Cross and long shelf variations in reef fish assemblage structure: Implications for management.

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Abstract

Fish communities are an important cultural, recreational and commercial resource that also have an important role in the functioning of marine ecosystems. Around the world fish assemblages are experiencing pressures from anthropogenic activities, and marine spatial planning is being established to mitigate these impacts and assist with biodiversity conservation. Information about how fish assemblages are structured across a range of spatial scales which encompass variations in physical, biotic and environmental parameters will assist marine spatial planning and management. We investigated differences in reef fish assemblage composition over three reef lines across an inshore to offshore gradient (3–23 m depth) at two marine reserves (70 km apart) in the Perth metropolitan region, Western Australia. There were significant increases in the number of individuals, species richness, and relative abundance of fish species across the shallow shelf depth gradient in the two locations. There were distinct fish assemblages associated with each reef line, correlated to depth and distance from shore. The differences across the shelf gradient, even over this small depth range, were greater than the differences between the two locations. These findings have implications for marine spatial management and the design of marine reserves that aim to conserve biodiversity. It may be most appropriate for such marine reserves to encompass a wide depth gradient, rather than a large longshore area. At the very least, cross and longshore patterns in fish assemblages should be taken into consideration and used to guide spatial management plans for biodiversity conservation.

Highlights

- Differences in fish assemblages were found across a shallow reefline gradient.
- Species richness and abundance increased from inshore to offshore reefs.
- Patterns in composition between reeflines were consistent among locations.
- Between reefline differences were greater than differences between locations.

- These differences have implications for fisheries and marine biodiversity conservation.

Keywords: demersal fish, cross-shelf, marine reserve, marine spatial planning, shallow-water, stereo-BRUVs

1. Introduction

Understanding how multi-scale processes control ecological patterns has become a central tenant of ecology and ecosystem management (Peters et al., 2007; Levin, 1992; Peterson and Parker, 1998). These processes act on individual species within a community from local to landscape scales and include abiotic (e.g. disturbance and depth) and biotic (predation and competition) influences (Turner et al., 2001). Models that bridge across spatial scales and environmental gradients need to be developed to understand the impact of these multi-scale processes (Chave, 2013), and the resulting implications for spatial management. In the marine environment, environmental processes affecting fish assemblage composition include depth (Charton et al., 2000; Fitzpatrick et a;. 2012), habitat type & complexity (Harman et al., 2003, Harvey et al., 2013), oceanographic features (e.g. water temperature, salinity and hydrodynamics) (Lecchini et al., 2003; Travers et al., 2011; 2010) and wave exposure (Letourneur, 1996; Clark, 1996; Fulton et al., 2005), all of which can be associated with biological factors such as predation and competition (Friedlander et al., 2007). The importance of depth as a key factor in structuring fish assemblages has been highlighted in a number of studies (García-Charton and Pérez-Ruzafa, 2001; Friedlander et al., 2003; Anderson and Millar, 2004; Gårdmark et al., 2011; Monk et al., 2010, 2011; Moore et al., 2009, 2011; Fitzpatrick et al., 2012). Environmental and biotic characteristics change across depth gradients, affecting fish assemblage composition (Brokovich et al., 2006). For example, on temperate shallow reefs in New Zealand, Anderson & Millar (2004) found that depth had a significant effect on the reef fish assemblage, with species richness and the number of individuals increasing along an inshore to offshore gradient. Conversely, Fitzpatrick et al. (2012) found that species richness and diversity and the number of fish declined with depth. The direction of these changes is likely related to localised environmental and biotic characteristics at each study location interacting with depth (e.g. habitat, complexity). Depth can also affect the trophic composition of fish communities, as resources change across depth gradients (Friedlander et al., 2010; Friedlander and Parrish, 1998; Travers et al., 2006; Newman and Williams, 2001). Many of these studies have focused on broader scale depth changes (up to hundreds of metres), while the influence of finer scale changes in depth on fish assemblages remains largely understudied (Pittman and Brown, 2011; Goatley and Bellwood, 2012; Sala et al., 2012).

A number of studies have shown that ecological processes are impacted by spatial variation, which makes inference and extrapolation of research over wider scales challenging (Newman et al., 1997; Newman and Williams, 1996; Wiens et al., 1993; Thrush et al., 2000; Horne and Schneider, 1994). Therefore, multi-scale nested sampling designs become imperative to understand underlying ecological processes (Dayton et al., 1999; Thrush et al., 2000). In the marine environment, smaller (100's meters) and larger (100's of km) spatial scales have characteristic patterns of patchiness and heterogeneity in community assemblages (Curley et al. 2003; Anderson & Millar 2004; Holmes & McCormick 2006). These differences in community composition are associated with changes in physical and biological processes (Andrew and Mapstone, 1987; Wiens, 1989; Tolimieri, 1995; Chesson, 1998). The overwhelming majority of studies to date have focused on community changes across large spatial scales (100s km) and environmental gradients (Williams and Martinez, 2000). While a number of studies have investigated spatial variation of individual fish species over smaller spatial scales (Tolimieri, 1995; García-Charton and Pérez-Ruzafa, 2001; Doherty, 1987; Fowler et al., 1992) and across a range of environmental variables (Friedlander et al., 2007; Clark, 1996; Fulton et al., 2005; Gårdmark et al., 2011), there has been a paucity of studies using structured hierarchical designs to assess fish assemblage composition across reefs, particular on temperate macro-algal dominated reefs (but see Anderson and Millar 2008).

Effective marine spatial management requires knowledge of the environmental and biological factors that shape fish assemblages at a hierarchy of spatial scales. Furthermore, ensuring connectivity between habitats is of vital importance, because fish species within habitat patches are dependent on one another through networks of predator – prey relationships, mutualism and competition (Schultz et al., 2014; Curley et al., 2003). In many cases marine spatial planning relies on incomplete knowledge of species inventories, distributions and habitat association (Schultz et al., 2014; Curley et al., 2003), and are often driven by social and economic considerations, rather than sustainable management of whole assemblages (McNeill, 1994).

This study investigated small-scale ecological patterns across three reeflines from an inshore to offshore gradient to characterise variation in fish assemblages. Differences in reef fish assemblage structure between inshore, mid shore and offshore reeflines were examined, focussing on species richness, the relative abundance and the relative biomass of fish. The aim of this study was to understand how small-scale variation with depth between shallow reeflines compared with medium scale spatial variation between sample locations at a distance of 70 km apart. It was hypothesised that: 1) there would be significant differences in the abundance and biomass of reef fish species between reeflines, and 2) there would be significant differences in the abundance and biomass of reef fish species between the two locations sampled after accounting for any confounding habitat factors.

2. Materials and Methods

2.1 Study area

This study was conducted within and immediately adjacent to the Marmion and Shoalwater Islands Marine Parks, two near-shore marine parks located to the north and south of the Perth metropolitan area (approximately 70km apart), Western Australia (31° 57.552’S, 115° 51.164’E; Fig. 1). Both marine parks encompass a range of spatial management areas, ranging from areas completely closed to fishing to general use areas. The benthic habitat is characterised by shallow macroalgal-dominated limestone reefs, interspersed with sand and sea grass. The limestone reefs form distinct lines that run parallel to the coastline, gradually increasing in depth to approximately 23m. Sampling occurred on three distinct and separate reeflines across this inshore to offshore gradient, at both the Marmion and Shoalwater Islands locations. The reeflines were depth stratified at each location: depths ranged from 3-7m (inshore), 9-12m (midshore) and 14-23m (offshore) for Shoalwater; and 3-9m (inshore), 6-12m (midshore) and 9-14m (offshore) for Marmion. Rugose, macroalgal-dominated reef was targeted for sampling at each reefline.

