

Demersal fish assemblages of South Passage and Blind Strait, Western Australia: a unique subtropical embayment in a World Heritage Property



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Jock McRae Clough BE

School of Plant Biology, The University of Western Australia, 35 Stirling Highway, Crawley, Western Australia 6009, Australia

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Supervisors: Professor Jessica Meeuwig and Professor Euan Harvey

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ABSTRACT: In 2009 a comprehensive and quantitative fish survey was undertaken to assess the distribution and composition of the demersal fish assemblages at South Passage and Blind Strait, Shark Bay, Western Australia. This is an ecologically rich region and forms part of the World Heritage Property of Shark Bay. Two hundred and ninety seven baited remote underwater stereo-video samples were collected over a study area of 160 km². Two hundred and thirty five species from 62 families of fish were recorded. Samples were categorized by their dominant habitat and zone: oceanic, embayment, and transition. Benthic habitat had the greatest influence on the fish assemblage and explained 17.4% of the variation, with zone and depth explaining 4.6% and 1.4% respectively. Environmental variables – temperature, salinity, dissolved oxygen and visibility – combined, explained less than 1.5% of variation in these assemblages. Species richness in the oceanic zone was more than twice that of the embayment zone with reef habitats supporting double and triple the species richness of seagrass and sand habitats respectively. Within reefs, those with at least 10% living coral had 50% greater species richness and 42% greater total abundance than limestone reefs while higher profile reefs (i.e. >0.5m from seabed) had 59% greater species richness than lower profile reefs, with no affect on abundance. A qualitative comparison of this survey with a 1979 visual survey indicated that some recreationally-targeted fish species such as *Choerodon rubescens* and *Lethrinus nebulosus* are now much less abundant. This survey provides confirmation of the diversity of fish assemblage within this World Heritage Property and is the first quantitative baseline for monitoring the region, taking into account the influence of habitat on the fish assemblage.

KEY WORDS: Demersal fish • Assemblage structure • Species richness • Mean total abundance • Stereo-BRUVs • World Heritage Property • Shark Bay • Western Australia

Introduction

Shark Bay is a large, shallow sub-tropical embayment which occupies an area of approximately 20,000 km² on the mid-west coast of Western Australia. In 1991 it was inscribed on the World Heritage List for its 'outstanding natural universal values'. For the marine environment some of these included: its unique hydrological structure, banks and sills, salinity gradients, high genetic biodiversity, seagrass meadows and abundance of megafauna (dugongs, whales, dolphins, turtles, sharks and rays) and its high species diversity (e.g. 323 fish, 218 bivalves and 80 coral species) and its location as the northern

limit of transition between temperate and tropical environments (Department of Environment and Conservation, www.sharkbay.org). This location's unique marine ecosystem has also been recognized by the Government of Western Australia by its designation of 70% of Shark Bay as a marine park in 1990. Shark Bay hosts the greatest diversity and largest area of seagrass meadows in the world (Walker et al. 1988, Walker 1990) and is considered to be one of the world's most pristine seagrass systems (Heithaus 2007). These extensive seagrass meadows provide a significant carbon sink and the region is important for commercial and recreational fishing and other recreational tourism (McClusky 2008). Shark Bay contributes to the ecological value of the marine system (Costanza 1997) providing important marine refugia. These include: a protected embayment for migrating cetaceans, a large turtle population and an internationally significant resident dugong population (Preen et al. 1997). Effective management of such a unique area requires a sound knowledge of the marine ecosystem and the impact of natural or human-caused disturbances (Preen et al. 1997, Chabanet et al. 2010).

Much of Shark Bay's marine ecosystem remains enclosed within two large gulfs and is relatively protected, however the exposed oceanic coastline is subject to substantial swell. Openings along this coastline also introduce significant marine environmental influences, including the impact of the Leeuwin Current, to Shark Bay's protected Eastern and Western Gulfs (Hutchins 1990, Cresswell 1991, Watson & Harvey 2009). This occurs from the north via the large opening between the mainland and the north end of Dirk Hartog Island and also at South Passage which forms a relatively narrow but important opening between the mainland and the southern end of Dirk Hartog Island. Most previous fish studies on Shark Bay have focused on fauna within the Eastern and Western Gulfs (Lenanton 1977, Black 1990, Linke et al. 2001, Travers & Potter 2002, White & Potter 2004, Wakefield et al. 2007, Wirsing et al. 2006, Heithaus 2001, et al. 2002, 2007, Jackson et al. 2005, 2007, 2010, Mitchell et al. 2007, Vaudo & Heithaus 2009). Only two previous studies (Hutchins 1990, Fairclough et al. 2008) specifically included the fish assemblage at South Passage and the embayment immediately to the east, Blind Strait. These studies indicated this particular area was more ecologically complex and diverse than the broader gulfs of Shark Bay, but neither study developed a quantitative and comprehensive baseline of the fish assemblage. Such baseline knowledge is important because it allows detection of change through time, resulting potentially from, for instance, macro-environmental impacts such as increasing sea surface temperature (Carpenter et al. 2008) and ocean acidification (Jokiel et al. 2008) as well as human overexploitation primarily through fishing pressure (Pauly 1995, Hutchings & Baum 2005, Myers & Worm 2005). Solid baseline data and monitoring of minimally-impacted ecosystems such as those found at South Passage – Blind Strait may also become

increasingly important in assessing changes to marine ecosystems as a result of climate change (Knowlton & Jackson 2008, Vroom et al. 2010).

An important component of marine ecosystem management is the understanding of how patterns in fish distribution related to underlying biotic and abiotic variables. Of the biotic variables benthic habitat can often have an important effect on the spatial distribution of fish populations. Previous studies have demonstrated this in coral reefs (Roberts & Ormand 1987, Caley & St. John 1996, Friedlander & Parrish 1998, Jones & Syms 1998, Parrish & Boland 2004, Krajewski & Floeter 2011), temperate reefs (Holbrook et al. 1990, Connell & Jones 1991, Morton & Gladstone 2011) and other habitat types such as kelp (Angel & Ojeda 2001, Anderson & Millar 2004, Pérez-Matus et al. 2007) and seagrass (Jenkins & Wheatley 1998, Travers & Potter 2002). Habitat-related patterns in fish assemblages exhibit significant variability depending on the spatial scale (García-Charton & Pérez-Ruzafa 2001, Anderson & Millar 2004, Jackson et al. 2010, Morton & Gladstone 2011). For example, temperate fish assemblages were examined by Anderson & Millar (2004) in northeastern New Zealand over three spatial scales: tens of meters (transects), hundreds to thousands of meters (sites) and hundreds of kilometers (locations). Variability was highest at the smallest scale (transects) with comparable variability at the larger scales of site to site and location to location.

Abiotic variables (e.g. substratum type, depth, water temperature) may also be important in the determination of fish distribution (Heithaus 2001, Jaureguizar et al. 2004, Jackson et al. 2010, Krajewski & Floeter 2011, Bosman et al. 2011). Further, complexity and size of reef substructure can also influence species richness and abundance (Ebeling et al. 1980, Howard 1989, Harman et al. 2003, Watson et al. 2005). For example, Harman et al. (2003) observed a positive correlation of species diversity to the size of the limestone reefs in the temperate waters of Western Australia.

Fishing pressure also impacts assemblage composition with fishers tending to target larger, high-trophic level species which may lead to changes in the composition of the fish community (Pauly et al. 1998 & 2002, Pauly 1995, Stevens et al. 2000, Hutchings & Baum 2005, Mitchell et al. 2007, Watson et al. 2007). Shark Bay has had a long history of commercial fishing and is attracting an increasing level of recreational fishing (McClusky 2008, Jackson et al. 2010). Commercial fishing in the Western Gulf as a whole (Freycinet Estuary, Denham Sound and the South Passage – Blind Strait area) and operating out of the nearest port, Denham, had an average annual catch over the previous decade of $224 \text{ t} \pm 9 \text{ SE}$ (Fletcher & Santoro 2010), comprised primarily of whiting (*Sillago schomburgkii* and *Sillago analis*), mullet (*Mugil cephalus*), tailor (*Pomatomus saltatrix*) and yellowfin bream (*Acanthopagrus latus*). Commercial fishing in the South Passage – Blind Strait area is confined to low level beach seine and mesh net fishing adjacent to the southern shorelines and along the western side of Bellefin Prong and targets almost exclusively *S. schomburgkii*,

S. analis and *M. cephalus*. There has been no commercial shark fishing in Shark Bay since 1994 and sharks are not generally targeted by recreational fishers, but are caught occasionally as bycatch (Heithaus 2001, Dept of Fisheries unpubl data). Recreational fishers, generally in small boats, primarily target baldchin groper (*Choeroden rubescens*), blackspot tuskfish (*Choeroden schoenleinii*), yellowfin whiting (*S. schomburgkii*), grass emperor (*Lethrinus laticaudis*), redthroat emperor (*Lethrinus miniatus*), spangled emperor (*Lethrinus nebulosus*), pink snapper (*Pagrus auratus*), western butterflyfish (*Pentapodus vitta*) and tailor (*P. saltatrix*) (Fletcher & Santoro 2010, Dept of Fisheries unpubl data). Total recreational catch (including charter) for 2007 was approximately 18.5 t. No recreational fish survey was conducted in 2009 but catches were assumed to be similar to those of 2007 (Fletcher & Santoro 2010). Specific commercial and recreational catch records are not available for the South Passage – Blind Strait area.

The only previous multi-species, fisheries-independent assemblage survey of South Passage was undertaken in April 1979 (Hutchins 1990). This qualitative survey, using multiple sampling methods, recorded 323 species, predominantly tropical, and provided a subjective graded estimate of relative fish abundance.

The current study is the first comprehensive and quantitative baseline fish survey of the most diverse and ecologically complex part of Shark Bay: the ecosystem of South Passage – Blind Strait. The main goal is to describe species diversity, relative abundance and assemblage composition, identifying patterns in these with the underlying ecosystem structure. Specifically I test the hypothesis that there were significant differences in species richness, total abundance and assemblage: (i) among the four dominant benthic habitats (ii) among three zones (iii) between stations with substratum represented by high reef profile versus relatively low reef profile and (iv) between coral reef and limestone reef. I also assess the degree to which the abiotic variables of depth, temperature, distance from ocean, salinity, dissolved oxygen and visibility influence the assemblage. A highly qualitative comparison is also made between the results of this and the 1979 survey.

