JJ, Pease BC, Middleton MJ (1984) Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. *Aust J Mar Freshw Res* 35:33–46
- Clynick B, Chapman MG (2002) Assemblages of small fish in patchy mangrove forests in Sydney Harbour. *Mar Freshw Res* 53:669–677
- Cocheret de la Morinière E, Nagelkerken I, van der Meij H, van der Velde G (2004) What attracts juvenile coral reef fish to mangroves: habitat complexity or shade? *Mar Biol* 144:139–145
- Cocheret de la Morinière E, Pollux BJA, Nagelkerken I, van der Velde G (2002) Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. *Estuar Coast Shelf Sci* 55:309–321
- Connolly RM (1994a) A comparison of fish assemblages from seagrass and unvegetated areas of a southern Australian estuary. *Aust J Mar Freshw Res* 45:1033–1044
- Connolly RM (1994b) Comparison of fish catches from a buoyant pop net and a beach seine net in a shallow seagrass habitat. *Mar Ecol Prog Ser* 109:305–309
- Dorenbosch M, van Riel MC, Nagelkerken I, van der Velde G (2004) The relationship of reef fish densities to the proximity of mangrove and seagrass nurseries. *Estuar Coast Shelf Sci* 60:37–48
- Ferrell DJ, Bell JD (1991) Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. *Mar Ecol Prog Ser* 2:15–24
- Gray CA, Chick RC, McElligott DJ (1998) Diel changes in assemblages of fishes associated with shallow seagrass and bare sand. *Estuar Coast Shelf Sci* 46:849–859
- Guest MA, Connolly RM, Loneragan NR (2003) Seine nets and beam trawls compared in the day and night for sampling fish and crustaceans in shallow seagrass habitat. *Fish Res* 64:185–196
- Hindell JS, Jenkins GP (2004) Spatial and temporal variability in the assemblage structure of fishes associated with mangroves (*Avicennia marina*) and intertidal mudflats in temperate Australian embayments. *Mar Biol* 144:385–395

- Hindell JS, Jenkins GP, Connolly RM, Hyndes G (2004) Assessment of the importance of different nearshore marine habitats to important fishery species in Victoria using standardised survey methods, and in temperate and subtropical Australia using stable isotope analysis. Final report. Fisheries Research and Development Corporation. Project No. 2001/036
- Irlandi EA, Crawford MK (1997) Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. *Oecologia* 110:222–230
- Jelbart JE (2004) The influence of seascape spatial features on the fish and macroinvertebrates in seagrass beds. PhD Thesis, University of Western Sydney, Australia
- Jelbart JE, Ross PM, Connolly RM (2006) Edge effects and patch size in seagrass landscapes: an experimental test using fish. *Mar Ecol Prog Ser* (in press)
- Laegdsgaard P, Johnson CR (1995) Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangrove forests in eastern Australia. *Mar Ecol Prog Ser* 126:67–81
- Mumby PJ, Edwards AJ, Arias-Gonzalez JE, Lindeman KC, Blackwell PG, Gall A, Gorczynska MI, Harborne AR, Pescod CL, Renken H, Wabnitz CCC, Llewellyn G (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427:533–536
- Nagelkerken I, Kleijnen S, Klop T, van den Brand RACJ, Cocheret de la Morinière E, van der Velde G (2001) Dependence of Caribbean reef fishes on mangrove forests and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangrove forests/seagrass beds. *Mar Ecol Prog Ser* 214:225–235
- Nagelkerken I, van der Velde G (2004a) Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island. *Mar Ecol Prog Ser* 274:153–159
- Nagelkerken I, van der Velde G (2004b) Are Caribbean mangroves important feeding grounds for juvenile reef fish from adjacent seagrass beds? *Mar Ecol Prog Ser* 274:143–151
- Robertson AI, Duke NC (1987) Mangrove forests as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangrove forests and other nearshore habitats in tropical Australia. *Mar Biol* 96:193–205
- Sheaves M (2005) Nature and consequences of biological connectivity in mangrove systems. *Mar Ecol Prog Ser* 302:293–305
- Sheridan PF (1992) Comparative habitat utilization by estuarine macrofauna within the mangrove ecosystem of Rookery Bay, Florida. *Bull Mar Sci* 50:21–39
- Skilleter GA, Olds A, Loneragan NR (2005) The value of patches of intertidal seagrass to prawns depends on their proximity to mangroves. *Mar Biol* 147:353–365
- Thayer GW, Colby DR, Hettler WF (1987) Utilisation of the red mangrove prop root habitat by fishes in south Florida. *Mar Ecol Prog Ser* 35:25–38