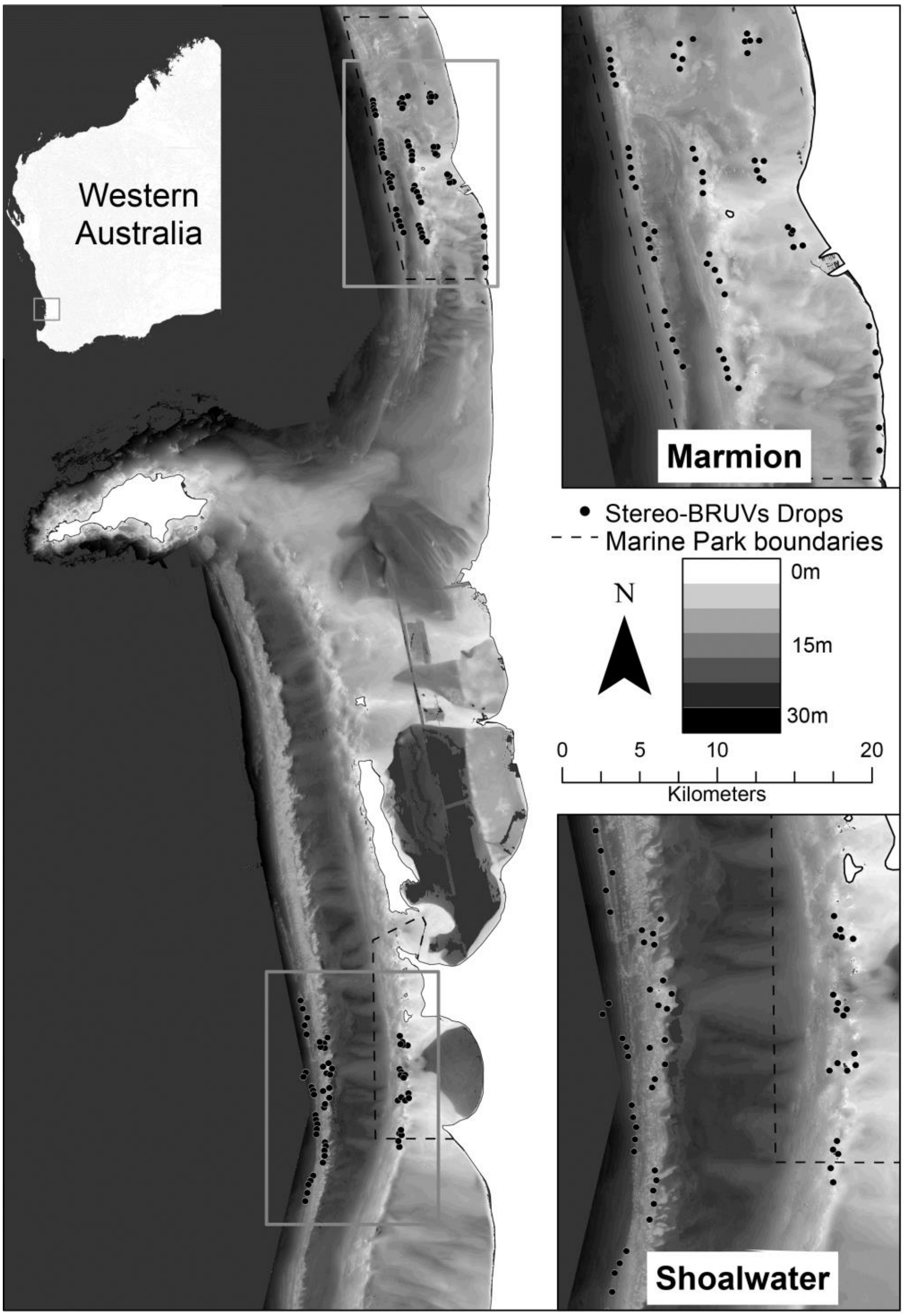

Figure 1. Sampling locations at Marmion and Shoalwater, to the north and south of the Perth metropolitan area respectively in Western Australia. Bathymetric information (depth, m) is overlaid. The boundaries of the marine parks are illustrated with dashed black lines. Each black point is a stereo-BRUV deployment.

2.2 Sampling

Sampling took place between the 25th April and 25th May 2012. Baited Remote Underwater stereo-Video systems (stereo-BRUVs) were used to record fish community composition. The stereo-BRUVs were the same as those described by Hardinge et al. (2013). Bait consisted of approximately 1kg of Western Australian pilchards (*Sardinops sagax*). These were crushed prior to deployment in order to maximise the dispersal of fish oil. The stereo-BRUV systems were deployed off a boat and were left to film continuously on the seafloor for at least 60 minutes. Watson et al. (2007) reported that 36 minutes of elapsed video is sufficient to capture the majority of fish within an assemblage on temperate reefs, but 60 minutes obtained a greater number of measurements of species targeted by fishers.

2.3 Experimental Design

The study comprised a three-factor design including location (two levels, fixed: Shoalwater, Marmion), reefline (three levels, fixed: inshore, midshore, offshore reef) and site (four levels at each reef: random and nested within reefline). Five replicate stereo-BRUVs were deployed per site, resulting in a total of 20 replicates for each of the three reeflines at each location.

2.4 Image analysis

Stereo-video imagery was downloaded and converted to avi format using Xilisoft Video Converter Ultimate (www.xilisoft.com/) and the Xvid codec (www.xvid.com). The imagery was analyzed using the software EventMeasure Stereo (Seager, 2008). Relative abundance of each species present in a replicate was measured by obtaining the maximum number of fish (MaxN) belonging to one species present in the field of view at one time. MaxN is a conservative estimate of relative abundance, but prevents any recounting of fish (Willis and Babcock, 2000; Cappo et al., 2003, 2006).

2.5 Biomass

The fork length of each fish visible in both of the stereo-pair of cameras was measured from the MaxN frame. For each sample, length estimates were converted to biomass using length – weight relationships derived from relevant published articles (Taylor and Willis, 1998; Kulbicki et al., 2005) or Fishbase (Frose and Pauly, 2010). Where length – weight information was not available for specific species, information for a similar congener was applied. For each sample the mean mass of fish of each species was calculated, and multiplied by MaxN to give an estimate of the total relative biomass of each species per deployment.

2.6 Statistical analysis

2.6.1 Multivariate analysis

Homogeneity of variance assumptions were examined using permutational analysis of multivariate dispersions (PERMDISP), which is a test equivalent to Levene's test for homogeneity of variance, but in a multivariate context (Anderson, 2006). Where necessary, abundance data were square-root transformed to minimise heterogeneity of multivariate dispersion between levels within the factors Location and Reefline.