Methods

Study site. The study focused on South Passage and Blind Strait in the south-western area of Shark Bay (Fig. 1). This 160 km² study area is situated between the south and south east end of Dirk Hartog Island and the mainland and is part of the Shark Bay World Heritage Property. The width of the study area varied from 1.5 km at its narrowest point, adjacent to Cape Ransonnet, to 10 km at its widest point at Cape Bellefin. The entrance to South Passage is about 2.8 km wide and provides the only access point to the sheltered embayment along a 280 km cliff coastline. The study area was mostly shallow (3 – 4 m) with

the deepest sections at the western entrance at about 30 m. The entrance has a rocky bar which extends from Steep Point, on the mainland, to Surf Point on Dirk Hartog Island. A small no-take sanctuary area of approximate areal size 1.7 km² is located to the east of Surf Point (Department of Environment and Conservation, www.dec.wa.gov.au). During spring tide periods, with a tidal range of 1.2m, the entrance becomes turbulent. The proximity to the ocean and the Leeuwin Current both warm and moderate the water temperature fluctuations within the passage relative to those experienced in the eastern gulfs of Shark Bay (Cresswell 1991, Heithaus 2001) with mean water temperature at Surf Point varying from 21.1 °C for the coolest period (October) to 24.3 °C in the warmest period (April) (Department of Fisheries 2009). This compares with the Eastern and Western Gulfs where the mean water temperature, adjacent to Peron Peninsular, ranges from 18.5 °C – 20 °C in the coolest period to 27 °C – 28 °C in the warmest period (Travers & Potter 2002). The benthic habitat is dominated by topographically complex limestone reefs, upon which corals recruit and grow in some locations, as well as large areas of seagrass meadows and unvegetated sand. Hard corals, primarily from the families Acroporidae and Pocilloporidae, are predominantly found at the western parts of South Passage with some soft coral (Alcyoniidae) located to the east of Surf Point (Bancroft 2009). Macroalgae is primarily from family Phaeophyta (primarily *Sargassum* spp.) and limestone reef pavements, particularly in the western area, typically had a cover of turf algae (Hutchins 1990, Bancroft 2009). The most dense and prevalent seagrasses are *Posidonia australis* and *Amphibolis antarctica* (Walker et al. 1988) which are generally found in conjunction with unvegetated sand.

The study area was partitioned into three zones based on the relative influence of the ocean, degree of shelter, and benthic habitats (Fig. 1). The oceanic zone, located at the west of the survey area and at the entrance to South Passage, was characterized by: persistent swell, greater influence of the Leeuwin Current, a mostly reef habitat in relatively deep water and the zone's comparative inaccessibility to smaller recreational boat fishers. The embayment zone comprised the marine area to the east of Cape Ransonnet at the most southerly point of Dirk Hartog Island. This zone was the largest of the three and encompassed relatively sheltered and shallow waters dominated by seagrass meadows and sand substrate. A transitional zone was identified between the oceanic and embayment zones as an intermediate area presenting a combination of characteristics found within the other zones. The transitional zone benthos was characterized by limestone and coral reefs in its northern area and mostly sand in the southern part. The sanctuary area was sampled, but not specifically analyzed as substantial differences in benthic habitat, within and adjoining this area, would likely distort comparisons of fish fauna inside and outside the sanctuary.

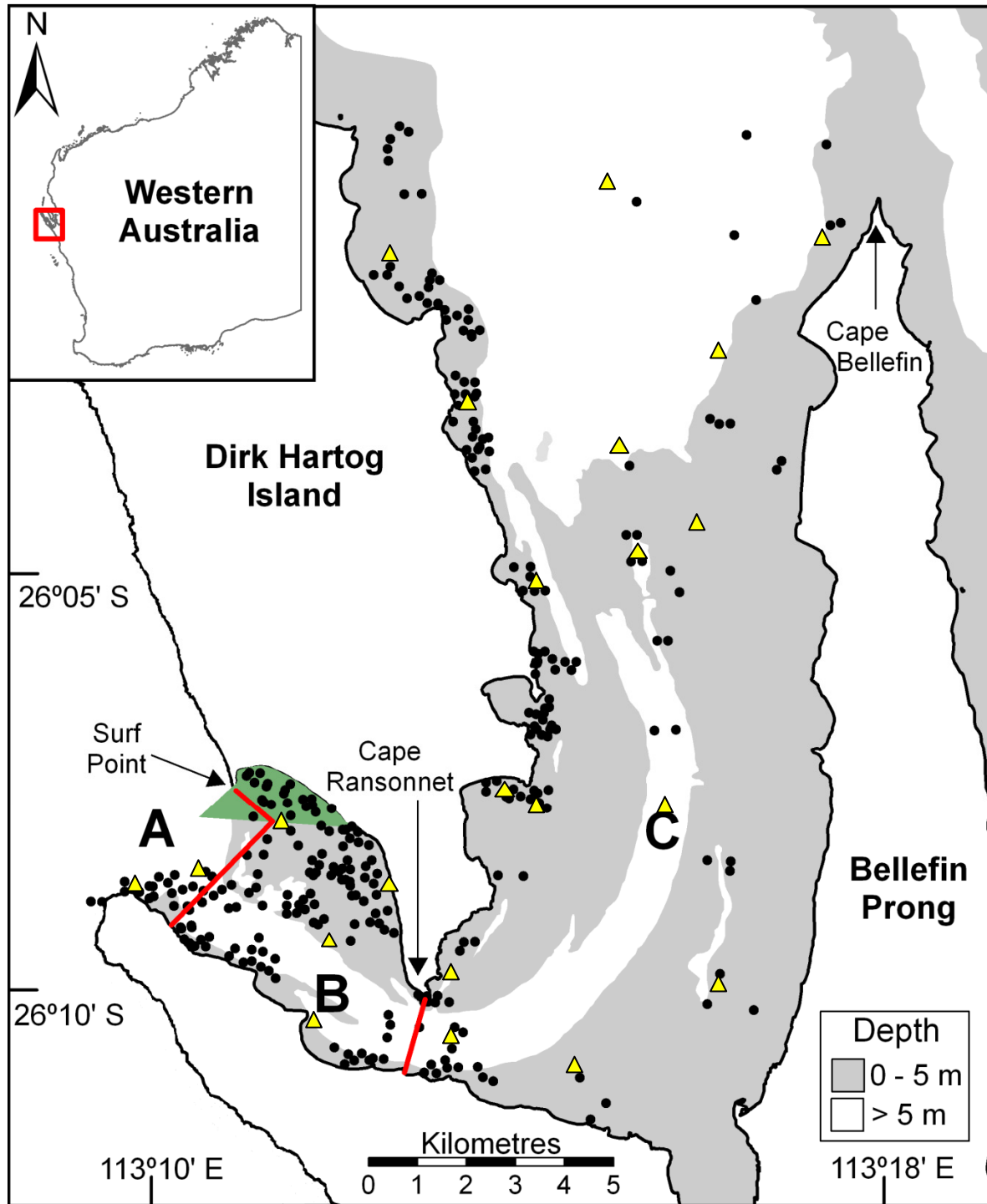


Fig. 1. South Passage and Blind Strait, Shark Bay, Western Australia. Stereo-BRUV deployment stations are shown as black dots. The three zones (A = oceanic, B = transitional, C = embayment) are partitioned by red lines. CTD sampling stations are shown as yellow triangles. The no-take sanctuary area, adjacent to Surf Point, is marked in green.

Sampling methods and design. The survey was carried out over seven days from 16th – 22nd September using baited remote underwater stereo-video systems (stereo-BRUVs). This method was chosen as it enabled a relatively rapid, quantitative and safe approach to sampling a large number of stations. Details of relative accuracy compared to other sampling

approaches as well as design and use can be found in the literature (Willis & Babcock 2000, Harvey et al. 2002, Cappo et al. 2003, 2004, Harvey et al. 2004, 2007, Watson et al. 2005, 2010, Langlois et al. 2010).

Sampling stations were selected to ensure all habitat types and depth ranges in each zone were comprehensively sampled with adjoining deployments being at least 200 m distant to ensure the bait plume did not result in the same fish being observed at neighboring stations and recorded more than once. The bait was approximately 1 kg of Australian pilchard (*Sardinops sagax*) and the stereo-BRUVs were deployed for a minimum of 60 minutes per station.

Laboratory image analysis commenced from when the stereo-BRUVs settled on the seabed for 60 minutes. Raw video footage (MT2S format) was converted to de-interlaced AVI (Xvid codec) video files using Xilisoft video converter (www.xilisoft.com) prior to calibration and image analysis. The program EventMeasure (Stereo) version 3.14 (<http://www.seagis.com.au/event.html>) enabled data collected from the field operations and video to be managed, the timing of events to be recorded, and reference images of the sea floor and fish in the field of view to be captured (Langlois et al. 2010). For a detailed description of calibration and measurement procedures see, Harvey and Shortis (1995,1998). The maximum number of each species observed at any one time (MaxN) for the whole video duration provided a conservative estimate of the abundance of each species at each station, standardized to within 7 m of the camera (Cappo et al. 2003, Harvey et al. 2007).

Video analysis also formed the basis for the categorization of the benthic habitat with the percentage cover of different habitat types visually estimated from freeze-framed video images for each station (Watson et al. 2007). A still image was captured from each video. Each image was then classified as being dominated by one of eleven different habitat categorizations: sand, seagrass, limestone reef (which had 6 different sub-categories), algae, rubble and sessile invertebrates (see classification in Radford et al. 2008). Reef had three relief profiles categorized: low (0 m – 0.5 m from the seabed), medium (0.5 m – 1.5 m) and high (1.5 m +). Each of these three profiles were further categorized by biota: having either turf algae or, where the live coral cover was estimated as being greater than 10%, coral. The purpose of this greater level of categorization within reef habitat was to enable species abundance and richness comparisons for different reef profiles and biota. The category algae designated macroalgae habitat (primarily *Sargassum* spp.), whether this was attached to the substratum or unattached. Loose and broken limestone reef or coral fragments which were not capable of forming a substrate for either algae or coral were termed rubble habitat and sessile invertebrates referred specifically to sponge habitat.

Environmental variables. Two sets of temperature, salinity and dissolved oxygen measurements, with 24 – 36 hours between each set, using a conductivity, temperature and depth (CTD) analyzer ('Seabird' - model 19+), were taken adjacent to the seabed. These were recorded at 22 locations throughout the study area, with three replications (at approximately 200 m separation) per location (Fig. 1). The first measurement set was recorded on 19th September and the second measurement set was recorded on the 20th and the morning of the 21st September.

