Edge effects in patchy seagrass landscapes: The role of predation in determining fish distribution

Timothy M. Smith [a,b,*], Jeremy S. Hindell [b,c], Gregory P. Jenkins [b,d], Rod M. Connolly [e], Michael J. Keough [b]

[a] Victorian Marine Science Consortium, PO Box 114, Queenscliff, Vic 3225, Australia
[b] Department of Zoology, The University of Melbourne, Parkville, Vic 3052, Australia
[c] Arthur Rylah Institute, Department of Sustainability and Environment Victoria, PO Box 137, Heidelberg, Vic 3084, Australia
[d] Marine and Freshwater Fisheries Research Institute, DPI Queenscliff Centre, PO Box 114, Queenscliff, Vic 3225, Australia
[e] Australian Rivers Institute — Coast and Estuaries, and Griffith School of Environment, Griffith University, Queensland, 4222, Australia

ABSTRACT

Predation is often described as an underlying mechanism to explain edge effects. We assessed the importance of predation in determining edge effects in seagrass using two approaches: a video survey to sample predators at small scales across seagrass edges, and a tethering experiment to determine if predation was an underlying mechanism causing edge effects. Underwater videos were placed at four positions: middle of seagrass patches; edge of seagrass; sand immediately adjacent to seagrass and sand distant from seagrass. Fish abundances and the time fish spent in view were measured. The main predatory fish (Australian salmon, *Arripis* spp.) spent more time over adjacent sand than other positions, while potential prey species (King George whiting, *Sillaginodes punctata* (Cuvier), recruits) were more common in the middle of seagrass patches. Other species, including the smooth toadfish, *Tetractenos glaber* (Freminville), and King George whiting adults, spent more time over sand adjacent to seagrass than distant sand, which may be related to feeding opportunities. King George whiting recruits and pipefish (*Stigmatopora* spp.) were tethered at each of the four positions. More whiting recruits were preyed upon at outer than inner seagrass patches, and survival time was greater in the middle of shallow seagrass patches than other positions. Relatively few pipefish were preyed upon, but of those that were, survival time was lower over sand adjacent to seagrass than at the seagrass edge or middle. Video footage revealed that salmon were the dominant predators of both tethered King George whiting recruits and pipefish. The distribution of predators and associated rate of predation can explain edge effects for some species (King George whiting) but other mechanisms, or combinations of mechanisms, are determining edge effects for other species (pipefish).

1. Introduction

Edge effects are a fundamental concept in landscape ecology, and, as habitats continue to fragment. Understanding of edge effects is increasingly important for management and conservation (Ries et al., 2004; Hinchey et al., 2008). Habitat edges can change species abundances and distributions by altering physical conditions, resource distribution and species interactions (Murcia, 1995; Ries and Sisk, 2004). Predation can be an underlying mechanism changing species abundances at edges by increasing encounter rates between species, lowering refuge value, or enhancing foraging potential (Murcia, 1995; Ries and Sisk, 2004).

Seagrass is a nearshore habitat that supports a rich and diverse array of fauna including many predatory species (Jackson et al., 2001). However, seagrass is under threat from a range of anthropogenic and natural sources including eutrophication, dredging and storms (Duarte, 2002), leading to habitat fragmentation and increasing relative amounts of patch edges (Horinouchi, 2007b). The seagrass/sand interface forms a distinct structural boundary that affects water flow (Fonseca and Fisher, 1986; Hovel et al., 2002; Peterson et al., 2004), light levels (Carruthers and Walker, 1997), and sedimentation (Scoffin, 1970; Fonseca and Fisher, 1986). Changes to structural properties at the edge of seagrass can affect species abundance by increasing planktonic food supply and recruitment (Eckerman, 1987) or changing foraging and escape behaviour (Orth et al., 1984).

Edge effects in seagrass habitats are varied and inconsistent (Connolly and Hindell, 2006). Invertebrate abundances can increase (Bologna and Heck, 2002), decrease (Sanchez-Jerez et al., 1999) or remain consistent (Hovel et al., 2002) across seagrass edges, while recruitment (Bologna and Heck, 2000), survivorship (Irlandi, 1997; Hovel, 2003) and growth (Irlandi and Peterson, 1991) of invertebrates can be affected at seagrass edges. Fish responses to seagrass edges show similar inconsistent patterns. Overall fish density and species richness can increase at seagrass edges (Smith et al., 2008; Macreadie

* Corresponding author at: Victorian Marine Science Consortium, PO Box 114, Queenscliff, Victoria 3225, Australia. Tel.: +61 3 5258 0257; fax: +61 3 5258 0270.
E-mail address: timsmith11@hotmail.com (T.M. Smith).

et al., 2009, 2010) but often show little response (Hovel et al., 2002; Uhrin and Holmquist, 2003; Johnson and Heck, 2006; Jelbart et al., 2006). Individual species however can show different responses to overall patterns, increasing or decreasing at the edge (Hovel et al., 2002; Jelbart et al., 2006; Smith et al., 2008; Macreadie et al., 2009). Response of small fish species to seagrass edges may be related to predation from larger fish (Smith et al., 2008; Macreadie et al., 2010). However, detecting edge effects of predatory, often transient fish in seagrass patches requires effective sampling at small spatial scales and adequate sampling design (Connolly and Hindell, 2006). Although the relative effect of an edge can vary according to patch size (Smith et al., 2010), such patterns cannot be confidently detected without sampling both the edge and interior of a patch.

The presence of predators does not necessarily equate to greater predation levels. Predators may alter prey behaviour or predator themselves may be under predation stress and alter behaviour causing little change in predation levels (Bernot and Turner, 2001; Werner and Peacor, 2003). Assessing the role of predation in determining species distributions can be difficult and may vary according to water depth, seagrass structure and diel cycles (Edgar and Shaw, 1995; Jackson et al., 2006; Horinouchi, 2007b; Gorman et al., 2009). Tethering provides an experimental method of assessing predation, and has been used in a variety of habitats including coral reefs (Danilowicz and Sale, 1999; Chittaro et al., 2005), seagrass (Bologna and Heck, 1999; Peterson et al., 2001; Hovel and Lipcius, 2002; Haywood et al., 2003; Horinouchi, 2007a; Gorman et al., 2009) and unvegetated mudflats (Peterson et al., 2001; Haywood et al., 2003). Organisms that have been used in tethering experiments include fish (Dahlgren and Eggleston, 2000; Smith and Hindell, 2005), crustaceans (Peterson et al., 2001; Haywood et al., 2003), plankton (Bullard and Hay, 2002) and seagrass seeds (Orth et al., 2006).

Our study aims to: (1) assess predator abundances in different positions across seagrass landscapes, and (2) determine if predation of small seagrass fish species varies across seagrass patches using a tethering experiment.

2. Materials and methods

2.1. Field site

Video surveys and tethering experiments were done at Blairgowrie (38° 21′ 46″ S, 144° 47′ 21″ E), on the southern side of Port Phillip Bay, Victoria, Australia, between December 2007 and February 2008. Blairgowrie supports patches of the seagrass *Heterozostera nigricaulis* which supports many small seagrass-associated species of fish (Smith et al., 2008) and large predator fish species (Hindell et al., 2001).