Permutational multivariate analysis of variance (PERMANOVA with 9999 permutations) was used to analyse differences in the composition and relative biomass of the reef fish assemblage, and the composition by feeding guild, using the PERMANOVA+ add on (Anderson, 2001; Anderson et al., 2008) to the PRIMER 6 statistical package (Clarke and Gorley, 2006). Assemblage composition and relative biomass was analysed using a Bray-Curtis dissimilarity matrix and fourth root transformation. The relative abundance by feeding guild was analysed using a Bray-Curtis dissimilarity matrix and square root transformation. The Bray-Curtis coefficient was selected as it has the property of independence of joint absences. If the main effects were significant, pair wise tests were run between levels of each factor and interaction effects ($P<0.05$).

Principal coordinate ordinations (PCO) (Gower, 1966) were used to illustrate the grouping of samples for the location and reefline interaction. The use of PCOs enabled investigation of broad patterns in the multivariate data (Anderson and Robinson, 2003). Initially, patterns in the trophic levels of the fish assemblage were investigated using the relative abundance of feeding guilds. Vectors illustrating the Spearman rank correlation of the relative abundance of fishes within different feeding guilds, and of individual species were overlaid. A Spearman rank correlation was used to determine the species that were strongly correlated with the PCO axes, as these contributed significantly to the observed dissimilarity between sites. For those species with a correlation to either PCO axis of greater than 0.4 or less than -0.4, vectors were overlaid on the PCO. These vectors illustrate the strength and direction of the linear correlation to the PCO axes. These species were chosen for further univariate analysis.

2.6.2 Univariate analysis

Univariate analyses were conducted on species richness, total relative number of individuals and the relative abundance of individual species using PERMANOVA. After investigation for homogeneity of variance, data on the total relative number of individuals and species richness were left untransformed for analysis. The species that showed a strong Spearman rank correlation to either of the PCO axes were selected for univariate analysis of relative abundance. Upon investigation of homogeneity of variances, the data for each of the selected species were fourth root transformed. All univariate data were analysed using a Euclidean distance resemblance matrix.

The pattern of change in the relative biomass of selected species was analysed. However, to calculate an accurate biomass estimate for each sample it was necessary to make measurements of multiple fish of the same species during each sample, and for the species to be reasonably common in multiple samples. For these reasons, only four of the correlated species (*Coris auricularis*, *Epinephelides armatus*, *Neatypus obliquus*, and *Chrysophrys auratus*) were selected for the analysis of patterns in relative biomass. Homogeneity of variances in the biomass data of these species were investigated using Levene's test on the interaction between location and reefline. These data were then square root transformed where needed and analysed using the statistical design as described above.

Where the main tests found significant differences pairwise comparisons were carried out using PERMANOVA. Where the number of possible unique permutations was low pairwise tests were carried out using Monte Carlo sampling to calculate the Monte Carlo *P* value (P(MC)) (Anderson et al., 2008).

2.6.3 Model validation and the influence of potential confounding habitat factors

This study was designed to investigate the effect of reefline distance from shore on reef fish assemblages. To keep variation in habitat to a minimum, rugose limestone reef dominated by macro algae was targeted. In order to validate this model and to test for changes in the fish assemblages as a result of any confounding habitat factors a distance based linear model (DistLM) was used (Anderson and Robinson, 2003). A resemblance matrix of the relative abundance of the fish assemblage was constructed from the fourth root-transformed data using the Bray Curtis similarity coefficient. The DistLM was run on these five groups of environmental variables (distance from shore, depth, rugosity and dominant/ subdominant habitat variable) using the best selection procedure and the corrected AIC selection criteria (AICc) (Sugiura, 1978). Distance from shore and depth were continuous variables, measured in kilometres and metres respectively. Rugosity was estimated from the video footage and ranked on a scale from 1 to 4, 1 being flat and 4 being highly rugose. The habitat variables (sand, sand inundated reef, seagrass, foliose algae, algal canopy, coral) were assigned to two categories; being dominant or subdominant in the form of presence/ absence data. The selection of habitat was verified independently by at least two analysts. The variables that were selected in the most parsimonious model were plotted using distance based redundancy analysis (dbRDA) (Anderson, 2006).

3. Results

A total of 11 554 individuals from 101 fish species representing 49 families were recorded during the study. The three most abundant species were *Coris auricularis* (3921 individuals recorded), the genus *Pseudocaranx* spp (942 individuals recorded) and *Neatypus obliquus* (455 individuals recorded).

3.1 Model validation and the influence of potential confounding habitat factors

The DistLM procedure identified the most parsimonious model to explain variation in the fish assemblage using the predictor variables depth, distance from shore, and latitude (i.e. northing). Each of these variables were significant (Table 1), explaining 11%, 12%, and 6% of the variation in the fish assemblage (total of 22%, $r^2 = 0.22$, AICc = 878.41). As depth and distance from shore were less than 90% corellated (Pearson's r = 0.82), both were used in the model. The dominant and subdominant habitat groups were also found to be significant, but explained only a low proportion of the variation in the assemblage (7% and 8%) and were not selected by the AICc selection procedure for inclusion in the model. The statistical test for rugosity as a predictor variable was not significant (Table 1), suggesting that rugosity was consistent across samples, and that we were sucessful in targeting high rugosity reef.

Table 1. The proportion of variation in the fish assemblage explained by each of the environmental variables examined. The variables highlighted in bold were selected to best model the fish assemblage through DistLM using the best selection procedure and AICc selection criteria.

Group	SS(trace)	F	P	Proportion
Distance from shore	**26440.0**	**16.47**	**<0.001**	**0.12**
Depth	**23638.0**	**14.51**	**<0.001**	**0.11**
Subdominant habitat type	16377.0	1.87	<0.001	0.08
Dominant habitat type	15024.0	2.15	<0.001	0.07

Northing	**13277.0**	**7.73**	**<0.001**	**0.06**
Rugosity	3079.3	1.71	0.059	0.01

The dbRDA ordination shows a clear separation in the fish assemblages between locations (correlated with latitude) and a gradient with depth and distance from shore which is consistent in both locations (Fig. 2). These results validate the efforts to control for habitat and rugosity when deploying the stereo-BRUVs, and indicate that the two most valuable explanatory variables are those which would be expected to be explicitly associated with reefline.