Each stereo-BRUVs sample station was allocated a value for mean temperature, mean dissolved oxygen and mean salinity measurement associated with the closest of the CTD locations to that station's position. Other variables recorded at each station included depth, visibility and distance of the station from the oceanic entrance to South Passage. Depth was recorded from the deploying vessel's depth finder (Garmin). Visibility was estimated during the laboratory video analysis as a multiple of the 1.2 m bait suspension rod located immediately in front of the two stereo cameras. The distance from entrance (hereafter termed 'distance') was calculated as the distance of each station from a 1.6 km arc with centre at point 26° 7' 45" S and 113° 10' 00" E. This point lay about 1.6 km to the north of Steep Point and 1.6 km to the west of Surf Point. The arc marked the approximate position of the rocky bar that extends, in a curve, from Steep Point to Surf Point. Stations lying to the west of this arc (i.e. those in the oceanic zone) were considered to have a nil distance.

Statistical analysis. The statistical design consisted of two categorical variables: zone (three levels, fixed: oceanic, transitional and embayment) and dominant habitat (four levels, fixed: reef, seagrass, sand and algae) with a number of environmental variables considered as covariates. As species abundances were both skewed and contained many zero counts, a permutational, distance-based analysis of variance of the multivariate data was employed (PERMANOVA) (Anderson 2001) utilizing the Primer-E statistical package (Anderson et al. 2008). All multivariate analyses were conducted using the Bray-Curtis dissimilarity matrix on square root transformed relative abundance data. The six environmental variables (distance, depth, mean temperature, mean salinity, mean dissolved oxygen and visibility) were included as covariates in the PERMANOVA multivariate analysis. The skewness evident in the draftsman plots of the environmental variable assemblage matrix was reduced through a normalized, square-root transformation of temperature, dissolved oxygen, salinity, visibility and distance and a fourth-root transformation of depth (Clarke & Gorley 2006). Correlations among a number of environmental variables existed suggesting multi-collinearity. To this end, the number of environmental variables was reduced to minimize collinearity and maximize the variance explained in assemblage composition. The contribution to variance of environmental variables and the two categorical variables (dominant habitat and zone) in assemblage composition was examined using the distance based linear modeling routine

(DistLM) (Anderson et al. 2008). In the DistLM treatment the environmental variables were considered individually and the different levels of the two categorical variables were expanded into a binary form and each treated as a set: dominant habitat and zone. A canonical analysis of principal coordinates (CAP) (Anderson & Willis 2003) was used to examine whether discrimination of assemblages was evident for dominant habitat and zone. Species most correlated with the observed differences were ranked using Spearman rank correlations with an arbitrary vector cut-off >0.6 for dominant habitat and >0.5 for zone (Anderson et al. 2008). The similarities percentages routine (SIMPER) (Clarke & Gorley 2006) was conducted using Bray-Curtis resemblance of square-root transformed assemblage data to determine species similarities between all pairs of sites within each dominant habitat and each zone and identify the species that most distinguish pairs of sites between dominant habitats and between zones. Due to the fundamental differences in sampling technique of the 1979 and 2009 surveys a comparison between these surveys of relative abundance, in absolute terms, could be misleading. As a consequence comparison between surveys of relative abundance for certain targeted recreational and commercial species used ranked z-scores.

Results

General Overview. In total 15,985 fish were identified, representing 235 species from 62 families. Mean species richness per station was 8.9 ± 0.4 SE and ranged from 1 to 37. The total MaxN per station was 53.8 ± 2.6 SE and ranged from 1 to 246. The most common species observed was the western butterflyfish (*Pentapodus vitta*) which was identified at 84% of the stations. It was also the most abundant fish in the survey (mean MaxN 16.0 fish per station ± 0.8 SE). The next most common species were the silver toadfish (*Lagocephalus sceleratus*), the western king wrasse (*Coris auricularis*) and the bartail goatfish (*Upeneus tragula*) observed at 39%, 36% and 30% of stations respectively. These four species were present in all zones, except for *U. tragula* which was not present in the oceanic zone. A total of 297 stations were sampled with stereo-BRUVs (Table 1 and Fig. 1). Stations were located from the open ocean to a distance of approximately 25 km from the entrance to South Passage. The oceanic zone was the smallest at approximately 3.5 km² and contained 20 stations at a station density of 5.7 per km² followed by the transitional zone at approximately 17 km² with 127 stations and a station density of 7.5 per km². The embayment zone was largest at 140 km², had more than 50% of all stations (150), but had the lowest station density (1.1 per km²). Stations were dominated by the following habitats: sand (40%), seagrass (30%), reef (26%) and algae (4%). Sampling stations often had a variety of different habitats as their benthic cover. The commonness of the habitat types (i.e. the number of stations having at least some cover of a particular habitat expressed as a

percentage of the total) were: sand (54%), seagrass (31%), reef (aggregating all six reef subcategories, 21%), sessile invertebrates (8%) and rubble (7%). Mean habitat cover of sessile invertebrates and rubble at the stations where this habitat occurred were $17\% \pm 2.7\%$ SE and $10\% \pm 2.2\%$ SE respectively. As these two types of habitat were relatively uncommon and when present were not, on average, the most representative habitat these were not considered as separate habitat in this analysis. Each station's dominant habitat was categorized as either reef, seagrass, algae or sand based on which of these habitat types had greatest percentage cover at that station.

Table 1. Summary of survey results and environmental data for zones.

Zones	Oceanic	Transitional	Embayment
Approx area (km ²)	3.5	17	140
Dom. habitat cover (% of total stations):			
Reef (77 stereo-BRUVs stations)	65%	38%	10%
Seagrass (88 stereo-BRUVs stations)	0%	11%	49%
Algae (12 stereo-BRUVs stations)	0%	9%	1%
Sand (120 stereo-BRUVs stations)	35%	42%	40%
Number of stereo-BRUVs stations	20	127	150
Station density (no/km ²)	5.7	7.5	1.1
Environmental variables:			
Mean depth (m)	14.0 \pm 2.0 SE	4.2 \pm 0.2 SE	3.4 \pm 0.2 SE
Minimum - maximum depth (m)	3.0 - 31.0	0.8 - 10.5	0.5 - 14.0
Mean distance from entrance (m)	0	1853 \pm 110 SE	14701 \pm 475 SE
Minimum - maximum distance (m)	0 - 270	86 - 4877	4589 - 25572
Mean salinity (ppt)	35.24 \pm 0.00 SE	35.27 \pm 0.01 SE	35.45 \pm 0.02 SE
Minimum - maximum salinity (ppt)	35.24 - 35.26	35.23 - 35.47	35.25 - 36.38
Mean dissolved oxygen (mg l ⁻¹)	7.42 \pm 0.03 SE	7.14 \pm 0.03 SE	7.41 \pm 0.02 SE
Minimum - maximum diss. oxygen	7.19 - 7.50	6.55 - 7.52	6.58 - 7.65
Mean visibility (m)	5.9 \pm 0.2 SE	5.2 \pm 0.1 SE	4.2 \pm 0.1 SE
Minimum - maximum visibility (m)	4.0 - 7.0	2.0 - 7.0	2.0 - 7.0
Mean temperature (°C)	20.71 \pm 0.05 SE	20.24 \pm 0.03 SE	19.89 \pm 0.05 SE
Minimum - maximum temperature (°C)	19.98 - 20.82	19.77 - 20.82	18.03 - 20.73

Moderated by the marine influence the mean sea temperature was highest in the oceanic zone (20.71 °C \pm 0.05 SE) and lowest in the embayment zone (19.89 °C \pm 0.05 SE). Mean dissolved oxygen was relatively consistent across the study area being: oceanic (7.42 mg l⁻¹ \pm 0.03 SE), transitional (7.14 mg l⁻¹ \pm 0.03 SE) and embayment (7.41 mg l⁻¹ \pm 0.02 SE). Mean salinity was similar in the oceanic (35.24 ppt \pm 0.00 SE) and transitional zones (35.27 ppt \pm 0.01 SE) but, with further distance from the ocean, increased slightly in the embayment zone (35.45 ppt \pm 0.02 SE). Mean visibility declined from the oceanic zone (5.9 m \pm 0.2 SE) to the embayment zone (4.2 m \pm SE 0.1). Across all stations visibility varied between 2 m and 7 m with poorer visibility stations generally associated with localized turbulent conditions generated by surf near shorelines and wave breaks on reefs.

Correlations among environmental and categorical variables. A number of environmental variables were considered as predictors of fish assemblages. As such, we first considered correlations among these variables and a number of correlations were observed (Table 2). Not surprisingly the strongest correlation occurred between distance and zone (oceanic $r = -0.43$, transitional $r = -0.66$, embayment $r = +0.87$). There was also a strong positive correlation between distance and salinity ($r = +0.62$) reflecting the greater salinity of the enclosed embayment the further the distance from oceanic waters (Logan and Cebulski, 1970). Visibility declined with distance from the entrance ($r = -0.55$) and temperature was negatively correlated to distance ($r = -0.45$) and positively to depth ($r = +0.35$). Marginal test analysis using DistLM (Table 3) shows that all the six environmental and the two categorical sets explain a significant proportion of the variability in the fish assemblage, when considered alone (all $P < 0.001$). Sequential tests showed dominant habitat accounted for the greatest amount of variation in assemblage structure at 17.4%, with zone and depth the next most important explaining 4.6% and 1.4% respectively, of adjusted R^2 . The conditional tests on the remaining variables, mean salinity, distance, mean dissolved oxygen, visibility and mean temperature showed that while all, excepting mean temperature, were statistically significant ($P < 0.05$) each explained less than 1% of assemblage variability (on the basis of adjusted R^2). Altogether the 6 environmental variables and 2 categorical variables explained about a quarter (adjusted $R^2 = 0.251$) of the total variability in the fish assemblage. With the correlations and multi-collinearity that existed among a number of variables and the relatively low contribution to assemblage variance from the environmental variables this thesis focused on the two factors that most significantly influenced variance in fish assemblage structure at the study area: zone and dominant habitat. Depth was discussed where this variable had particular relevance.