2.2. Field sampling

2.2.1. Video sampling

Remote video sampling was used to assess the distribution of mobile fish species allowing transient fish to be sampled at fine scales required for seagrass edges studies. Sampling was done using four remote underwater cameras (3 Cannon HV20, 1 Sony CCD-TR16E). Cameras were fitted with wide-angled lenses (0.07 focal length) and placed inside an underwater housing and clamped to a post 40 cm above the sea floor. At night, 2 red lights attached to posts behind cameras illuminated the field of view. Camera field of view during the day was at least 4.0 m^2 (measured as the areas of a triangle from the camera point) and all fish that could be identified were recorded to ensure as many fish as possible were recorded. During the night however the field of view was only 2.25 m^2, restricting direct comparisons between night and day samples.

2.3. Sampling design

On each sampling occasion, 12 independent seagrass patches were sampled. Sampled patches varied in shapes, size and depth, including patches from two distinct seagrass bands, ensuring enough samples could be collected (Ball et al., 2006; Smith et al., 2010). Within each patch, cameras were randomly allocated to one of four positions: seagrass edge — within 1 m of the seagrass–sand interface; seagrass middle — halfway across the seagrass patch; adjacent sand — sand within 1 m of the seagrass–sand interface; and distant sand — sand at a distance from the seagrass edge equal to the distance to the middle of the seagrass patch (Smith et al., 2008). Therefore, three replicates were recorded from each position on each sampling occasion. Cameras were retrieved after one hour. Sampling was done on five non consecutive days ($n = 4 \times 3 \times 5 = 60$). Night sampling was done similar to day sampling. At night cameras were retrieved after 30 min, and samples were taken in as many positions as batteries would allow on each sampling night (Table 1). Sampling was done on 6 non consecutive nights.

2.3.1. Analysis of video footage

Video footage was assessed using two different methods that describe fish abundance (MaxN average) and the amount of time fish spend in each habitat (Time in View). MaxN (the greatest fish abundance within a short block of time or single frame) has been used recently to represent fish abundance (Cappo et al., 2003). When tested against other measures, MaxN has been shown to accurately reflect fish and species densities (Willis et al., 2000) and eliminates problems associated with fish being counted multiple times by ensuring an individual fish cannot be counted more than once in a single frame (Cappo et al., 2003). However, MaxN is a very conservative estimate of fish abundance, and is most effective when bait is used to attract fish and, therefore, large numbers of fish stay within the field of view. Baited designs are, however, unsuitable for fine-scale sampling where fish may be attracted from nearby locations. To ensure variation between MaxN samples and to prevent overestimation of fish abundance caused by sampling a few large schools MaxN average was used. MaxN average was calculated by averaging the maximum number of fish recorded in five 30 s blocks for each video. When fish were recorded in fewer than five 30 s blocks, the number of fish was still divided by five. Australian salmon (*Arripis* spp.) were recorded in 10 s blocks because of the fast swimming nature of that species. MaxN average will be referred to as MaxN. Time in View (TiV) at each position provided an estimate of how each position was used by fish. TiV was recorded as the total time in seconds that at least one fish of a given species was in the frame. Two rules were established to further reduce fish recounting and overestimation of TiV; 1) if a fish left the screen and returned from the same direction within 10 s it was deemed to be the same fish and was not recounted in MaxN; 2) if a fish was lost from view (i.e. hidden in seagrass) and did not reappear within 30 s it was deemed to have left the sampling area. Disturbance effects that may affect fish behaviour were restricted by only beginning video analysis after 1 min. During this time there was no evidence to suggest that deployment of cameras altered fish behaviour (T. Smith pers obs). Small schooling fish were impossible to identify from video samples

Table 1
Number of video replicates taken at each position during day and night sampling.

Position	Day	Night
Seagrass middle	15	8
Seagrass edge	13	6
Adjacent sand	14	8
Distant sand	14	9
Total	56	31

and classified as "bait fish." Seine netting on nearby seagrass patches revealed schools consisted of Atherinids and Clupeids.

2.4. Tethering experiment

Tethering experiments used two common seagrass-associated fish: King George whiting (*Sillaginodes punctata*) recruits (+0 age class) and pipefish *Stigmatopora* spp. Greater densities of pipefish have been found at seagrass edges compared with the seagrass interior, and the species is regularly collected on sand adjacent to seagrass (Smith et al., 2008).

Fish were collected from nearby seagrass patches using a 10 m seine net and tethered using a 40 cm length of 0.006 mm monofilament nylon line through the lower jaw (whiting) or around the tail (pipefish). Tethers were attached to a timing device similar to that used by Peterson et al. (2001). Briefly, fishing line was connected to a 'trigger' that activates a reed switch, starting a clock. Tethered fish were videoed to document behaviour and predator interaction for 82 whiting and 77 pipefish tethering trials. Tethering has limitations that are well documented (Peterson and Black, 1994; Aronson et al., 2001) but is nevertheless a useful means of studying relative predation.

2.4.1. Experimental design

Tethered fish were placed at each of the four positions within six replicate seagrass patches over four non consecutive sampling days ($n = 4 \times 6 \times 4 = 96$) for each species. Seagrass patches occurred in two distinct bands; a shallow inner band and a deeper outer band. Fewer patches were required on each sampling occasion for the tethering experiment than video survey allowing seagrass band to be included in the experimental design and provide an opportunity to explore tethering in a landscape context. Three patches were used in each band, and seagrass band (outer, inner) treated as a factor. Tethered fish were assessed after 30 min, and their status recorded as eaten, alive or dead. Leaving fish any longer than 30 min increased the likelihood of fish mortality for reasons other than predation.

In the laboratory, footage of eaten or missing fish was assessed and the fate of the fish recorded. If a fish was missing but the timer was not triggered, and there was no video footage, the fish was recorded as dead. Dead fish and fish taken without setting of timers were omitted from analysis.

2.4.2. Seagrass and depth

Water depth and seagrass length were measured to assess any relationship with predator distribution and fish survival time. Depth measurements to the nearest 5 cm were taken prior to, and at the completion of, each video and tethering sample. Seagrass length measurements to the nearest mm were taken from 5 seagrass blades from different shoots at the completion of video and tethering samples at the seagrass middle and edge.

2.5. Data analysis

2.5.1. Video survey

TiV and MaxN were converted to fish min^{-1} to account for any video samples that did not record for 60 min (four replicates), and four replicates were omitted from the analysis because of poor visibility restricted the field of view so no fish could be seen (Table 1). All data were checked for normality and homogeneity of variance and 4th root transformed where appropriate. TiV and MaxN for the most abundant species were analysed using a two-factor ANOVA, where Position (Distant Sand, Adjacent Sand, Seagrass Edge, Seagrass Middle) was treated as a fixed factor and sampling date was treated as a random factor. This was followed by three planned comparisons: vegetated and unvegetated habitats; sand and adjacent sand; seagrass edge and seagrass middle. Type III Sum of Squares was used to reduce problems associated with uneven sample sizes where replicates had

been omitted (Quinn and Keough, 2002). All positions during night sampling were not represented on every sampling date, therefore there was no position × date interaction data for night samples, and consequently analysis was not done. Depth and seagrass length were averaged for each replicate and regression analyses were used to compare each of TiV and MaxN with water depth and seagrass length (for seagrass length, sand positions were excluded).