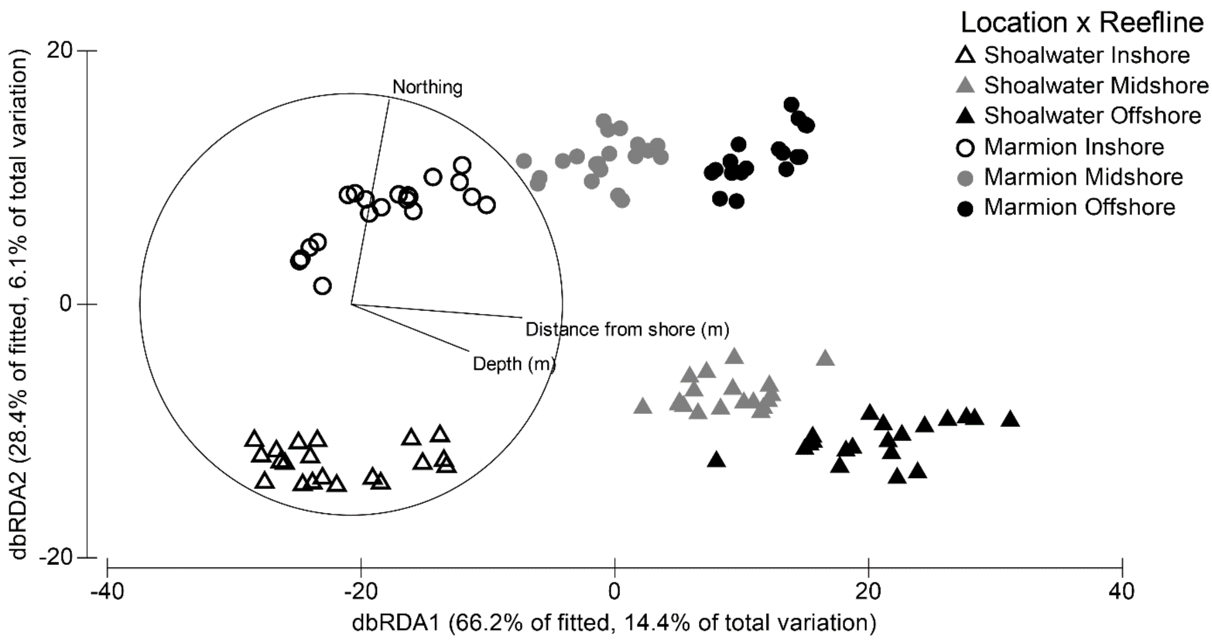

Figure 2. Distance based RDA ordination of the fish assemblage. The overlaid vectors indicate the strength and direction of the multiple partial correlations to the dbRDA axes of the explanatory variables that were selected by the model using AICc selection criterion and best selection procedure.

3.2 Relative number of individuals and species richness

Significant differences were found in the number of individual fish between reeflines (Table 2a). The mean relative number of individuals per deployment increased from inshore to offshore in both locations (Fig. 3a). And pairwise tests indicated that the number of individual fish was significantly greater at offshore reefs than at inshore reefs (t(6) = 8.85, P(perm) = 0.026)

Table 2. PERMANOVA results of the (a) relative number of individuals (untransformed) based on Euclidean distance resemblance matrix, (b) species richness (untransformed) based on Euclidean distance resemblance matrix, (c) assemblage composition based on Bray-Curtis dissimilarity matrix of the relative abundance (fourth root transformed), and (d) feeding guild composition based on Bray-Curtis dissimilarity matrix of the relative abundance (square root transformed). Significant values are highlighted bold.

		a) Number of individuals			**b) Species richness**		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Location	1	7422.2	3.64	0.088	2.9	0.23	0.640
Reefline	2	20248.0	8.17	**0.020**	188.6	7.58	**0.013**
Site (Reefline)	9	2478.4	1.55	0.135	24.9	1.53	0.150
Location x Reefline	2	158.46	0.08	0.925	19.0	1.55	0.261
Location x Site	9	2038.1	1.27	0.256	12.6	0.77	0.631
Residual	96	1599.8			16.3		
Total	119						

		c) Assemblage composition			**d) Feeding guild**		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Location	1	13226.0	63.60	**<0.001**	5079.3	7.58	**0.002**
Reefline	2	16756.0	7.40	**<0.001**	4919.6	4.12	**0.004**
Site (Reefline)	9	2260.6	18.03	**<0.001**	1194.8	2.68	**<0.001**
Location x Reefline	2	4864.6	23.40	**0.013**	410.9	0.614	0.758
Location x Site	9	2080.6	16.60	**<0.001**	669.7	1.50	**0.029**
Residual	96	1253.5			445.4		
Total	119						

Significant differences between reeflines were found for species richness (Table 2b). Pair wise tests indicated that inshore and offshore reefs were significantly different (t(6) = 4.40, P(perm) = 0.026), with species richness increasing from inshore to offshore (Fig. 3b).

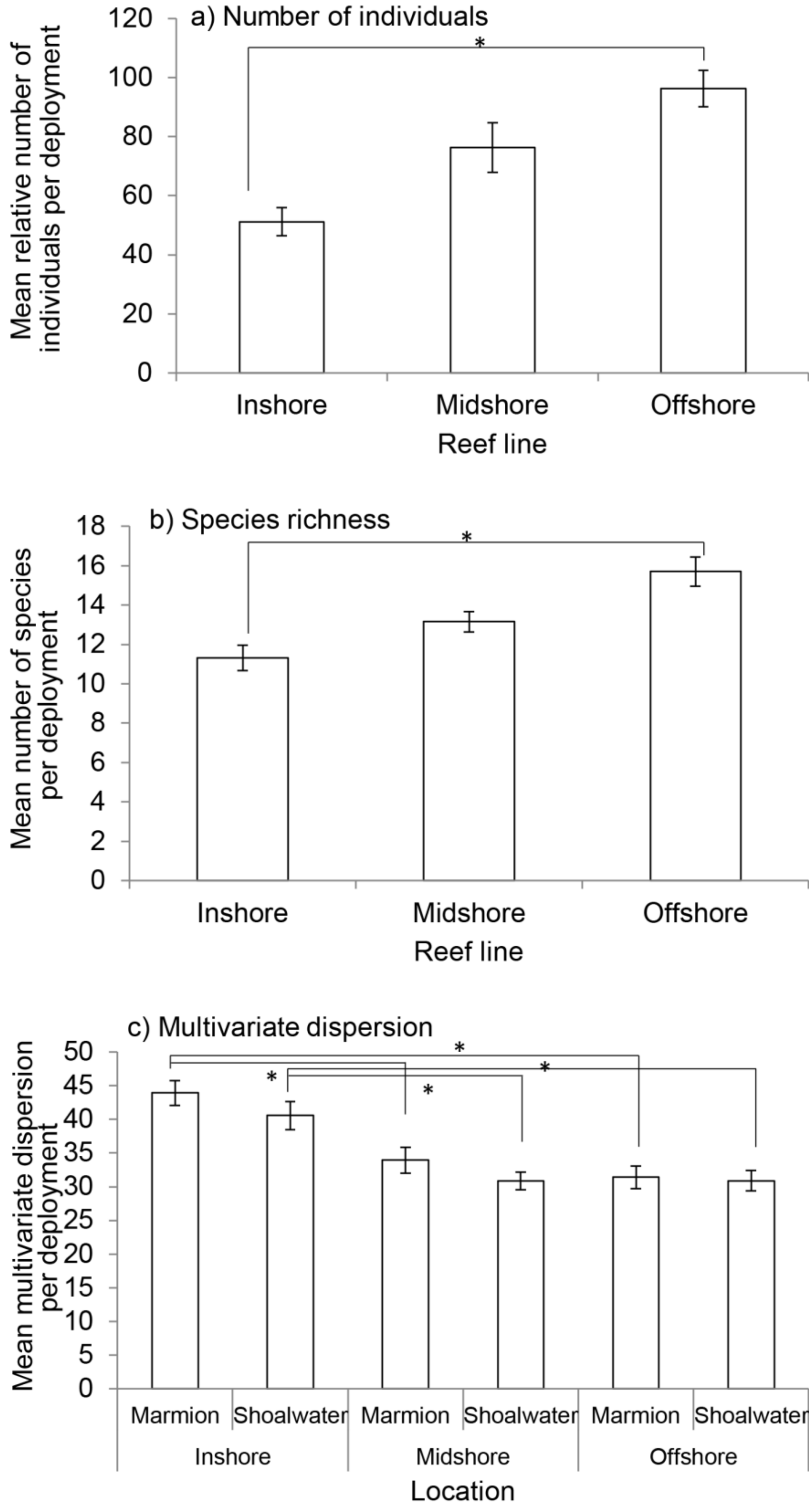

Figure 3. a) Mean relative number of individuals per deployment (± 1SE, n = 40); b) Mean species richness (± 1SE, n = 40) for each reefline; and c). Mean multivariate dispersion for each reefline and location (± 1SE, n=20) based on PERMDISP. Significant differences at α=0.05 are indicated by *.