Species Richness. Species richness varied as a function of both zone ($df = 2$, $MS = 602$, $F = 3.1$, $P = 0.045$) and habitat ($df = 3$, $MS = 5884$, $F = 30.1$, $P < 0.001$) with no significant interaction between zone and habitat ($P = 0.080$) (Table 4a). Depth was not a significant factor in relation to species richness ($P = 0.536$). Pair-wise comparisons showed significant differences in species richness among all three zones with the oceanic zone having nearly twice as many species as the transitional zone which had moderately more species than the embayment zone (Fig. 2, Fig. 3a and Table 4b). The species diversity in the oceanic zone (mean = 16.30 ± 2.48 SE, $n = 20$) was similar to that of the reef habitats notwithstanding 7 of the 20 stations being sited on sand. The species richness declined for the transitional (mean = 9.38 ± 0.71 SE, $n = 127$) and embayment zones (mean = 7.52 ± 0.32 SE, $n = 150$).

Table 2. Fish Assemblage. Pearson correlation coefficients (-1 to +1) for categorical variables (dominant habitat and zone) and environmental variables (distance, depth, mean temperature, mean salinity, mean dissolved oxygen and visibility).

Environmental	Categorical variable (level)	Distance	Depth	Mean temperature.	Mean salinity.	Mean d.o.	Visibility
Distance							
Depth		-0.34					
Mean temp.		-0.45	0.35				
Mean salinity		0.62	-0.12	-0.43			
Mean d.o.		0.30	0.00	0.43	0.24		
Visibility		-0.55	0.15	0.35	-0.42	-0.02	
Dominant habitat							
	Reef	-0.46	0.12	0.31	-0.29	0.00	0.24
	Sand	0.01	0.20	-0.02	0.05	-0.04	0.05
	Seagrass	0.49	-0.34	-0.24	0.26	0.17	-0.27
	Algae	-0.14	0.01	-0.09	-0.10	-0.29	-0.05
Zone							
	Oceanic	-0.43	0.48	0.31	-0.17	0.11	0.26
	Transitional	-0.66	0.05	0.21	-0.39	-0.44	0.31
	Embayment	0.87	-0.29	-0.36	0.47	0.38	-0.43

Table 3. Results of distance-based linear modelling (DistLM) for fitting the environmental variables (distance, depth, mean temperature, mean salinity, mean dissolved oxygen and visibility) and the categorical variables (dominant habitat and zone) for assemblage composition. Selection procedure was step-wise with selection criteria being adjusted R^2 (Anderson et al 2008). Conditional tests associated with each of the environmental variable sequential additions which increased adjusted $R^2 < 1\%$ have been omitted.

Marginal tests				
Group	<i>df</i>	Pseudo- <i>F</i>	P	Prop.
Distance	2	36.5	<0.001	0.110
Depth	2	12.4	<0.001	0.040
Mean temperature	2	11.3	<0.001	0.037
Mean salinity	2	13.8	<0.001	0.045
Mean diss. oxygen	2	4.5	<0.001	0.015
Mean visibility	2	11.4	<0.001	0.037
Dominant habitat	4	21.8	<0.001	0.182
Zone	3	19.2	<0.001	0.116
Sequential tests				
Group	<i>df</i>	Pseudo- <i>F</i>	P	Adjusted R^2
Dominant habitat	4	21.8	<0.001	0.174
Zone	6	9.6	<0.001	0.220
Depth	7	6.5	<0.001	0.234
Mean salinity	8	3.9	<0.001	0.242
Distance	9	2.2	0.006	0.245
Mean diss. oxygen	10	2.0	0.014	0.248
Mean visibility	11	1.8	0.029	0.250
Mean temperature	12	1.6	0.059	0.251

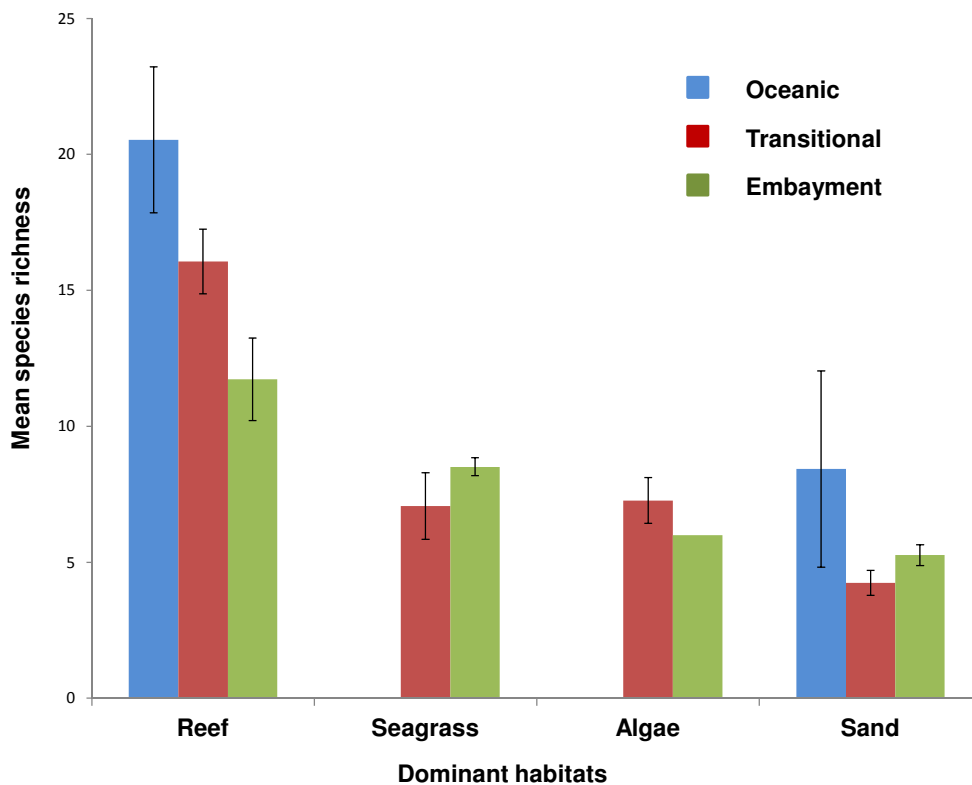


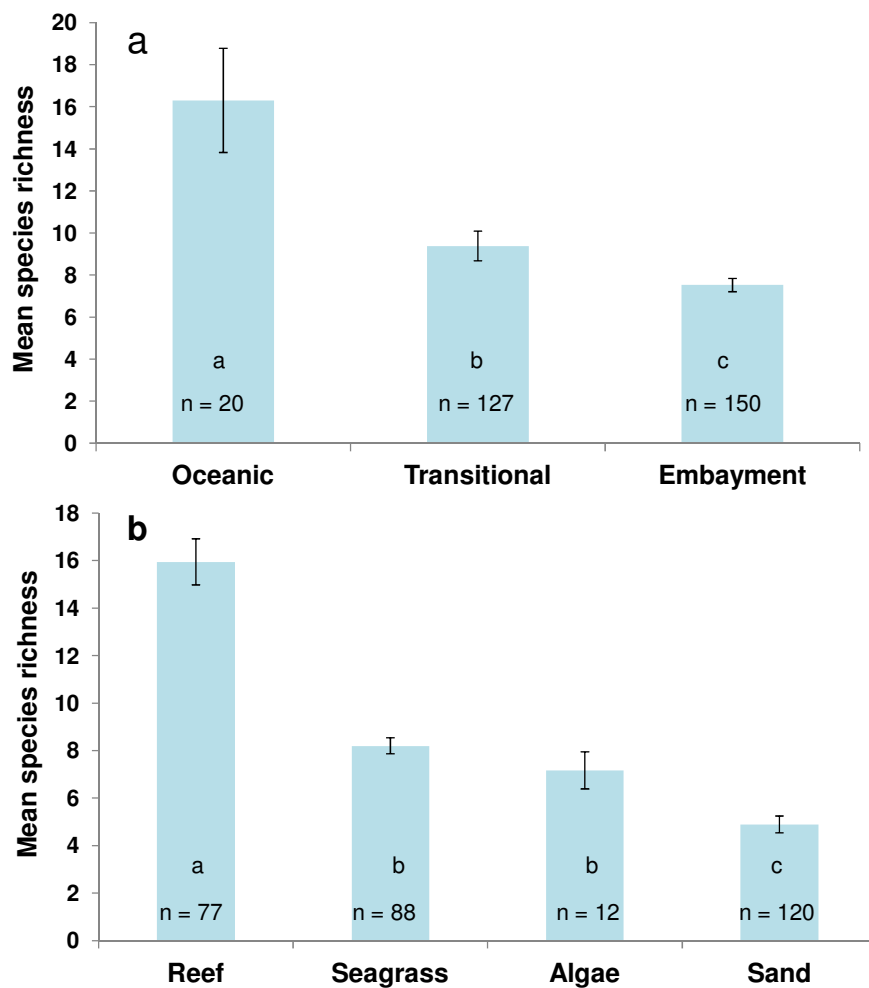
Fig. 2. Mean species richness (\pm SE) within dominant habitat for zone. Note: Insufficient data precludes error bars for Embayment – Algae.

Table 4a. South Passage – Blind Strait: Results of two-factor PERMANOVA analyses examining effects of dominant habitat and zone and their interaction on the mean species richness, mean total abundance and assemblage composition based on Bray-Curtis dissimilarities of square-root transformed relative abundance data for 235 fish species. **Bold values:** $P < 0.05$.