2.5.2. Tethering experiment

Presence/absence data from the tethering experiments were analysed using chi-square analyses comparing positions and seagrass bands in separate analysis. Survival time was converted to a proportion of 30 min to provide a relative measure across positions, and was assessed for normality and homogeneity of variance, arcsine transformed where required, and analysed using ANOVA. Unreplicated split-plot analyses were used to analyse survival times and fish lengths for each species. Seagrass band (outer, inner) was treated as a between subjects factors, and patch was treated as a random factor nested within seagrass band. Position (distant sand, adjacent sand, seagrass edge, seagrass middle) was treated as a within subjects factor. Response variables were averaged over sampling days. Tukey's tests were done where there was a significant position effect. Logistic regression analysis (Wald statistic) was used to determine if survival was affected by fish length, water depth or seagrass length. We did not test for effects of fish length, water depth or seagrass length on survival time, because the statistical model was a partly-nested design, and including 3 covariates in such a design would be problematic, because there was little replication at the scale at which covariates would be applied.

3. Results

3.1. Video survey

3.1.1. Day samples

Over five sampling days, nineteen fish species from seventeen families were recorded. Smooth toadfish, *Tetractenos glaber* was the most commonly recorded fish species, with bait fish, Australian salmon and both juveniles and adult King George whiting also common (Table 2).

3.1.1.1. Australian salmon.
Australian salmon MaxN did not differ among positions, but TiV was significantly greater at the sand edge than distant sand, and was intermediate at both seagrass positions (Table 3, Fig. 1). TiV and MaxN of salmon increased with water depth (TiV: $F_{1, 54} = 8.6$, $p = 0.005$, MaxN: $F_{1, 54} = 9.7$, $p = 0.003$, Fig. 3). TiV decreased with increasing seagrass length ($F_{1, 26} = 8.5$, $p = 0.007$, Fig. 3) but there was no relationship for MaxN.

3.1.1.2. Smooth toadfish.
Smooth toadfish were closely associated with seagrass and adjacent sand. Smooth toadfish TiV was significantly greater in vegetated positions than unvegetated positions, and at the adjacent sand than distant sand (Table 3, Fig. 1). Planned comparisons showed that toadfish MaxN was greater at adjacent sand than distant sand (Table 3, Fig. 2).

Regression analysis revealed that when water depth increased, toadfish TiV ($F_{1, 54} = 16.9$, $p < 0.001$) and MaxN ($F_{1, 54} = 18.831$, $p < 0.001$) increased (Fig. 3), but there was no relationship with seagrass length.

3.1.1.3. Bait fish.
Bait fish TiV and MaxN were significantly greater in seagrass than sand positions (Table 3, Figs. 1 and 2). Bait fish TiV increased with seagrass length ($F_{1, 26} = 12.4$, $p = 0.002$, Fig. 3) but there was no significant relationship between MaxN and seagrass length or either TiV or MaxN and depth.
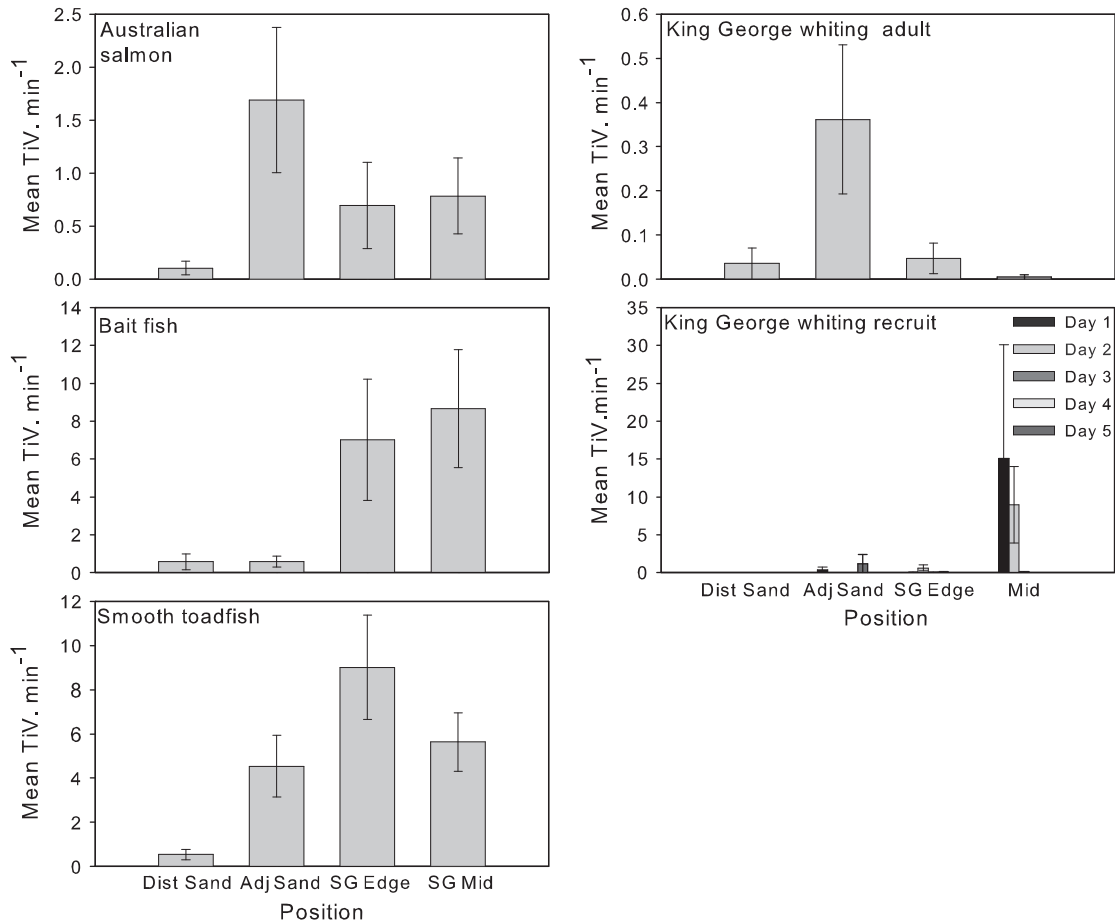
Table 2
Frequency of each fish species recorded in video sampling during the day and night at each position.