3.3 Assemblage composition

A permutational test for dispersion (PERMDISP) showed that the assemblage composition was heterogeneous for the interaction between reefline and location ($P<0.05$). The multivariate dispersion at inshore reefs at both Marmion and Shoalwater was significantly greater (Fig. 3c, PERMDISP, $P<0.05$) than those at midshore and offshore reefs, which were not significantly different (PERMDISP, $P>0.05$).

PERMANOVA results for the overall reef fish assemblage showed an interaction between location and reefline (Table 2c). Pair wise tests indicated a significant difference in assemblage composition between each reefline within each location (all $t(6) > 1.5$, $P(perm) < 0.05$), and for the reeflines between the locations ($t(3) > 2.1$, $P(perm) < 0.05$). The exception was in the test for differences at inshore reeflines between locations. The fish assemblage composition at inshore reefs was statistically similar at both Marmion and Shoalwater ($t(3) = 1.48$, $P(perm) = 0.105$).

Significant differences were detected in the relative abundances of the feeding guilds of fishes between reefline and location (Table 2d). Offshore reefs were dominated by Piscivores, Planktivores, and Invertivores, with Planktivores being most characteristic of offshore reefs at Shoalwater, and Invertivores being most characteristic of offshore reefs at Marmion (Fig. 4). The PCO plot of multivariate fish assemblages by species (Fig. 5) illustrates a horseshoe shaped pattern indicative of a gradient in the species composition of the fish assemblage from near shore to offshore reefs. The overlaid vectors illustrate the strength and direction of the linear correlation of the fish species to the PCO axes based on Spearman rank correlations > 0.5. These species were selected for univariate analysis to determine their variation with reefline or location.

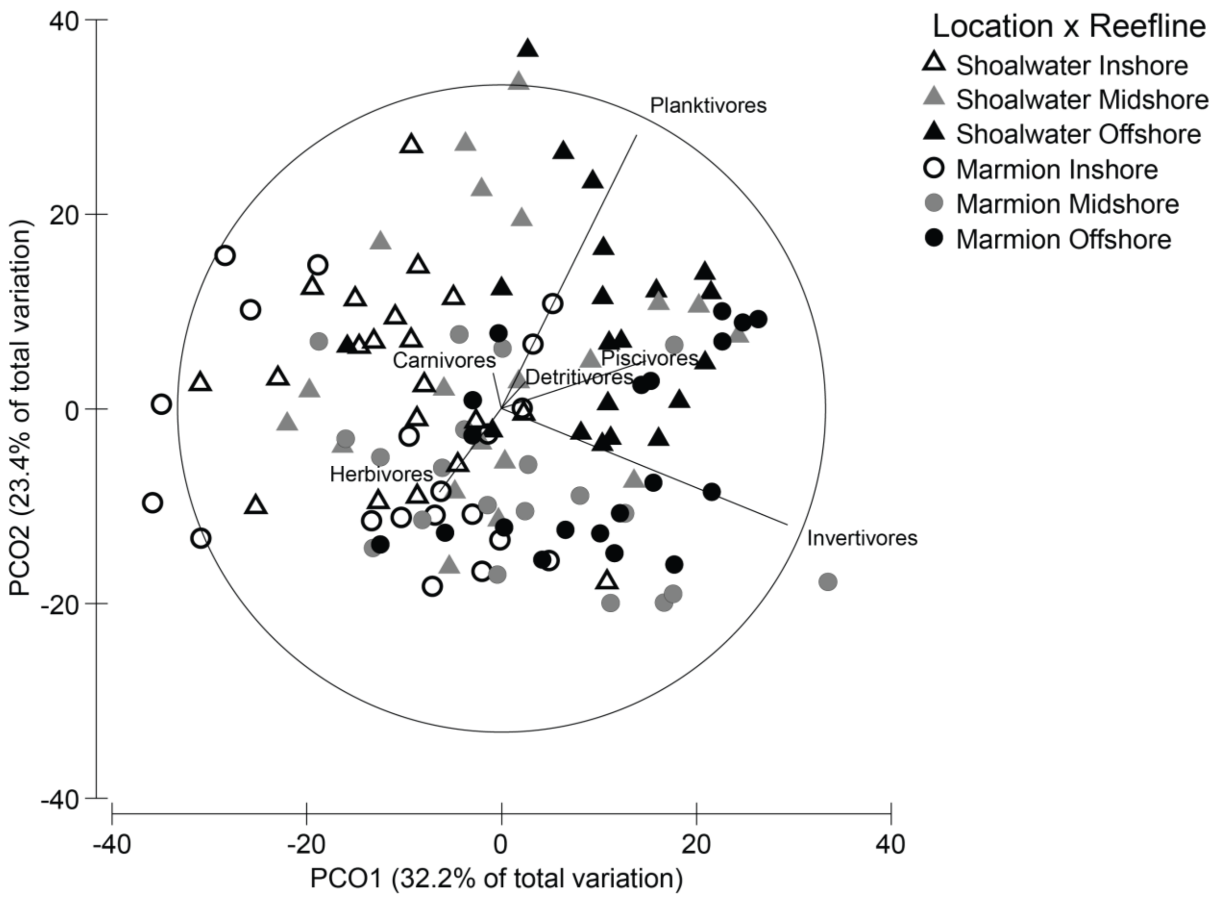

Figure 4. Principal coordinate ordination (PCO) plot of the composition of the fish assemblages by feeding guilds, using Bray-Curtis dissimilarity matrix on square root transformed assemblage data. The overlaid vectors indicate the strength and direction of the spearman rank correlations of each feeding guild to the PCO axes. Each point is a stereo-BRUV deployment.