Source	Species richness				Mean total abundance			Assemblage composition		
	<i>df</i>	MS	Pseudo- <i>F</i>	<i>P</i>	MS	Pseudo- <i>F</i>	<i>P</i>	MS	Pseudo- <i>F</i>	<i>P</i>
Dom. Habitat	3	5885	30.1	< 0.001	7089	17.2	< 0.001	21596	10.5	< 0.001
Zone	2	602	3.1	0.045	142	0.3	0.800	19271	9.4	< 0.001
Dom. Hab. x Zone	4	391	2.0	0.080	514	1.2	0.275	7531	3.7	< 0.001
Residual	287	195			413			2059		
Total	296									

Table 4b. South Passage – Blind Strait: Results of pair-wise tests among dominant habitat groups and zone groups on the mean species richness, mean total abundance and assemblage composition for 235 fish species. **Bold values:** P < 0.05

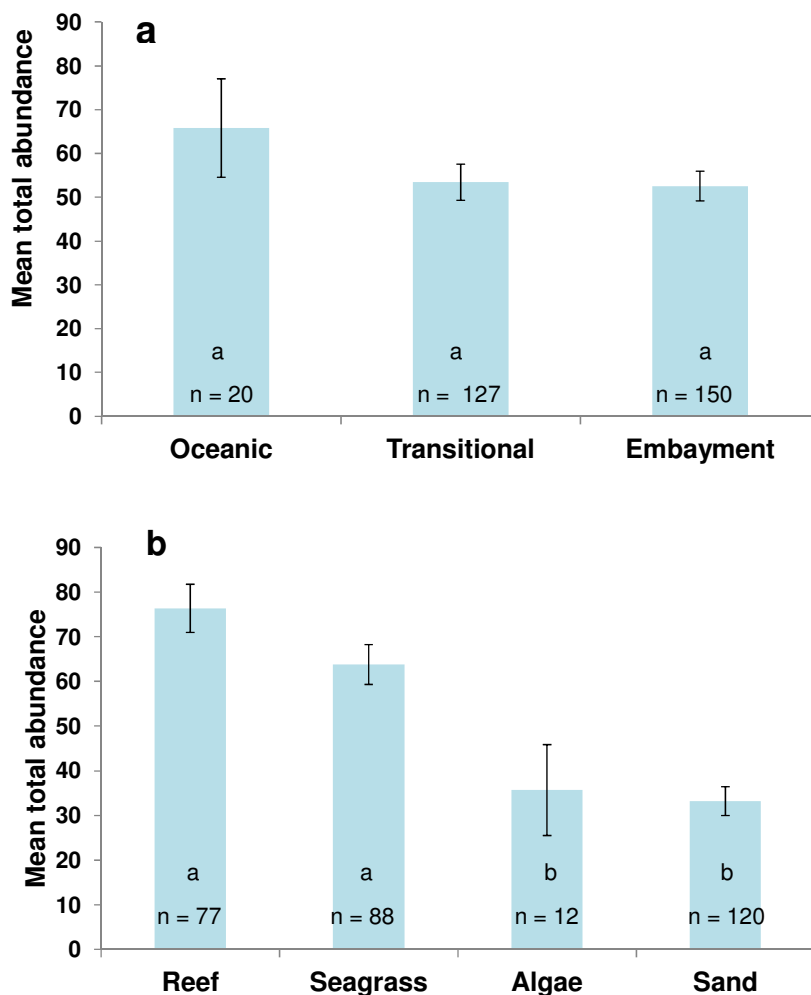
	Species richness		Mean total abundance		Assemblage composition	
	t	P	t	P	t	P
Dominant Habitat Groups						
Reef, Sand	12.0	< 0.001	5.8	< 0.001	4.1	< 0.001
Reef, Algae	3.7	< 0.001	2.1	0.025	1.8	< 0.001
Reef, Seagrass	6.6	< 0.001	1.1	0.275	4.1	< 0.001
Sand, Algae	2.8	0.005	0.4	0.850	2.0	< 0.001
Sand, Seagrass	7.9	< 0.001	4.9	< 0.001	3.2	< 0.001
Algae, Seagrass	1.0	0.343	2.0	0.032	2.3	< 0.001
Zone Groups						
Transitional, Oceanic	1.9	0.043	0.5	0.784	2.6	< 0.001
Transitional, Embayment	2.7	0.005	0.5	0.727	3.3	< 0.001
Oceanic, Embayment	2.7	0.005	1.0	0.350	3.0	< 0.001



Figs. 3a and 3b. Mean species richness (± SE) by (a) zone and (b) dominant habitat. Letters indicate significant differences between means at P < 0.05 and the number of stations (n) is indicated for each zone and habitat.

Pair-wise comparisons for dominant habitat showed significant differences in species richness across all habitats ($P < 0.05$) except between the algae and seagrass habitat ($P = 0.343$) (Fig. 3b and Table 4b). The reef stations (mean = 15.9 ± 1.0 SE, $n = 77$) displayed almost double the species diversity of seagrass (mean = 8.2 ± 0.3 SE, $n = 88$) and algae (mean = 7.2 ± 0.8 SE, $n = 12$) with the least speciose stations on sand (mean = 4.9 ± 0.4 SE, $n = 120$).

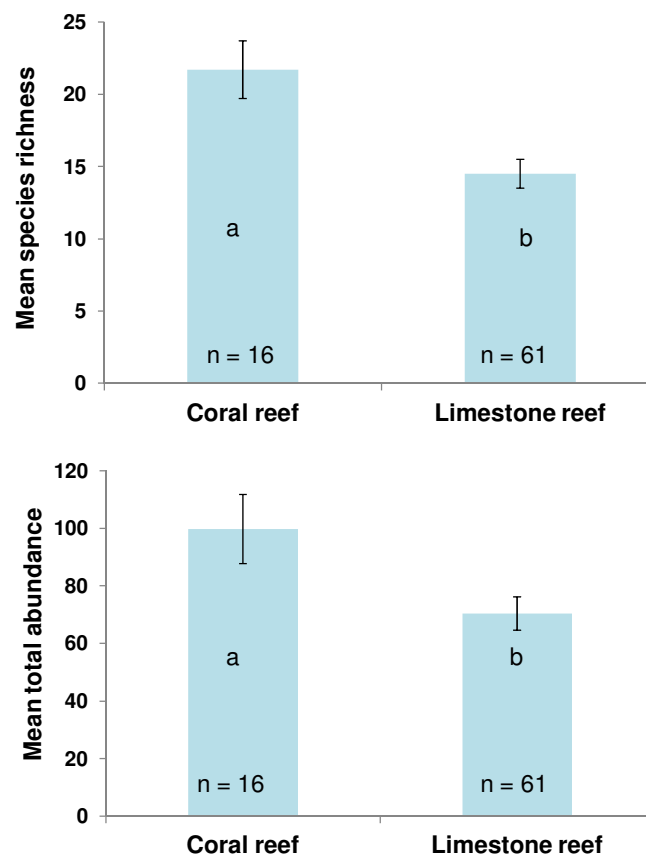
Relative Abundance. Mean total relative abundance did not vary significantly with zone ($P = 0.800$) (Fig. 4a), but varied significantly for dominant habitat ($df = 3$, $MS = 11821$, $F = 29.5$, $P < 0.001$) (Table 4a). Depth was significant ($P = 0.005$) and there was a significant interaction between dominant habitat and depth ($P = 0.038$). Pair-wise comparisons for dominant habitat indicated that abundance differed between reef and sand, sand and seagrass, algae and seagrass and reef and algae (all $P < 0.05$) (Table 4b). There was however no significant difference in abundance between reef and seagrass ($P = 0.275$) and



Figs. 4a and 4b. Mean total abundance (\pm SE) by (a) zone and (b) dominant habitat. Letters indicate significant differences between means at $P < 0.05$ and the number of stations (n) is indicated for each zone and habitat.

between sand and algal habitats ($P = 0.850$). In general, reef (mean = 76.8 ± 5.4 SE, $n = 77$) and seagrass habitats (mean = 64.0 ± 4.4 SE, $n = 88$) had about twice the fish abundance of algal (mean = 35.7 ± 10.2 SE, $n = 12$) and sand habitats (mean = 33.7 ± 3.2 SE, $n = 120$) (Fig. 4b). On reef habitat, *Pentapodus vitta* (33%) and *Coris auricularis* (17%) represented about half of the mean total abundance. The seagrass habitat was dominated by *P. vitta* (55%), and *Pelates sexlineatus* (16%) and the less species-rich sand habitat was on average dominated by *P. vitta* (66%), and *Lagocephalus sceleratus* (17%).

Effect of coral cover and reef relief. Of the 77 stations characterized as reef 16 stations had at least 10% live coral cover on reefs and were termed coral reefs for this study. The remaining 61 stations were classified as limestone reefs. Mean species richness and mean total abundance both varied significantly ($P < 0.001$) between coral and limestone reefs. Mean species richness on coral reefs (mean SR 21.7 ± 2.0 SE) was 50% higher than on limestone reefs (mean SR 14.5 ± 1.0 SE). Mean total abundance (TA) on coral reefs (mean TA 99.7 ± 12.0 SE) was 42% greater than on limestone reefs (mean TA 70.4 ± 5.8 SE) (Fig. 5).

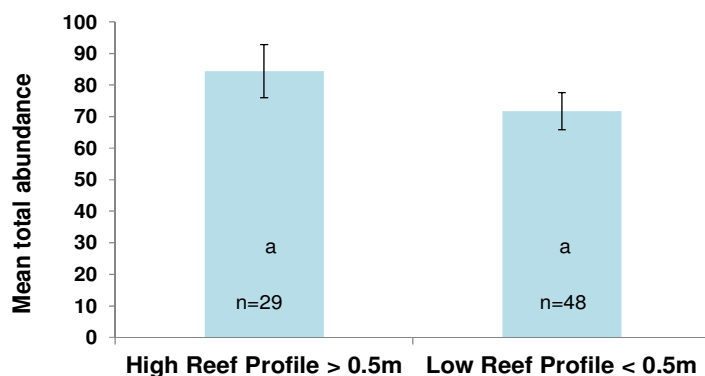
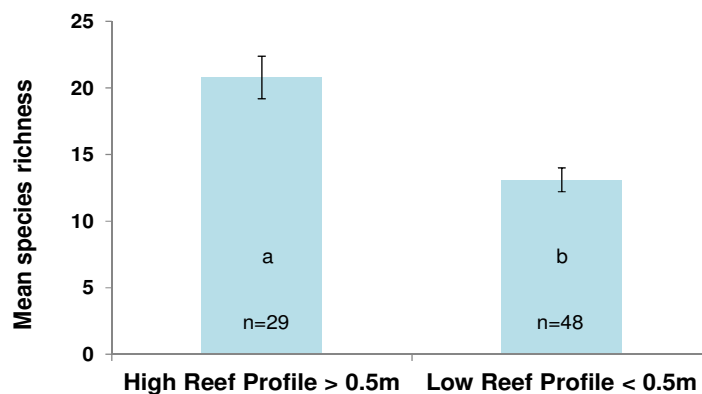


Figs. 5a and 5b. Mean species richness (\pm SE) (a) and mean total abundance (\pm SE) (b) for coral reef (i.e. with at least 10% live coral cover) and limestone reef. Letters indicates significant differences between means at $P < 0.05$ and the number of stations (n) is indicated for each reef type.

To further explore the effect of reef relief on species diversity, 29 of the 77 dominant reef habitat stations were classified as high relief stations where the reef height was greater than 0.5 m from the surrounding seabed and the remaining 48 stations were classified as low relief stations where the height of the reef structure was less than 0.5 m (Table 5). Mean species richness was significantly different between high and low profile reefs ($P < 0.001$) while there was no significant difference in mean total abundance ($P = 0.26$). High profile reefs (mean SR 20.8 ± 1.6 SE) had 59% greater species richness than low profile reef stations (mean SR 13.1 ± 0.9 SE) (Fig. 6).