| | | Day | | | | | Night | | | | |
| | | Sand | | Seagrass | | | Sand | | Seagrass | | |
Species		Distant	Adjacent	Edge	Middle	Total	Distant	Adjacent	Edge	Middle	Total
Smooth toadfish	*Tetractenos glaber*	10	12	12	12	46	7	4	4	4	19
Bait fish	Atherinids, Clupeids	4	6	7	10	27	8	7	5	6	26
Australian salmon	*Arripis* sp.	6	8	6	6	26					0
Small leatherjacket	Monacanthidae		1	6	7	14				1	1
Goby	Gobiidae	6	8			14	1				1
King George whiting recruit	*Sillaginodes punctata*		2	5	6	13					0
Banjo shark	*Trygonorrhina faciata*	3	3	1	3	10					0
King George whiting adult	*Sillaginodes punctata*	1	5	2	1	9	1				1
Globe fish	*Diodon nichthemerus*	2	4	2	1	9					0
Sea mullet	*Mugil cephalus*	2	1	2	3	8				1	1
Silver trevalley	*Pseudocaranx dentex*		2	1		3					0
6 Spine leatherjacket	*Meuschenia freycineti*		1	1	1	3					0
Weed whiting	*Neodax balturs*			1	1	2					0
Flounder	Pleuronectidae	1				1					0
Southern garfish	*Hyporhamphus melanochir*				1	1	1		1		2
Old Wife	*Enoplosus armatus*				1	1					0
Flathead	Platycephalidae		1			1					0
Woods siphon fish	*Siphamia cephalotes*				1	1					0
Rough leatherjacket	*Scobinichthys granulatus*				1	1					0

3.1.1.4. King George whiting. King George whiting adults and recruits showed different patterns; adults were associated with adjacent sand and recruits with the seagrass middle. Adult King George whiting were recorded in only nine replicates, restricting analysis, but over 50% of recordings (5) were in adjacent sand where TiV was much greater (Fig. 1). King George whiting recruit TiV showed an interaction between positions and days, being greater in the middle than other positions on the first two sampling days (Table 3, Fig. 1). There was no significant difference for MaxN (Table 3). There was no relationship between King George whiting recruits and either water depth or seagrass length.

3.1.2. Night samples

There was little difference in fish distribution among positions at night. A total of 31 night samples were taken over six nights, nine at the distant sand, eight at the adjacent sand and seagrass middle but only six at the seagrass edge (Table 1). Only 7 species were recorded in night samples with bait fish and smooth toadfish the most common (Table 2). Australian salmon were not seen at night. However, TiV in each position and MaxN for both bait fish and toadfish showed little difference among positions (Fig. 4).

3.2. Tethering experiment

A total of 96 of each of King George whiting recruits and pipefish were tethered over 8 days. Of these, 47 King George whiting were eaten by predators. Only 15 pipefish were eaten, and none were eaten in the middle of seagrass patches. Additionally, 13 pipefish were

removed from analysis because they were dead, escaped, or gone and the timing devices had not been triggered. Tethered fish length was not different across positions or seagrass bands for either species (Table 4).

Analysis comparing eaten and surviving fish revealed few significant results, with no difference across positions for either King George whiting or pipefish. Comparisons across seagrass bands, however, found more King George whiting were eaten at outer seagrass patches than inner patches ($\chi^2 = 10.150$, df = 1, p = 0.001), but there was no difference for pipefish.

3.2.1. King George whiting recruit survival time

King George whiting recruit survival time was greatest in the middle of inner seagrass patches where only one fish was eaten, while in outer patches survival time was lowest in the middle of seagrass patches, but there was no overall difference among positions or seagrass bands (Table 4, Fig. 5). Survival was not significantly related to water depth, seagrass length was marginally non-significant ($Z = -1.94$, p = 0.053) but as King George whiting length increased, chance of survival decreased ($Z = 2.62$, p = 0.001, Fig. 6).

3.2.2. Pipefish survival time

Pipefish survival time was greatest at the middle of seagrass patches where no fish were eaten. Pipefish survival time was lower over adjacent sand than both the seagrass edge (p = 0.036) and middle (p = 0.012) but there was no difference between other positions or seagrass bands (Table 4, Fig. 5). There was no relationship

Table 3
Analysis of variance comparing the TiV and MaxN in each position for each species sampled with videos. Significant values in bold (p<0.05).

| | | Australian salmon | | | | Smooth toadfish | | | | Baitfish | | | | King George whiting recruit | | | |
| | | TiV | | MaxN | | TiV | | MaxN | | TiV | | MaxN | | TiV | | MaxN | |
	df	F	P	F	p	F	p	F	P	F	p	F	p	F	p	F	p
Day	4	3.35	**0.020**	1.61	0.344	0.72	0.584	1.94	0.124	5.23	**0.002**	5.72	**0.001**	2.98	**0.032**	2.65	**0.049**
Position	3	2.62	0.319	1.30	0.319	9.65	**0.002**	2.54	0.106	5.89	**0.010**	5.62	**0.012**	1.85	0.192	1.67	0.225
SG E v SG M	1	<0.01	0.984	0.16	0.695	2.66	0.129	0.03	0.872	0.40	0.541	1.88	0.196	0.98	0.342	0.05	0.820
Adj Sand v Dist Sand	1	7.56	**0.018**	3.11	0.103	7.90	**0.016**	7.11	**0.021**	0.13	0.541	0.12	0.738	0.62	0.446	1.50	0.244
SG v Unveg	1	0.30	0.596	0.60	0.451	19.42	**0.001**	0.49	0.449	16.73	**0.001**	14.12	**0.003**	3.69	0.079	3.39	0.090
Position × Day	12	0.65	0.788	0.35	0.970	0.57	0.854	1.45	0.190	0.97	0.496	0.71	0.496	2.13	**0.039**	1.92	0.065
Error	36																

Fig. 1. Mean (± 1 SE) TiV in each position for Australian salmon, smooth toadfish, bait fish and King George whiting adults and TiV at each position on each sampling day for King George whiting recruits.

between survival and either water depth or pipefish length. Logistic regression analysis was not done between survival time and seagrass length because only four fish were preyed upon in seagrass.
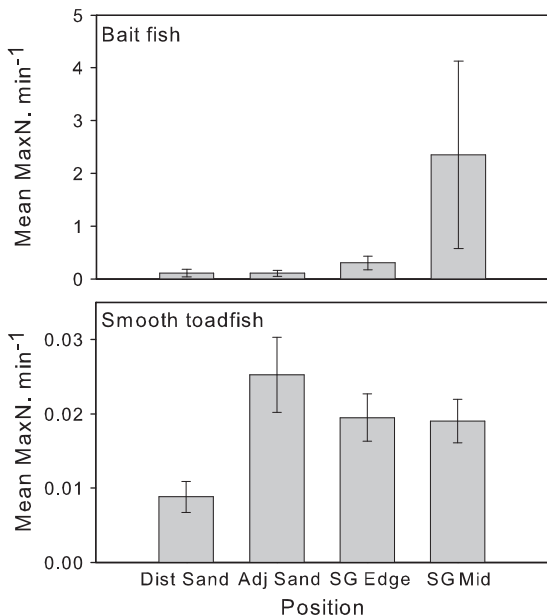

Fig. 2. Mean MaxN (± 1 SE) at each position for bait fish and smooth toadfish.

3.2.3. Predators

Australian salmon were the most common predator of both King George whiting recruits and pipefish. Salmon accounted for 43 predation events on King George whiting, followed by silver gulls, *Larus novaehollandiae* (Stephens) (3 predation events) and flathead (Platycephalidae spp. 1 predation event). Salmon accounted for 14 of the 15 predation events on pipefish; the other predation event was by a shrimp from the family Callianassidae.