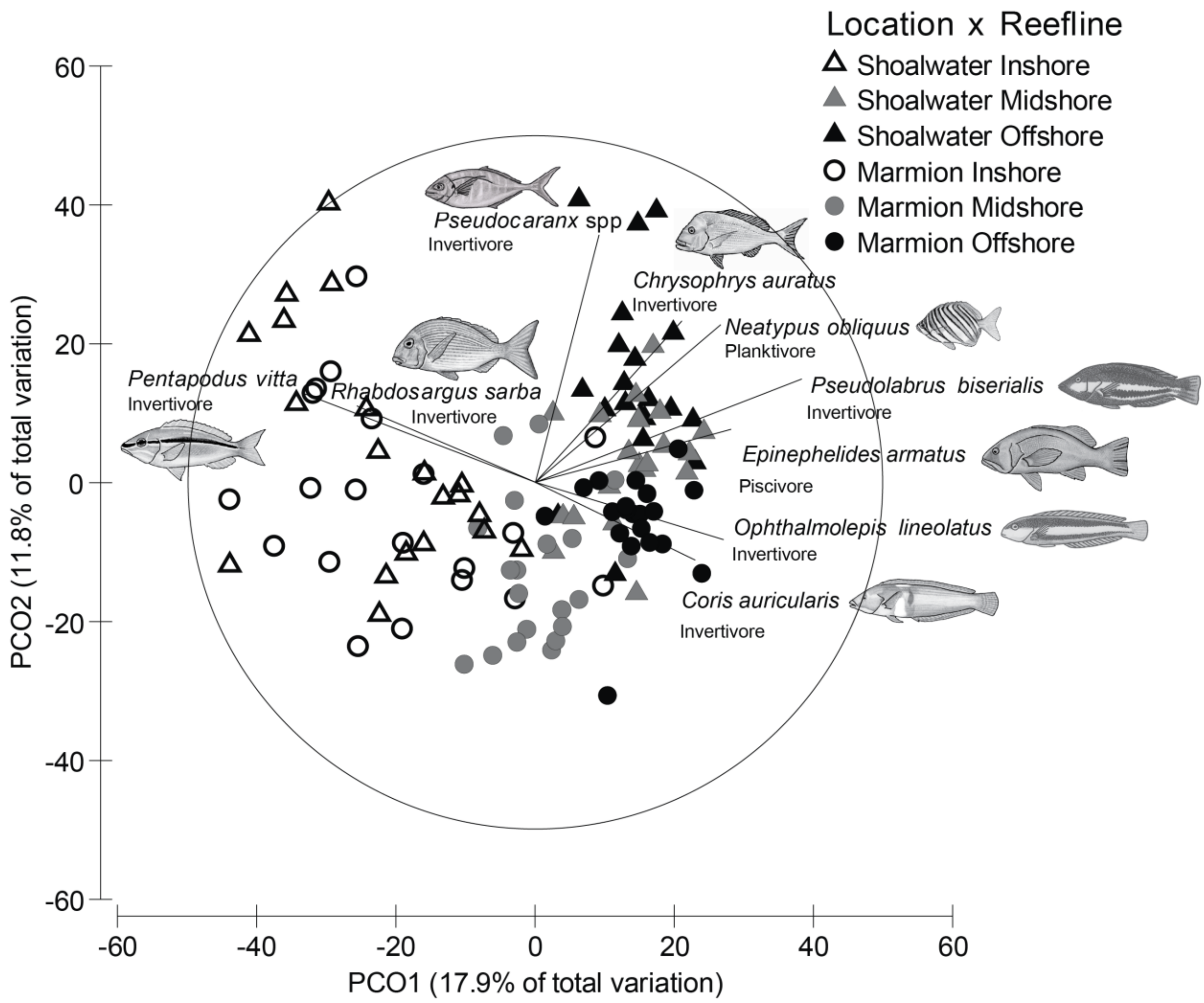

Figure 5. Principal coordinate ordination (PCO) plot of fish assemblages as assessed by location and reefline, using Bray-Curtis dissimilarity matrix on fourth root transformed assemblage data. The overlaid vectors indicate the strength and direction of the spearman rank correlations of each species to the PCO axes. All species selected have a positive or negative correlation to the axes of more than 0.5. Each point is a stereo-BRUV deployment.

3.4 Relative abundance and biomass of key and iconic species

Overall, there was a trend of increasing relative abundance from inshore to offshore reefs for many species. There were also some significant differences between locations (Table 3 and 4). *Coris auricularis*, *Epinephelides armatus*, *Opthalmolepis lineolatus*, *Pseudolabrus biserialis* and *Rhabdosargus sarba* all increased in abundance from inshore to offshore reefs (Table 3a, b; 4a, d, e; Fig. 6 a, c; 7 a, d, e). Similarly, *Neatypus obliquus*, *Chrysophrys auratus*, and *Pseudocaranx* spp increased in abundance from inshore to offshore, however the pattern was observed only at Shoalwater for these species (Table 3c, d;

4 c; Fig. 6e, g; 7c). These patterns were also reflected in the mean relative biomass per deployment of *Coris auricularis*, *Epinephelides armatus*, *Neatypus obliquus* and *Chrysophrys auratus*, (Table 3, Fig. 6). *Pentapodus vitta* exhibited a contrasting trend in abundance, being abundant only at inshore reefs, and not recorded at offshore reefs in either location (Table 4b; Fig. 7b).

Table 3. Results of univariate PERMANOVA tests of the relative abundance and biomass (grey) of the key and iconic species as identified as having a spearman rank correlation to the PCO axes of greater than 0.5. Significant values are highlighted in bold. Refer to methods section for details of the selection and analysis process.

	Mean relative abundance				**Mean relative biomass**			**Mean re**	
	a) *Coris auricularis*							**b) *Epine***	
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Ps
Location	1	5.13	41.96	**<0.001**	5121.2	3.9	0.085	0.05	
Reefline	2	8.88	8.19	**0.005**	6998.1	10.42	**0.006**	3.24	
Site(Reefline)	9	1.08	4.49	**<0.001**	671.9	1.28	0.25	0.22	
Location x Reefline	2	0.26	2.16	0.169	848.1	0.65	0.546	0.53	
Location x Site(Reefline)	9	0.12	0.51	0.86	1313.7	2.5	**0.01**	0.09	
Res	96	0.24			524.9			0.25	
Total	119								
	c) *Neatypus obliquus*							**d) *Chrys***	
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Ps
Location	1	19.76	28.21	**<0.001**	10347	26.45	**<0.001**	0.15	
Reefline	2	9.13	21.26	**<0.001**	4593.7	13.97	**0.004**	3.3	
Site(Reefline)	9	0.43	2.29	**0.023**	328.9	2.15	**0.028**	0.3	
Location x Reefline	2	6.25	8.92	**0.009**	4119	10.53	**0.004**	0.28	
Location x Site(Reefline)	9	0.7	3.73	**<0.001**	391.2	2.55	**0.009**	0.12	
Res	96	0.19			153.2			0.22	
Total	119								

Table 4. Results of univariate PERMANOVA tests of the relative abundance of the species identified as having a spearman rank correlation to the PCO axes of greater than 0.5. Significant values are highlighted in bold.

Mean relative abundance				
a) *Opthalmolepis lineolatus*				
Source	df	MS	Pseudo-F	P(perm)
Location	1	0.36	1.78	0.218
Reefline	2	9.28	33.05	**<0.001**
Site(Reefline)	9	0.28	1.85	0.070
Location x Reefline	2	1.86	9.13	**0.005**

Location x Site(Reefline)	9	0.2	1.34	0.222
Res	96	0.15		
Total	119			

b) *Pentapodus vitta*

Source	df	MS	Pseudo-F	P(perm)
Location	1	1.05	4.24	0.068
Reefline	2	8.89	56.63	**0.007**
Site(Reefline)	9	0.16	1.44	0.180
Location x Reefline	2	1.36	5.47	**0.026**
Location x Site(Reefline)	9	0.25	2.27	**0.021**
Res	96	0.11		
Total	119			

c) *Pseudocaranx* spp

Source	df	MS	Pseudo-F	P(perm)
Location	1	8.15	10.44	**0.013**
Reefline	2	4.4	8.19	**0.009**
Site(Reefline)	9	0.54	0.94	0.492
Location x Reefline	2	0.27	0.34	0.720
Location x Site(Reefline)	9	0.78	1.37	0.211
Res	96	0.57		
Total	119			

d) *Pseudolabrus biserialis*

Source	df	MS	Pseudo-F	P(perm)
Location	1	2.03	13.78	**0.005**
Reefline	2	7.48	34.08	**<0.001**
Site(Reefline)	9	0.22	1.62	0.117
Location x Reefline	2	3.17	21.51	**<0.001**
Location x Site(Reefline)	9	0.15	1.08	0.383
Res	96	0.14		
Total	119			

e) *Rhabdosargus sarba*

Source	df	MS	Pseudo-F	P(perm)
Location	1	0.23	0.23	0.648
Reefline	2	3.83	15.29	**0.006**
Site(Reefline)	9	0.25	1.33	0.223
Location x Reefline	2	0.85	0.86	0.458
Location x Site(Reefline)	9	0.99	5.24	**<0.001**
Res	96	0.19		
Total	119			