Table 5. Mean fish species richness and mean total abundance for differing reef profiles. High profile reef >0.5 m. Low profile reef <0.5 m.

	Mean species richness	Mean total abundance	Mean depth (m)
High profile reef	20.8 ± 1.6 SE	84.4 ± 8.4 SE	5.1 ± 0.9 SE
Low profile reef	13.1 ± 0.9 SE	71.7 ± 5.9 SE	5.1 ± 0.6 SE



Figs. 6a and 6b. Mean species richness (\pm SE) (a) and mean total abundance (\pm SE) (b) for high (>0.5 m) and low (<0.5 m) reef profiles for all stations having reef as the dominant habitat (i.e. >50% of benthic habitat as reef). Letters indicate significant differences between means at $P < 0.05$ and the number of stations (n) is indicated for each reef profile type.

Assemblage Composition. Both zone and dominant habitat were significant factors in relation to fish assemblage structure ($P < 0.001$) and there was also significant interaction between and zone and dominant habitat ($P < 0.001$) (Table 4a). The canonical analysis of principal coordinates (CAP) clearly distinguished fish assemblages among the dominant habitats: reef, sand and seagrass (Fig. 7). The first two canonical correlations were reasonably large (CAP: $N = 297$, $m = 30$, $\delta_1 = 0.86$ and $\delta_2 = 0.72$). From these data, the first canonical axis differentiated the fish assemblages between reef and seagrass habitat while the second canonical axis clearly separated the fish assemblage associated with sand from the other two (upper) groups. Allocations between habitat groups was relatively high (78% overall) with a success rate of 75% for reef, 79% for sand and 84% for seagrass, whilst the successful allocation rate for algae was relatively low (42%) (Table 6). While algae were considered the dominant habitat for 12 stations, most of these stations were relatively heterogeneous in terms of habitat: 9 had estimated 10% - 40% sand while 3 had an estimated 30% - 40% reef habitat. This overlap of habitat type may explain some of the misallocations to Algae for the original Reef and Sand groups and misallocation to Reef and Sand for the original Algae habitat group. Using a Spearman rank correlation cutoff of >0.6 showed that nine species (with the largest ordinal ranking) have a strong correlation with either reef or seagrass habitat (Fig. 7). The CAP plot for zone shows evident species assemblage differences (CAP: $N = 297$, $m = 27$, $\delta_1 = 0.82$ and $\delta_2 = 0.67$) (Fig. 8). The first canonical axis shows the clearest assemblage discrimination between the oceanic and transitional zones with the embayment zone. A Spearman rank correlation cutoff of >0.5 showed nine species with largest ordinal ranking being correlated with the transitional and the embayment zones. The clustering of the species associated with the transitional zone is not as tight as those species associated with either the embayment zone (which is primarily a seagrass habitat) or the seagrass and reef habitat of Fig. 7. This appears to reflect the strong habitat focus and specialty of these species. The cross validation for the CAP analysis among the three zones shows similar high allocation success to that of habitat with an overall success rate of 84% and successful allocations of 85%, 80%, and 87% in the oceanic, transition and embayment zones respectively (Table 6).

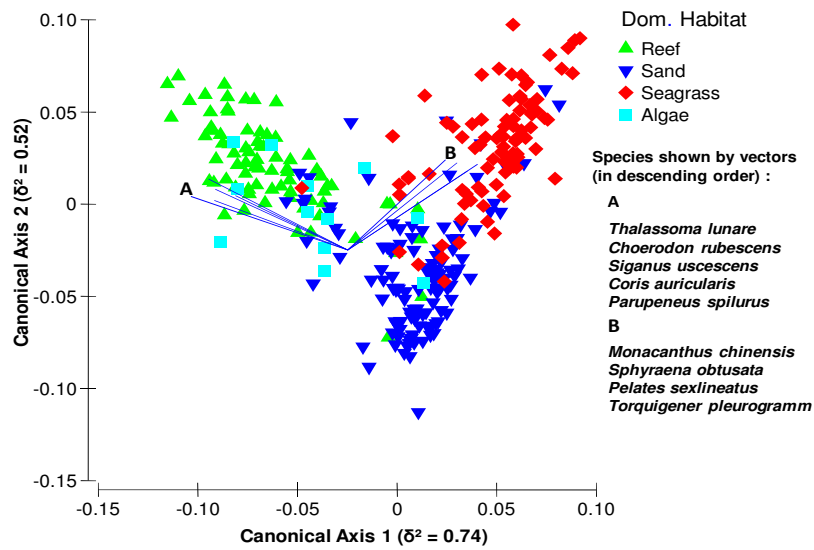


Fig. 7. Canonical analysis of principal coordinates (CAP) ordination of assemblage for dominant habitat. Analysis uses Bray Curtis resemblance (including dummy variable) of the square-root transformed relative abundance of 235 fish species. Spearman rank correlation vectors, using a cut-off >0.6, identify 9 species. These have been grouped as A (positively correlated to the x- axis) and B (negatively correlated to the x – axis). The axes also report squared correlation coefficients (δ^2).

Table 6. Allocation success of replicates to dominant habitat and zone. Note that with four dominant habitat groups and three zones a 25% and 33.3% success rate (respectively) would be expected if results were no better than random.

Dominant habitat	
Reef	58/77 (75%)
Seagrass	74/88 (84%)
Algae	5/12 (42%)
Sand	95/120 (79%)
Total	232/297 (78%)
Zone	
Oceanic	17/20 (85%)
Transitional	101/127 (80%)
Embayment	130/150 (87%)
Total	248/297 (84%)

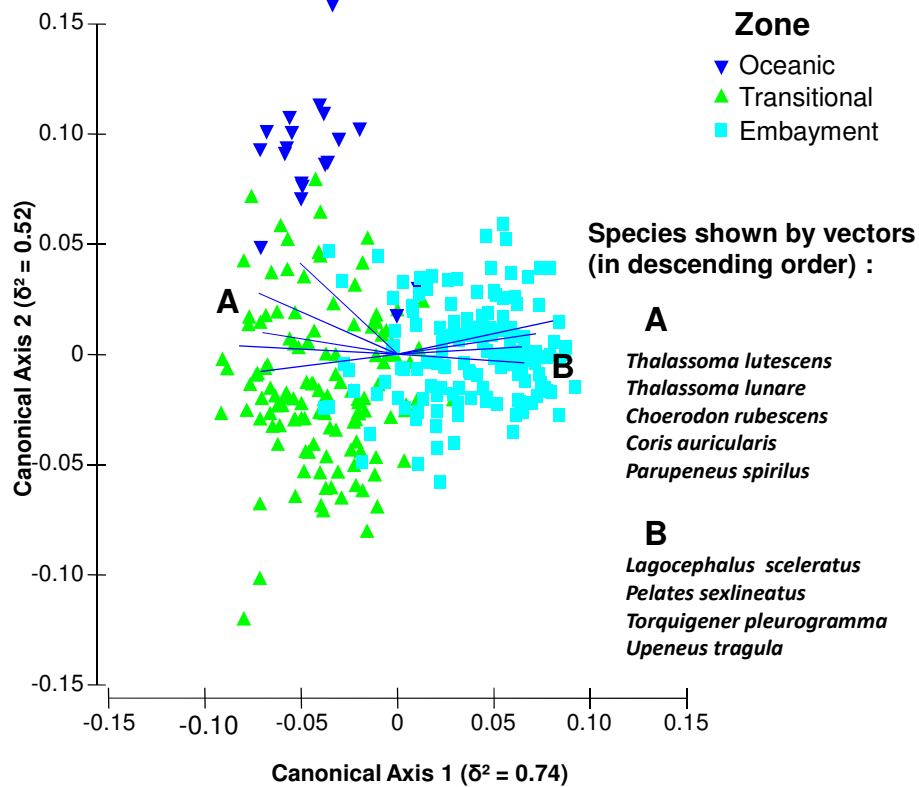


Fig. 8. CAP of assemblages for zone. Spearman rank correlation vectors, using a cut-off >0.5, identify 9 species. The axes also report squared correlation coefficients (δ^2).

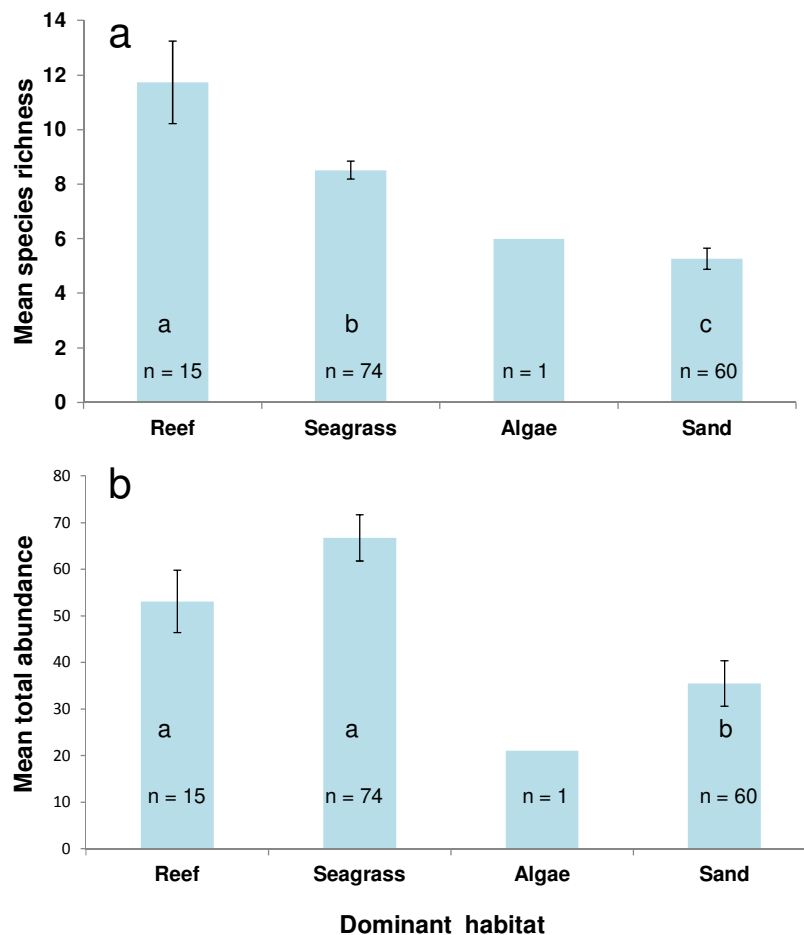
Within zones, average species similarities between all pairs of stations increased with the zone distance from the ocean. Oceanic zone had a relatively low similarity of 18.7, compared to the transitional (24.9) and embayment (30.3) zones (Table 7). *Pentapodus vitta* was the species that contributed most to the similarities between stations within zones – (except the oceanic zone) – and interestingly also had the greatest contribution to the dissimilarity between zones: oceanic-transitional (11% contribution to dissimilarity), oceanic-embayment (10%) and transitional-embayment (12%). The similarities within each dominant habitat were greatest on seagrass (40.3) and lowest on sand (21.1). The species *P. vitta* most typified the three most represented dominant habitats: reef, seagrass and sand. Two species most contributed to distinguishing between stations on different habitats: *Pelates sexlineatus* between algae-seagrass (13% contribution to dissimilarity) and reef-seagrass (9%) and *P. vitta* between algae-reef (10%) and sand-reef (10%).