4. Discussion

Predation can influence the distribution of species in and around seagrass habitats. This study found that both predator and prey distribution and prey survival times during the day can change according to both position within a seagrass patch, and the location of that patch within seagrass habitats. Our findings support previous work suggesting predation at seagrass edges is greater than at other seagrass locations (Bologna and Heck, 1999; Gorman et al., 2009). Edges can facilitate greater encounter rates between predators and prey, decreasing prey abundances at edges through greater mortality rates or predator avoidance (Ries et al., 2004). Australian salmon were the predominant predator of tethered King George whiting and pipefish and is a common predator of many small fish in seagrass (Robertson, 1982; Hindell et al., 2000). Salmon spent more time over sand adjacent to seagrass than other positions and can be linked to predation and distribution of King George whiting recruits, and, pipefish predation. Presence of salmon over adjacent sand was directly related to lower pipefish survival times over adjacent sand. Likewise, survival times of King George whiting recruits were greater
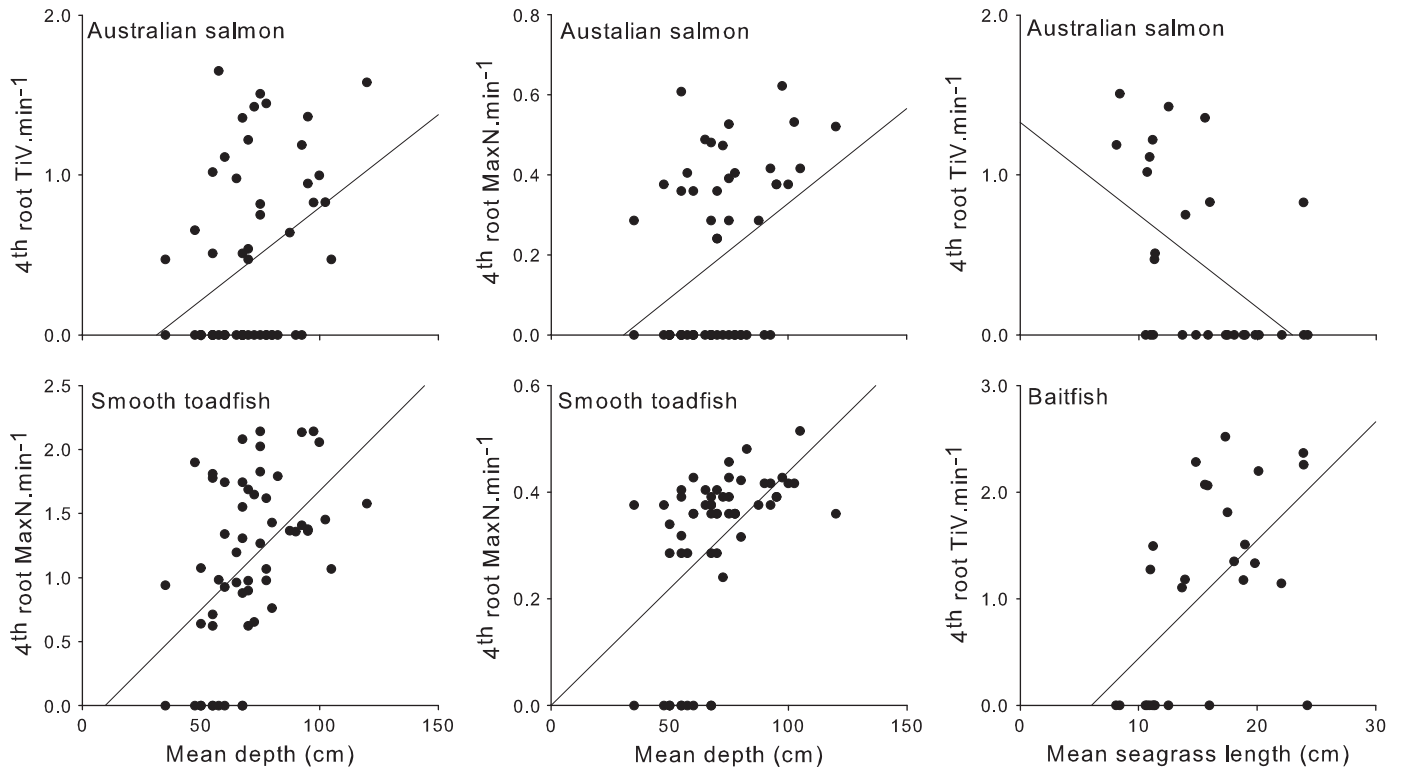
Fig. 3. Significant relationship (p<0.05) between each of TiV and MaxN and water depth for Australian salmon and smooth toadfish, and, between TiV and seagrass density at the middle and edge of patches for Australian salmon and bait fish.

in the middle of inner patches where water was shallower and few salmon were recorded, but not in outer patches where the water was deeper and more salmon were recorded. King George whiting recruits spent more time in the middle of patches on the initial two days of sampling, suggesting greater TiV of salmon over sand adjacent to seagrass was effecting King George whiting distribution within patches. King George whiting recruits undergo ontogenetic changes, moving from seagrass to sand habitats during January (Jenkins and Wheatley, 1998), which may explain the lack of consistency in King George whiting recruit TiV over days. Moving to sand habitats

coincides with changes in colouration and may initiate schooling behaviour, making recruits less susceptible to predation from salmon, and therefore spending less time in the middle of patches.

Seagrass edges can provide a foraging area or barrier for transient predators (Horinouchi, 2007b). Syngnathids and King George whiting recruits are common prey of salmon (Robertson, 1982; Hindell et al., 2000) and are more abundant at seagrass edges, "spilling" onto sand adjacent to seagrass (Smith et al., 2008). The seagrass edge and adjacent sand therefore provide salmon with a favourable foraging area creating a positive edge response (Ries et al., 2004). Survival
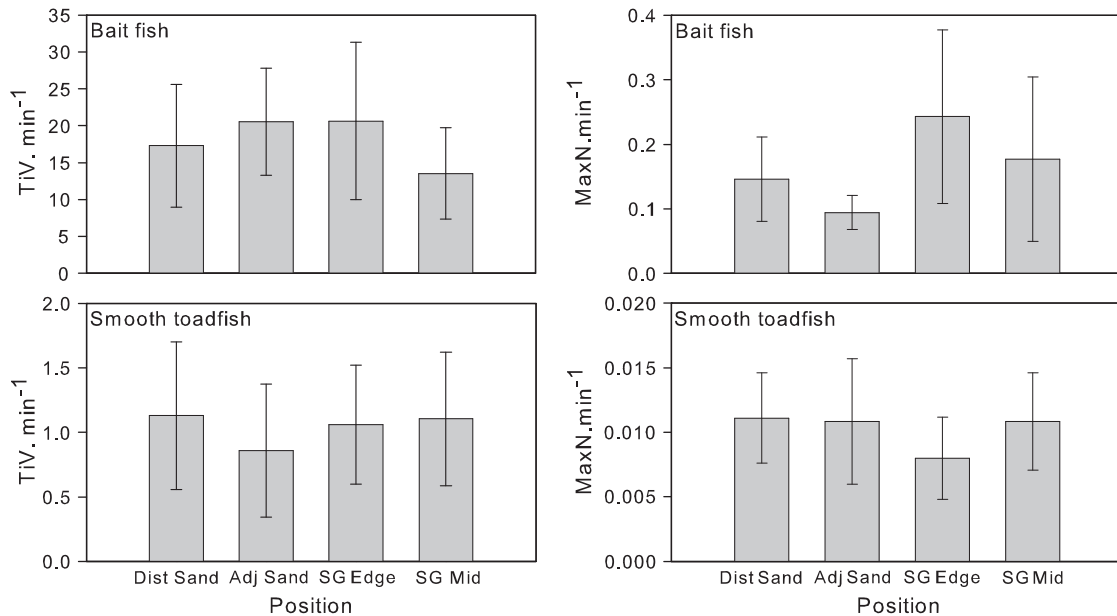
Fig. 4. Mean (±1 SE) TiV and MaxN in each position during night samples for bait fish and smooth toadfish.