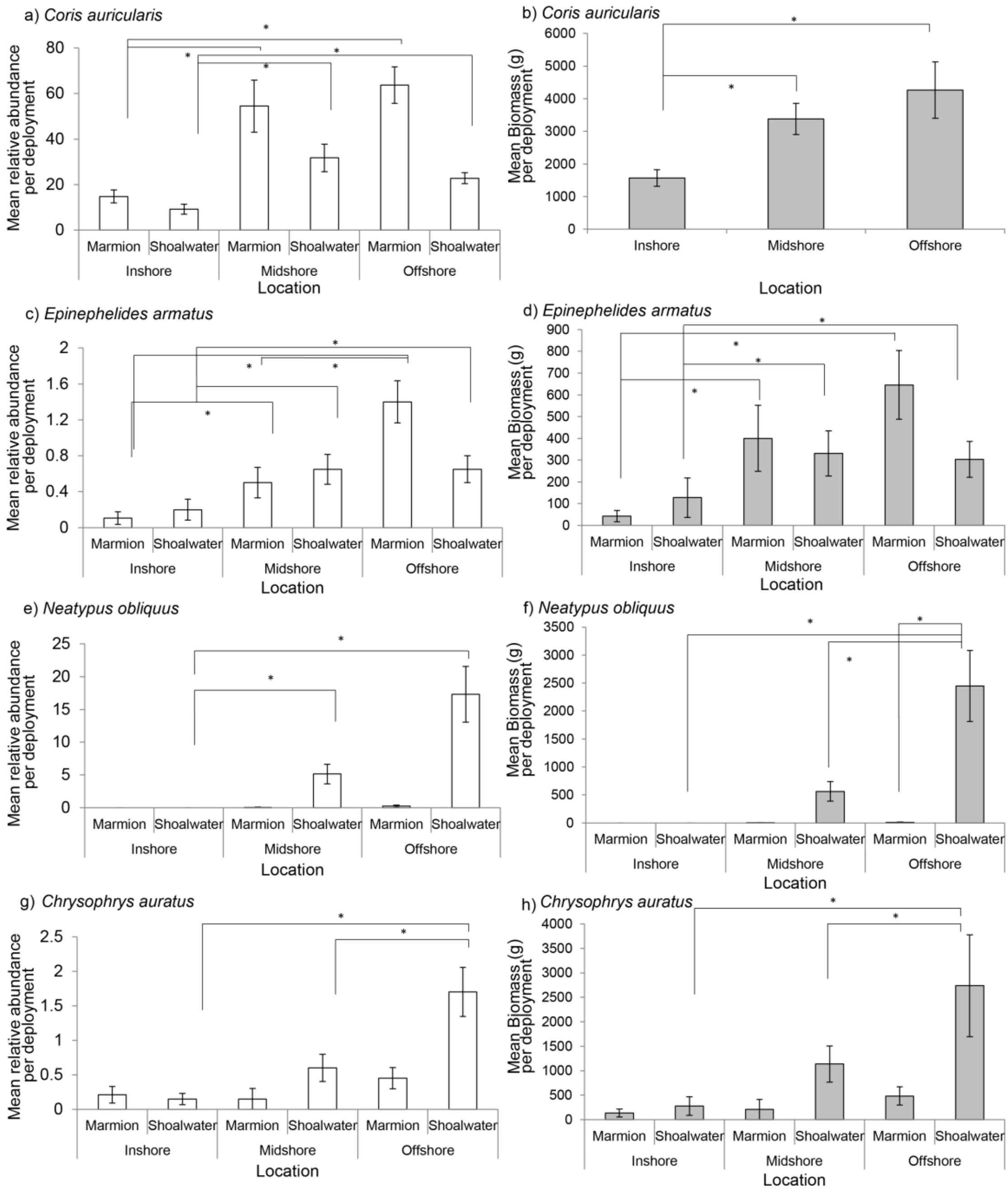

Figure 6. Mean relative abundance and mean total relative biomass (grey) per deployment (± 1SE) of selected species with spearman rank correlations to either PCO axis of greater than 0.4. Significant differences in relative abundance were highlighted using *. Relative abundance and biomass contrasts for significant factors only are displayed.

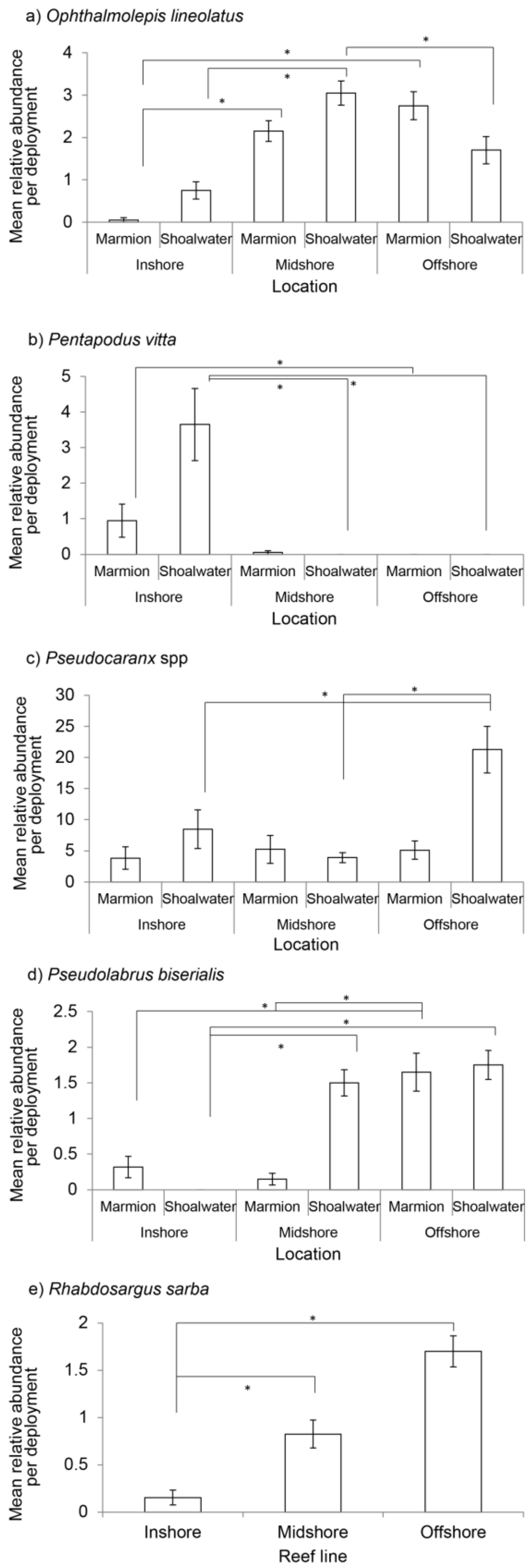

Figure 7. Mean relative abundance of selected species (± 1SE) with spearman rank correlations to either PCO axis of greater than 0.4. Significant differences in relative abundance were highlighted using *. Relative abundance contrasts for significant factors only are displayed.