Tables 7a and 7b. Top four species contributing most (and the cumulative percentage) to typifying the fish assemblage within zones (7a) and within dominant habitats (7b) (shaded) and the species that most distinguish between zones (7a) and between dominant habitats (7b) (non-shaded) using SIMPER (Clarke & Gorley 2006). Average Bray-Curtis similarities (shaded) and dissimilarities (non-shaded) between all pairs of stations are also shown.

7a		Zone					
		Oceanic		Transitional		Embayment	
		Species	Cum.%	Species	Cum.%	Species	Cum.%
Oceanic	Av. Similarity: 18.7						
	<i>Coris auricularis</i>		16				
	<i>Thalassoma lunare</i>		29				
	<i>Kyphosus cornelii</i>		36				
		<i>Pentapodus vitta</i>	44				
Transitional	Av. Dissimilarity: 85.2			Av. Similarity: 24.9			
	<i>Pentapodus vitta</i>		11	<i>Pentapodus vitta</i>	63		
	<i>Coris auricularis</i>		16	<i>Coris auricularis</i>	74		
	<i>Kyphosus cornelii</i>		21	<i>Parupeneus spilurus</i>	79		
		<i>Thalassoma lunare</i>	25	<i>Thalassoma lunare</i>	82		
Embayment	Av. Dissimilarity: 91.1			Av. Dissimilarity: 79.8		Av. Similarity: 30.3	
	<i>Pentapodus vitta</i>		10	<i>Pentapodus vitta</i>	12	<i>Pentapodus vitta</i>	54
	<i>Pelates sexlineatus</i>		16	<i>Pelates sexlineatus</i>	21	<i>Lagocephalus sceleratus</i>	68
	<i>Coris auricularis</i>		20	<i>Coris auricularis</i>	26	<i>Pelates sexlineatus</i>	79
		<i>Kyphosus cornelii</i>	24	<i>Lagocephalus sceleratus</i>	31	<i>Upeneus tragula</i>	85

7b		Dom. Hab.							
		Reef		Seagrass		Algae		Sand	
		Species	Cum.%	Species	Cum.%	Species	Cum.%	Species	Cum.%
Reef	Av. Similarity: 30.5								
	<i>Pentapodus vitta</i>		33						
	<i>Coris auricularis</i>		49						
	<i>Parupeneus spilurus</i>		58						
	<i>Thalassoma lunare</i>		67						
Seagrass	Av. Dissimilarity: 81.2			Av. Similarity: 40.3					
	<i>Pelates sexlineatus</i>		9	<i>Pentapodus vitta</i>	55				
	<i>Coris auricularis</i>		15	<i>Pelates sexlineatus</i>	71				
	<i>Pentapodus vitta</i>		21	<i>Lagocephalus sceleratus</i>	77				
	<i>Thalassoma lunare</i>		25	<i>Upeneus tragula</i>	83				
Algae	Av. Dissimilarity: 74.5			Av. Dissimilarity: 82.6		Av. Similarity: 26.1			
	<i>Pentapodus vitta</i>		10	<i>Pelates sexlineatus</i>	13	<i>Coris auricularis</i>	33		
	<i>Coris auricularis</i>		16	<i>Pentapodus vitta</i>	25	<i>Pentapodus vitta</i>	64		
	<i>Thalassoma lunare</i>		22	<i>Coris auricularis</i>	32	<i>Choerodon rubescens</i>	76		
	<i>Parupeneus spilurus</i>		27	<i>Lagocephalus sceleratus</i>	36	<i>Coris caudimacula</i>	81		
Sand	Av. Dissimilarity: 84.3			Av. Dissimilarity: 75.4		Av. Dissimilarity: 85.1		Av. Similarity: 21.1	
	<i>Pentapodus vitta</i>		10	<i>Pelates sexlineatus</i>	16	<i>Pentapodus vitta</i>	16	<i>Pentapodus vitta</i>	66
	<i>Coris auricularis</i>		17	<i>Pentapodus vitta</i>	30	<i>Coris auricularis</i>	26	<i>Lagocephalus sceleratus</i>	83
	<i>Thalassoma lunare</i>		22	<i>Lagocephalus sceleratus</i>	35	<i>Choerodon rubescens</i>	30	<i>Carangidae spp</i>	87
	<i>Parupeneus spilurus</i>		26	<i>Upeneus tragula</i>	40	<i>Lagocephalus sceleratus</i>	35	<i>Scomberomorus queenslandicus</i>	89

Embayment Zone. The embayment zone was approximately 8 times larger than the transitional zone and 40 times larger than the oceanic zone and contained more than half of the total number of sampled stations. Thus, a separate analysis was undertaken for this zone. Species richness, abundance and assemblage varied significantly among dominant habitats (all $P < 0.001$). Seagrass and sand were the most common dominant habitat. Species richness was greater on seagrass (mean SR = 8.5 ± 0.3 SE, $n = 74$) than on sand (mean SR = 5.3 ± 0.4 SE, $n = 60$) with reef the most speciose habitat (mean SR = 11.7 ± 1.5 SE, $n = 15$) (Fig. 9a). Mean total abundance was almost twice as much on seagrass (mean TA = 66.7 ± 5.0 SE, $n = 74$) than sand habitat (mean TA = 35.5 ± 4.9 SE, $n = 60$) (Fig. 9b).



Figs. 9a and 9b. Mean species richness (\pm SE) (a) and mean total abundance (\pm SE) (b) for dominant habitat within the embayment zone. Letters indicate significant differences between means at $P < 0.05$ and the number of stations (n) is indicated for each dominant habitat type.

The seagrass habitat was found at shallower depths (mean depth seagrass $2.6 \text{ m} \pm 0.2 \text{ SE}$ compared to mean depth sand $4.3 \text{ m} \pm 0.3 \text{ SE}$). Depth was significant ($P = 0.015$) but as there was a significant interaction between depth and habitat ($P = 0.023$) it is difficult to draw any conclusions regarding the effect of depth to variance in embayment assemblage.

Comparison with former fish survey. The sampling methods employed in the 1979 and the 2009 surveys differed. The sampling method for the earlier survey was partly based on the visual census technique described by Wilson & Marsh (1979). This involved diving at 29 different sites and observing, during the course of each dive, the fish species, habitat preferences and their relative abundance in the form of a subjective graded estimate. The remaining 20 sites of this survey were sampled using spear, nets, dredges and rotenone. The sampling concentrated primarily on reef and coral habitat but some seagrass, sand and mangrove locations were also sampled. The differing sampling methods contributed to the large difference of recorded species between surveys. The 1979 survey recorded a greater number of the more furtive or rock or weed-hugging species including cardinal fishes (Apogonidae), blennies (Blenniidae) and gobies (Gobiidae). The stereo-BRUVs survey identified more of the free swimming fish families including surgeonfish (Acanthuridae), brems (Nemipteridae) and pufferfishes (Tetraodontidae). Twenty eight and fifteen families in the 1979 and 2009 surveys (respectively) were identified by one survey and not the other (Table 8).

Relative abundance estimates and ranked z-scores of primary targeted recreational and commercial fish species were compared for the April 1979 and September 2009 surveys for 43 similarly positioned stations (Table 9). The relative abundances were similar for most of these targeted species excepting *Choerodon rubescens* and *Lethrinus nebulosus* which were more common, by rank, in the 1979 survey and *Sillago analis* which was more common, by rank, in the 2009 survey (Fig. 10). *Sillago analis* was unrecorded in the 1979 survey and recorded at only two stations in the 2009 survey with 95% of the recorded abundance at one station. For both surveys *C. rubescens* and *L. nebulosus* were more widespread in 1979, being recorded at 28% and 44% of the 1979 survey stations, respectively and each at 16% of the 2009 survey stations.

Discussion

This baseline survey demonstrated the greatest variation in fish assemblages was at the fine scale or individual station level. At this level, although two stations may not be far apart, each station's unique ecological characteristics and the influence of other environmental factors not incorporated in this study's design contributed, on average, to around 75% of the variance to the fish assemblage structure. The survey demonstrated there was significant

variation in mean species richness, mean total abundance and assemblage as a function of a variety of specific factors including zone, habitat and environmental variables: distance, depth, mean temperature, mean salinity, mean dissolved oxygen and visibility. Of these the most significant factor in determining species diversity, abundance and assemblage composition was the dominant habitat which explained, on average, around 17.4% to the variance in fish assemblages. The relevance of habitat was largely consistent with other studies (Jenkins & Wheatley 1997, Friedlander & Parrish 1998, Travers & Potter 2002, Parrish & Boland 2004, Moreton & Gladstone 2011). Reef habitats, which afford protective refuge from predation as well as offering greater invertebrate, smaller teleost and algal prey,

Table 8. Differences in the number of Family observations between the 1979 survey and the 2009 survey.