Table 4
Analysis of variance comparing survival times of King George whiting recruits and pipefish at different positions and seagrass bands. Significant values in bold (p<0.05).

		Fish length				Survival time			
		King George whiting recruits		Pipefish		King George whiting recruits		Pipefish	
	df	F	p	F	p	F	p	F	p
Between subjects									
Seagrass band	1	0.06	0.798	0.00	0.985	5.13	0.086	0.07	0.807
Patch (Seagrass band)	4								
Within subjects									
Position	3	0.48	0.703	0.03	0.992	0.68	0.582	4.72	**0.021**
Position × Seagrass band	3	1.67	0.227	3.45	0.052	4.12	**0.032**	0.52	0.677
Position × Patch (Seagrass band)	12								

times of pipefish were lower on adjacent sand compared to other positions, and no fish were eaten from the middle of patches. Therefore, it would be expected that if predation was causing edge effects for pipefish, abundances would be greater in the middle of patches where predation is lower. However, pipefish abundances are greater at the edge of patches than the middle (Smith et al., 2008; Macreadie et al., 2009), suggesting that pipefish balance predation pressure with some other mechanism that maximises energy and growth at the edge (Orth et al., 1984). Planktonic food availability, through greater water flow at the seagrass edge, has been suggested to explain greater abundances of pipefish at the edge (Smith et al., 2008; Macreadie et al., 2009), and, although gut analysis has found little differences in prey consumption between the edge and middle (Smith unpublished data), supplementary food experiments have indicated that food availability may influence pipefish abundances within seagrass patches (Macreadie et al., 2010).

Seagrass provides small fish species with a refuge from predators (Jackson et al., 2001), and changes in seagrass structure and presence of predators can affect the refuge value of patches (Horinouchi, 2007b). Survival time in seagrass positions was generally greater than

sand positions, supporting the premise that the presence of seagrass structure provides a refuge from predators (Hindell et al., 2002). Survival time of King George whiting recruits in outer patches was the exception, where survival time was lower in seagrass than sand. Predator abundances are thought to increase in deep water (Sheaves, 2001), and we found salmon TiV and abundance increased with water depth. Seagrass may disrupt schooling behaviour (Flynn and Ritz, 1999), but deeper water in outer patches may allow salmon to maintain schooling behaviour within seagrass patches increasing salmon abundances within seagrass patches, making whiting more prone to predation in deeper beds. Seagrass density, however, did not influence survival of tethered fish, contrasting studies on crustaceans that found dense seagrass enhances survival (Haywood and Pendrey, 1996; Hovel and Fonseca, 2005). Predator/prey relationships between salmon and bait fish, however, may be influenced by seagrass density; as seagrass density increased, salmon TiV decreased and bait fish TiV increased. Foraging ability of chase and attack predators such as salmon can be affected by seagrass density (Flynn and Ritz, 1999), creating a refuge for bait fish. Similarly, in the absence of salmon at night, bait fish were recorded in all positions, suggesting they will move onto sand when predators are not present.

Sand adjacent to seagrass patches was used more than distant sand by salmon, smooth toadfish and adult whiting, supporting previous findings suggesting that unvegetated sand close to seagrass is more important than more distant sand (Ferrell and Bell, 1991; Smith et al., 2008). Sand adjacent to seagrass might represent a beneficial habitat for seagrass fishes (Smith et al., 2008). Salmon, toadfish and adult King George whiting may use adjacent sand as an enhanced habitat because there is greater food availability than distant sand. Toadfish and adult King George whiting feed on similar prey over sand (Robertson, 1980) that includes polychaetes and decapods which have shown patterns of greater abundances on sand close to seagrass than more distant sand (Tanner, 2005). Alternatively,
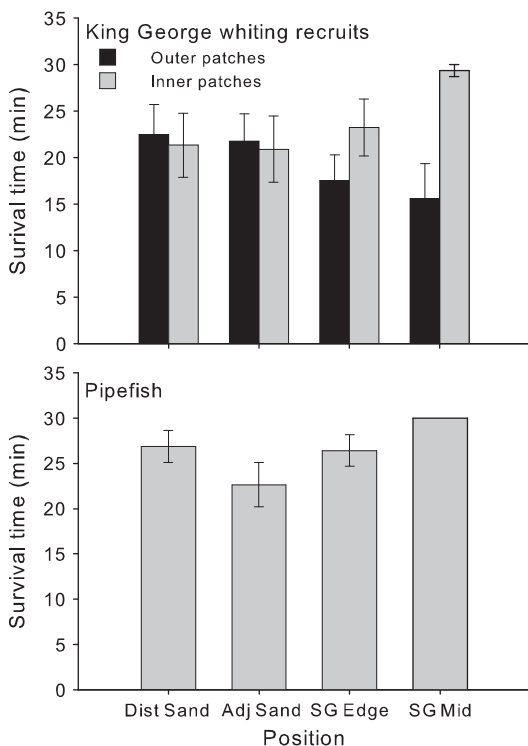

Fig. 5. Mean (± 1 SE) survival time of King George whiting recruits across positions and seagrass band, and pipefish survival time across positions (pooled across seagrass bands).
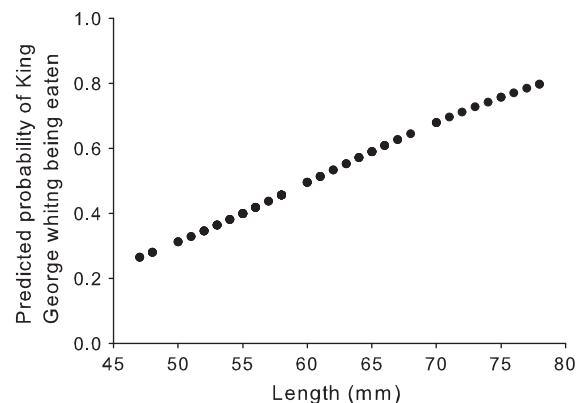

Fig. 6. Relationship between the probability of King George whiting recruits being eaten after 30 min and King George whiting length.

toadfish, spent more time in seagrass than sand positions and may be 'spilling over' from the preferred seagrass habitat onto adjacent non-preferred sand habitat.