Some species were significantly more abundant at one location than at the other. The abundance of *C. auricularis* was greater at Marmion than at Shoalwater (Fig.6a). However, the biomass was similar at both locations (Table 3a). This indicates that individuals of this species were generally larger at Shoalwater then they were at Marmion. The species complex *Pseudocaranx* spp, exhibited a contrasting pattern, being more abundant at Shoalwater than at Marmion (Fig. 7c, Table 4c).

A number of species showed a significant interaction between the factors location and reefline (Table 3, Table 4). At Marmion, *E. armatus* increased in both abundance and biomass from inshore to offshore, whereas at Shoalwater both the abundance and biomass of *E. armatus* were similar at midshore and offshore sites (Fig. 6c, Table 3b). *Neatypus obliquus* were abundant offshore at Shoalwater, but were rarely recorded at Marmion (Fig. 6e, Table 3c). *Chrysophrys auratus* were more abundant and had a higher biomass offshore at Shoalwater than at midshore or inshore sites. However, at Marmion the abundance and biomass remained similar across all reeflines (Fig. 6g, Table 3d). At Shoalwater *P. biserialis* were abundant at both midshore and offshore reefs, but at Marmion were only abundant offshore (Fig. 6d, Table 4d).

4. Discussion

There were differences in both the assemblage and trophic structure of reef fish assemblages from the inshore to offshore reefs sampled. The number of species and the relative number of individuals sampled per stereo-BRUVs deployment also increased from inshore to offshore. The variation in species richness and number of individuals across reeflines, separated by only a few kilometres, was greater than the variation at larger spatial scales, i.e. between the two locations which are separated by approximately 70 km. While this pattern was generally similar for both locations, each location had distinct fish assemblages. The offshore and inshore reeflines were significantly different from one another with respect to species richness, relative abundance of individuals and assemblage composition. Likewise, sites within a reefline had similar species richness, and relative abundance of individuals, despite being separated from one another by similar distances to the reeflines (kilometre scale). While we expected differences in the assemblage structure between the inshore and offshore reefs given that there was approximately 11-20 m difference in depths, the difference in fish assemblage structure between inshore and midshore and midshore and offshore reefs was unexpected given there was only 6-11 metres difference between them.

The more homogeneous assemblages in this study were associated with sites further offshore, which is in contrast to (Brokovich et al. 2006) who found more heterogeneous assemblages in deeper regions, albeit at sites much further offshore (i.e. up to 60m depth). These differences might be related to the proximity of a greater variety of habitat types at inshore reefs, or that the inshore sites encompassed a range of environmental gradients (e.g. exposure to wave energy). The differences in the reef fish assemblages between the two locations could be the result of large-scale physical processes. For example during the summer and autumn months a seasonal current called the Capes current flows northwards along the inshore waters of the South West of Australia (Pearce and Pattiaratchi, 1999).

Changes in the abundance and biomass of dominant fish species suggest pronounced changes in the composition of some trophic groups across reeflines. For example, there was an increase of invertivore species across the inshore to offshore gradient (e.g. *C. auricularis*, *C. auratus*, *P. biserialis* and *R. sarba*), which may be associated with increased food availability at greater depths. Bell (1983) found similar patterns in relative abundance across depth ranges, and suggested that ultimately trophic status and biology determine species presence at different depths. Some studies have also shown that the concentration of planktivores increased with depth (Friedlander and Parrish, 1998; Friedlander et al., 2010). The data from this study in part reflects this pattern, with an increasing abundance of planktivores (driven by *N. obliquus*) at Shoalwater, but not Marmion.

The general increase in relative abundance and biomass of the iconic carnivorous species *C. auratus* and *E. armatus* across reeflines may be due to the synergistic effects of fishing, life history and resource availability (plankton and invertivore guilds) in offshore areas. The relative abundance and biomass of *C. auratus* was lower and more similar across reeflines in Marmion compared to Shoalwater, where it was more abundant offshore. Sumner (2008) observed a gradient in activity of recreational fishers, with a greater number of fishing trips in the central and southern areas of the Perth metropolitan region (corresponding to the Shoalwater location), compared to the north and greater recreational fishing activity within the shallow and near shore areas (Sumner 2008). Moreover, Wakefield (2010) reported that *C. auratus* populations exhibit a variable distribution across the coastline of Western Australia correlated to spawning season (Wakefield 2010). However, spawning for this species is in summer and not in autumn, when this study was conducted. From a biological perspective, it is difficult to explain the variation in *C. auratus* over a distance of 70 km. Historically, the Marmion area has received more fishing pressure than the area around Shoalwater which may account for some of the differences seen in targeted species.

Depth (correlated to reeflines in this study) is a key factor affecting the structure of reef fish assemblages (Charton et al., 2000; Friedlander et al., 2003; Anderson and Millar, 2004; Friedlander et al., 2007; Moore et al. 2009, 2011; Gårdmark et al., 2011; Fitzpatrick et al. 2012; Harvey et al. 2013.). This study found that species assemblage composition differed across relatively small spatial scales between reeflines. Similar patterns of increasing species richness, and relative number of individuals with depth in the littoral zone were obtained by Friedlander et al. (2010).

Habitat complexity plays a key role in shaping fish assemblages (Grigg, 1994; Brokovich et al., 2006). Habitats that are structurally more complex have been associated with a greater relative abundance of fish and more heterogeneous fish assemblages (Luckhurst and Luckhurst, 1978; Harman et al., 2003; Friedlander et al., 2007). Chatfield et al. (2010) found that substrate type was the most influential variable structuring temperate fish assemblages, with strong species-specific habitat associations evident. Habitat type in this study was standardised by targeting macroalgal dominated rugose reef. The DistLM analysis suggests that any variation in habitat was less influential than the effects of distance from shore or depth. However, variation in habitat should be considered in marine spatial planning.

Habitat variability, even across small gradients of environmental variation and linked areas of specific importance (e.g. nursery and spawning areas), are also a consideration in marine spatial planning (Curley et al., 2003; McNeill, 1994). Clearly, species specific differences in relative abundance between reeflines correlate with the physical environmental characteristics of an area and the physical capabilities of the fish inhabiting it (Bellwood and Wainwright, 2001). It is important to understand the relationship between habitats and fish assemblage composition, in particular for consideration in marine spatial planning processes, as habitat degradation is a primary cause for biodiversity declines.

Understanding the factors and spatial variation that affect fish assemblages across inshore to offshore reef gradients has important management implications, in particular in relation to marine spatial planning. Both the Marmion and Shoalwater Marine Parks do not incorporate the significant changes in reef fish biodiversity that occur with depth across the continental shelf over fairly small distances and depths. Similarly, when monitoring the outcomes of marine spatial planning within a habitat type or at the same geographical location, it is important to stratify sampling to consider depth, habitat and distance from shore. If sampling is not stratified the variation with depth and distance from shore may overwhelm any variation due to the factors under investigation. This study clearly demonstrates that there is significant variation between reeflines over even relatively small depth ranges.

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