By using not only tethering timers, but also video, we were able to assess survival time between habitats, predators preying on tethered fish, and any artefacts associated with tethering. Video footage from tethering experiments showed tethering had little effect on the behaviour of King George whiting recruits compared to non tethered whiting seen during the video survey, except to restrict escape from predators (T. Smith pers obs). High mortality rates of pipefish not associated with predation suggests that pipefish may not be a suitable species for tethering because of their poor swimming ability. Predation on pipefish by Callianasid shrimp highlights the artefacts that can be associated with tethering experiments. Callianasids are not a natural predator of pipefish but were able to take advantage of the restricted mobility of the tethered fish. However, with the use of video, and carefully selected prey species and sampling design, tethering is a useful means of testing predation across positions and habitats.

Habitat edges can change species interactions by altering movement patterns, inducing species mortality, increasing cross boundary subsidies and creating new interactions (Fagan et al., 1999). Predation is the most commonly cited interaction used to explain edge effects, where one organism benefits at the expense of another (Ries et al., 2004). In the case of Australian salmon (predator) and King George whiting recruits (prey) in shallow seagrass, the seagrass edge is a complementary habitat for salmon, but negative for the whiting prey, reducing abundances or forcing prey species to the interior of the patch where encounter rates with the predator are lower. Although the same predation climate would apply for pipefish, abundances of pipefish are greater at the seagrass edge (Smith et al., 2008), indicating that some other resource, probably food availability, is outweighing the risk of predation. The role of predation and species interactions in determining edge effects can be great for some species (King George whiting recruits) or minimal for others (pipefish), where the distribution of other resources is of greater importance than the threat of predation. As fragmentation of seagrass and other habitats continues, it is becoming increasingly important to establish the effects that edges have on patch associated fauna, and the mechanisms underlying such effects.

Acknowledgments

References

Aronson, R.B., Keck, K.L., Valentine, J.F., 2001. Measuring predation with tethering experiments. Mar. Ecol. Prog. Ser. 214, 311–312.

Ball, D., Parry, G., Heislers, D., Blake, S., Werner, G., 2006. Analysis of Victorian Seagrass Health at a Multiregional Level. Department of Primary Industries Victoria, Queenscliff.

Bernot, R.J., Turner, A.M., 2001. Predator identity and trait-mediated indirect effects in a littoral food web. Oecologia 129, 139–146.

Bologna, P.A.X., Heck, K.L., 1999. Differential predation and growth rates of bay scallops within seagrass habitats. J. Exp. Mar. Biol. Ecol. 239, 299–314.

Bologna, P.A.X., Heck, K.L., 2000. Impacts of seagrass habitat architecture on bivalve settlement. Estuaries 23, 449–457.

Bologna, P.A.X., Heck, K.L., 2002. Impact of habitat edges on density and secondary production of seagrass-associated fauna. Estuaries 25, 1033–1044.

Bullard, S.J.M., Hay, M.E., 2002. Plankton tethering to assess spatial patterns of predation risk over a coral reef and seagrass bed. Mar. Ecol. Prog. Ser. 225, 17–28.

Cappo, M., Harvey, E.S., Malcolm, H., Speare, P., 2003. Potential of video techniques to monitor diversity, abundance and size of fish in studies of marine protected areas. In: Beumer, J.P., Grant, A., Smith, D.C. (Eds.), Aquatic Protected Areas — What Works Best and How Do We Know? World Congress on Aquatic Protected Areas. Australian Society of Fish Biology, Cairns, Australia, pp. 455–464.

Carruthers, T.J.B., Walker, D.I., 1997. Light climate and energy flow in the seagrass canopy of *Amphibolis griffithii* (J.M Black) den Hartog. Oecologia 109, 335–341.

Chittaro, P.M., Usseglio, P., Sale, P.F., 2005. Variation in fish density, assemblage composition and relative rates of predation among mangrove, seagrass and coral reef habitats. Environ. Biol. Fish. 72, 175–187.

Connolly, R.M., Hindell, J.S., 2006. Review of nekton patterns and ecological processes in seagrass landscapes. Estuar. Coast. Shelf Sci. 68, 433–444.

Dahlgren, C.P., Eggleston, D.B., 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81, 2227–2240.

Danilowicz, B.S., Sale, P.F., 1999. Relative intensity of predation on the French grunt, *Haemulon flavolineatum*, during diurnal, dusk, and nocturnal periods on a coral reef. Mar. Biol. 133, 337–343.

Duarte, C.M., 2002. The future of seagrass meadows. Environ. Conserv. 29, 192–206.

Eckerman, J.E., 1987. The role of hydrodynamics in recruitment, growth and survival of *Argopecten irradians* (L.) and *Anomia simplex* (D'Orbigny) within eelgrass meadows. J. Exp. Mar. Biol. Ecol. 106, 165–191.

Edgar, G.J., Shaw, C., 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia 1. Species richness, size structure and production of fishes in Western Port, Victoria. J. Exp. Mar. Biol. Ecol. 194, 53–81.

Fagan, W.E., Cantrell, R.S., Cosner, C., 1999. How habitat edges change species interactions. Am. Nat. 153, 165–182.

Ferrell, D.J., Bell, J.D., 1991. Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. Mar. Ecol. Prog. Ser. 72, 15–24.

Flynn, A.J., Ritz, D.A., 1999. Effect of habitat complexity and predatory style on the capture success of fish feeding on aggregated prey. J. Mar. Biol. Assoc. UK 79, 487–494.

Fonseca, M.S., Fisher, J.S., 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. Mar. Ecol. Prog. Ser. 29, 15–22.

Gorman, A.M., Gregory, R.S., Schneider, D.C., 2009. Eelgrass patch size and proximity to the patch edge affect predation risk of recently settled age 0 cod (*Gadus*). J. Exp. Mar. Biol. Ecol. 371, 1–9.

Haywood, M.D.E., Pendrey, R.C., 1996. A new design for a submersible chronographic tethering device to record predation in different habitats. Mar. Ecol. Prog. Ser. 143, 307–312.

Haywood, M.D.E., Manson, F.J., Loneragan, N.R., Toscas, P.J., 2003. Investigation of artifacts from chronographic tethering experiments — interactions between tethers and predators. J. Exp. Mar. Biol. Ecol. 290, 271–292.

Hinchey, E.K., Nicholson, M.C., Zajac, R.N., Irlandi, E.A., 2008. Marine and coastal applications in landscape ecology. Landscape Ecol. 23, 1–5.

Hindell, J.S., Jenkins, G.P., Keough, M.J., 2000. Variability in abundances of fishes associated with seagrass habitats in relation to diets of predatory fishes. Mar. Biol. 136, 725–737.

Hindell, J.S., Jenkins, G.P., Keough, M.J., 2001. Spatial and temporal variability in the effects of fish predation on macrofauna in relation to habitat complexity and cage effects. Mar. Ecol. Prog. Ser. 224, 231–250.

Hindell, J.S., Jenkins, G.P., Keough, M.J., 2002. Variability in the numbers of post-settlement King George whiting (Sillaginidae: *Sillaginodes punctata*, Cuvier) in relation to predation, habitat complexity and artificial cage structure. J. Exp. Mar. Biol. Ecol. 268, 13–31.

Horinouchi, M., 2007a. Distribution patterns of benthic juvenile gobies in and around seagrass habitats: effectiveness of seagrass shelter against predators. Estuar. Coast. Shelf Sci. 72, 657–664.

Horinouchi, M., 2007b. Review of within-patch scale structure complexity on seagrass fishes. J. Exp. Mar. Biol. Ecol. 350, 111–129.

Hovel, K.A., 2003. Habitat fragmentation in marine landscapes: relative effects of habitat cover and configuration on juvenile crab survival in California and North Carolina seagrass beds. Biol. Conserv. 110, 401–412.

Hovel, K.A., Lipcius, R.N., 2002. Effects of seagrass habitat fragmentation on juvenile blue crab survival and abundance. J. Exp. Mar. Biol. Ecol. 271, 75–98.

Hovel, K.A., Fonseca, M.S., 2005. Influence of seagrass landscape structure on the juvenile blue crab habitat-survival function. Mar. Ecol. Prog. Ser. 300, 179–191.

Hovel, K.A., Fonseca, M.S., Myer, D.L., Kenworthy, W.J., Whitfield, P.E., 2002. Effects of seagrass landscape structure, structural complexity and hydrodynamic regime on macrofaunal densities in North Carolina seagrass beds. Mar. Ecol. Prog. Ser. 243, 11–24.

Irlandi, E.A., 1997. Seagrass patch size and survivorship of an infaunal bivalve. Oikos 78, 511–518.

Irlandi, E.A., Peterson, C.H., 1991. Modification of animal habitat by large plants: mechanisms by which seagrasses influence clam growth. Oecologia 87, 307–318.

Jackson, E.L., Attrill, M.J., Rowden, A.A., Jones, M.B., 2006. Seagrass complexity hierarchies: influence on fish groups around the coast of Jersey (English Channel). J. Exp. Mar. Biol. Ecol. 330, 38–54.

Jackson, E.L., Rowden, A.A., Attrill, M.J., Bossey, S.J., Jones, M.B., 2001. The importance of seagrass beds as a habitat for fishery species. Oceanogr. Mar. Biol. Annu. Rev. 39, 269–303.

Jelbart, J.E., Ross, P.M., Connolly, R.M., 2006. Edge effects and patch size in seagrass landscapes: an experimental test using fish. Mar. Ecol. Prog. Ser. 319, 93–102.

Jenkins, G.P., Wheatley, M.J., 1998. The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: comparison of shallow seagrass, reef-algal and unvegetated sand habitats, with emphasis on their importance to recruitment. J. Exp. Mar. Biol. Ecol. 221, 147–172.

Johnson, M.W., Heck, K.L., 2006. Effects of habitat fragmentation per se on decapods and fishes inhabiting seagrass meadows in the northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 306, 233–246.

Macreadie, P., Hindell, J., Keough, M., Jenkins, G., Connolly, R., 2010. Resource distribution influences positive edge effects in a seagrass fish. Ecology 91, 2013–2021.

Macreadie, P.I., Hindell, J.S., Jenkins, G.P., Connolly, R.M., Keough, M.J., 2009. Fish responses to experimental fragmentation of seagrass habitat. Cons. Biol. 23, 644–652.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 10, 58–62.

Orth, R.J., Heck, K.L.J., von Montfrans, J., 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator–prey relationships. Estuaries 7, 339–350.

Orth, R.J., Kendrick, G.A., Marion, S.R., 2006. Predation on Posidonia australis seeds in seagrass habitats of Rottnest Island, Western Australia: patterns and predators. Mar. Ecol. Prog. Ser. 313, 105–114.

Peterson, B.J., Thompson, K.R., Cowan, J.H., Heck, K.L., 2001. Comparison of predation pressure in temperate and subtropical seagrass habitats based on chronographic tethering. Mar. Ecol. Prog. Ser. 224, 77–85.

Peterson, C.H., Black, R., 1994. An experimentalists challenge — when artifacts of intervention interact with treatments. Mar. Ecol. Prog. Ser. 111, 289–297.

Peterson, C.H., Luettich, R.A., Micheli, F., Skilleter, G.A., 2004. Attenuation of water flow inside seagrass canopies of differing structure. Mar. Ecol. Prog. Ser. 268, 81–92.

Quinn, G.P., Keough, M.J., 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

Ries, L, Sisk, T.D., 2004. A predictive model of edge effects. Ecology 85, 2917–2962.

Ries, L, Fletcher, R.J., Battin, J., Sisk, T.D., 2004. Ecological responses to habitat edges: mechanisms, models and variability explained. Annu. Rev. Ecol. Syst. 35, 491–522.

Robertson, A.I., 1980. The structure and organization of an eelgrass fish fauna. Oecologia 47, 76–82.

Robertson, A.I., 1982. Population-dynamics and feeding ecology of juvenile Australian salmon (Arripis trutta) in Western-Port, Victoria. Aust. J. Mar. Freshw. Res. 33, 369–375.

Sanchez-Jerez, P., Cebrian, C.B., Espla, A.A.R., 1999. Comparison of the epifauna spatial distribution in Posidonia oceanica, Cymodocea nodosa and unvegetated bottoms: importance of meadow edges. Acta. Oecol. 20, 391–405.

Scoffin, T.P., 1970. The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. J. Sed. Petrol. 40, 249–273.

Sheaves, M., 2001. Are there really few piscivorous fishes in shallow estuarine habitats? Mar. Ecol. Prog. Ser. 222, 279–290.

Smith, T.M., Hindell, J.S., 2005. Assessing effects of diel period, gear selectivity and predation on patterns of microhabitat use by fish in a mangrove dominated system in SE Australia. Mar. Ecol. Prog. Ser. 294, 257–270.

Smith, T.M., Hindell, J.S., Jenkins, G.P., Connolly, R.M., 2008. Edge effects on fish associated with seagrass and sand patches. Mar. Ecol. Prog. Ser. 359, 203–213.

Smith, T.M., Hindell, J.S., Jenkins, G.P., Connolly, R.M., 2010. Seagrass patch size affects fish responses to edges. J. Anim. Ecol. 79, 275–281.

Tanner, J.E., 2005. Edge effects on fauna in fragmented seagrass meadows. Aust. Ecol. 30, 210–218.

Uhrin, A.V., Holmquist, J.G., 2003. Effects of propeller scarring on macrofaunal use of the seagrass Thalassia testudinum. Mar. Ecol. Prog. Ser. 250, 61–70.

Werner, E.E., Peacor, S.D., 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84, 1083–1100.

Willis, T.J., Millar, R.B., Babcock, R.C., 2000. Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. Mar. Ecol. Prog. Ser. 198, 249–260.