Families found in 1979 survey but not in 2009 survey	Common name	Families found in 2009 survey but not in 1979 survey	Common name
<i>Aploactinidae</i>	Velvetfish	<i>Belonidae</i>	Longtoms
<i>Aracanidae</i>	Boxfish	<i>Chaetodontidae</i>	Margin coral fish
<i>Atennariidae</i>	Anglerfish	<i>Chanidae</i>	Milkfish
<i>Atherinidae</i>	Hardyheads	<i>Dasyatidae</i>	Rays
<i>Batrachoididae</i>	Frogfish	<i>Hemiramphidae</i>	Garfish
<i>Bythitidae</i>	Blindfish	<i>Hemiscylliidae</i>	Carpetshark
<i>Caesiocorpididae</i>	Perch	<i>Odacidae</i>	Whiting
<i>Callionymidae</i>	Stinkfish	<i>Paralichthyidae</i>	Flounders
<i>Cirrhitidae</i>	Hawkfish	<i>Pinguipedidae</i>	Grubfishes
<i>Clinidae</i>	Weedfish	<i>Pleuronectidae</i>	Flounders
<i>Clupeidae</i>	Herrings	<i>Rachycentridae</i>	Cobia
<i>Creediidae</i>	Sandburrowers	<i>Rhynchobatidae</i>	Guitarfish
<i>Cynoglossidae</i>	Soles	<i>Triakidae</i>	Shark
<i>Diodontidae</i>	Porcupine Fish	<i>Urolphidae</i>	Stingarees
<i>Enoplosidae</i>	Old Wife	<i>Zanclidae</i>	Moorish Idol
<i>Gobiesocidae</i>	Clingfish		
<i>Grammistidae</i>	Soapfish		
<i>Holocentridae</i>	Squirrelfish		
<i>Mobulidae</i>	Manta Ray		
<i>Monodactylidae</i>	Batfish		
<i>Mugiloididae</i>	Grubfish		
<i>Pempheridae</i>	Bullseye		
<i>Plotosidae</i>	Catfish		
<i>Priacanthidae</i>	Bigeyes		
<i>Rhincodontidae</i>	Whale Shark		
<i>Scorpaeniidae</i>	Scorpionfish		
<i>Syngnathidae</i>	Seahorses/Pipefish		
<i>Tripterygiidae</i>	Threefins		

Table 9. Approximate abundance, z-score and ranked z-scores of targeted recreational and commercial species from the 2009 and 1979 (Hutchins 1990) surveys. Species abundances at 43 sampling stations from the 2009 survey were compared with approximately similar station positions from the 1979 survey. Species abundances for the 1979 survey (unpublished JB Hutchins data) were derived from the sum of the midpoint value of the subjective range estimates of species relative abundance at each station the species was recorded (i.e. if one species estimated abundance of 4-9 and 28-81 occurred at a total of two stations, then abundance figure for that species is $7 + 55 = 62$). Total abundance for the 2009 survey was the sum of MaxN for species from each station. Recreational and commercially-targeted species are shown in light green and orange respectively.

Species	2009 survey			1979 survey		
	total abundance	z - score	ranked z-score	total abundance	z - score	ranked z-score
<i>Choerodon rubescens</i>	48	-0.14	9	545	2.28	11
<i>Choerodon schoenleinii</i>	10	-0.36	4	4	-0.64	3
<i>Lethrinus laticaudis</i>	12	-0.35	5	18	-0.57	4
<i>Lethrinus miniatus</i>	20	-0.30	7	19	-0.56	7
<i>Lethrinus nebulosus</i>	15	-0.33	6	229	0.57	9
<i>Pagrus auratus</i>	54	-0.10	10	126	0.02	8
<i>Pentapodus vitta</i>	577	2.99	11	376	1.37	10
<i>Pomatomus saltatrix</i>	0	-0.42	1	18	-0.57	4
<i>Sillago analis</i>	46	-0.15	8	0	-0.66	1
<i>Sillago schomburgkii</i>	1	-0.41	3	3	-0.65	2
<i>Mugil cephalus</i>	0	-0.42	1	18	-0.57	4

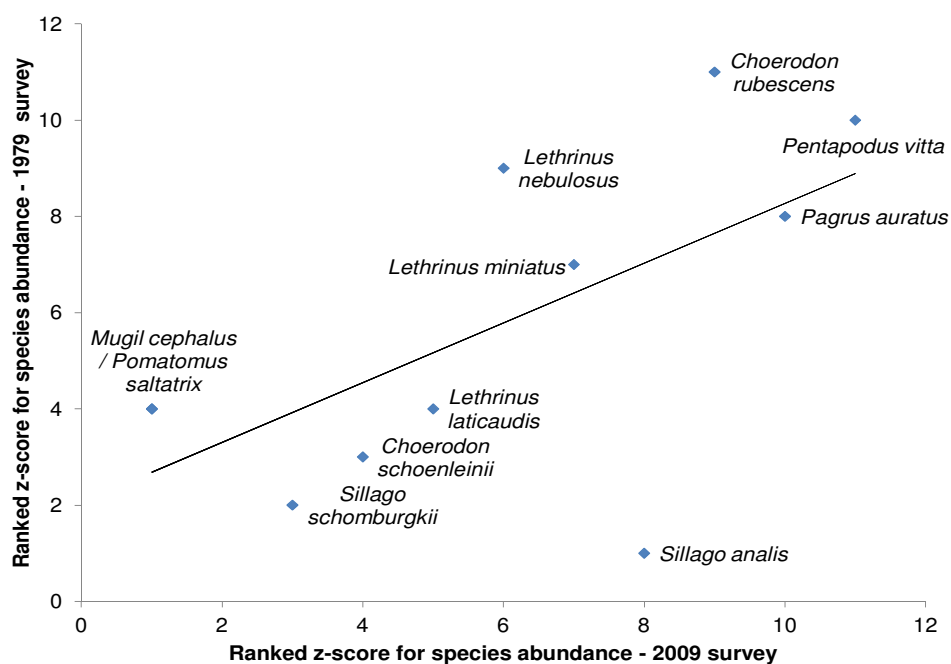


Fig. 10. Ranked z-score for abundance of 11 targeted recreational and commercial fish species as detailed in Table 9. The 2009 survey is depicted on the x-axis and the 1979 survey, the y-axis. The linear regression trendline is displayed ($y = 0.62x + 2.06$) with species shown above this trendline being relatively more common, by rank, in the 1979 survey while those below the trendline being more common, by rank, in the 2009 survey.

supported higher diversity and abundance than non-reef habitat. The interrelationships among biotic habitat and physical structure make it difficult to accurately attribute variability to any one factor such as the extent of coral cover, substratum rugosity, topographic complexity and degree of structural relief that occurs on reef habitat but their relative impact can be identified.

Coral reefs with a live coral cover of at least 10% are seen to drive the biotic community including coral reef fish (Bancroft 2009). Of the 77 reef stations sampled in the study 16 were recorded with at least 10% live coral cover (primarily Acroporidae and Pocilloporidae near the western entrance to South Passage and soft coral, mainly Alcyoniidae, to the east of Surf Point) and species diversity and abundance was greatest at these coral reef stations. This result is consistent with some previous studies: Jones & Kaly (1996) found that abundance and diversity was positively related to coral cover while Krajewski et al. (2011) found density and biomass positively correlated to coral cover and habitat complexity. Other studies, such as Roberts & Ormond (1987) found live coral cover in the Red Sea was not significantly correlated with either species richness or abundance.

Greater species richness and abundance in coral and limestone reef habitat could also be attributed to their topographic complexity which hosted many sites that afforded refuge for small and large herbivores and carnivores and supporting prey for such species. A similar pattern has been identified in other studies of coral reefs: Friedlander & Parrish (1998) found significantly greater species richness and abundance on more structurally complex coral reefs while Jones & Syms (1998) identified a positive correlation of coral fish abundance with reef topographic complexity. On temperate reefs Connell & Jones (1991) found that complex sites supported a greater proportion of older fish and had lower recruitment mortality and García-Charón & Pérez-Ruzafa (2001) found habitat heterogeneity of rocky substrate improved species richness and abundance.

Structural relief also contributed to increased species richness with structurally higher reefs having about one third greater species diversity than that found on relatively lower relief reefs. This is consistent with other Western Australian locations (Howard 1989, Harman et al. 2003, Watson et al. 2005).

While it appears that greater structural complexity and relief lead to greater species richness, some caution should be exercised in that the relatively more structurally complex and higher relief sites were located west of Cape Ransonnet and most were located in the far west where the oceanic influences and wave exposure were greatest. Such abiotic influences have been shown to effect assemblage composition with species-specific positive or negative correlations (Vroom et al. 2010, Krajewski & Floeter 2011).

Reef habitat had a number of species which had infrequent occurrences in other habitat suggesting they were habitat specialists. These included *Thalassoma lunare*, *Choeroden*

rubescens, *Siganus fuscescens*, *Coris auricularis* and *Parupeneus spilurus*. Consistent with the finding of Fairclough et al. (2008) *C. rubescens* was observed on reefs associated with marine influence, however in contrast, this study also found *Choeroden cauteroma* was not confined to inner gulf habitat but ranged over all reef habitat in all three zones.

The other dominant habitats were seagrass and sand. Consistent with previous studies (Jenkins & Wheatley 1997, Travers & Potter 2002) seagrass meadows, which comprised about half of the embayment stations, were significantly more speciose and had substantially higher fish abundances than sand. The observed mean species richness and abundance between seagrass and sand were however substantially less than previously observed by Travers & Potter (2002) (at more than 5x and 10x respectively) over similar habitat further into the enclosed gulf waters of Shark Bay. This may be partially attributable to the sampling approach (stereo-BRUVs compared to Travers otter trawl), but the proximity to marine influences may also affect the diversity and abundance of species associated with seagrass and sand habitat. For instance there was considerable dissimilarity between the current survey and the Travers 1999/2000 survey (sampling similar habitat adjacent to Peron Peninsular) regarding each survey's five most common species encountered on seagrass and sand habitat. For each survey there was little overlap in species inhabiting the seagrass habitat and sand habitats with only one species in common, *Pentapodus vitta*. Travers survey also observed the most common fish on both seagrass and sand habitat to be mostly temperate species compared to the current survey which observed the species on these habitats to be mostly tropical. The lower seasonal range in mean water temperature between South passage and the inner gulfs (3 °C – 4 °C at Surf Point compared with approximately twice this temperature range adjacent to Peron Peninsular) may have influenced this assemblage dissimilarity which possibly also confirms the concept that the inner gulf regions of Shark Bay may hold a higher proportion of temperate species while the marine influence evident in South Passage contributes to a predominantly tropical fauna (Hutchins 1990). Seagrass habitat specialists included *Monacanthus chinensis*, *Sphyaena obtusata*, *Pelates sexlineatus*, and *Torquigener pleurogramma*.

The second most significant factor to influence fish assemblage was zone which explained, on average 4.6% of the variability in fish assemblages. In assessing assemblage variance among the zones the choice of how many zones and where the particular zones are to be partitioned in the study area was important as the observed assemblage patterns are dependent on the scale of observation (García-Charton & Pérez-Ruzafa 2001, Anderson & Millar 2004). The spatial scale of the zone areas were chosen to reflect hypothesized differences in zone geomorphic protection and shelter, benthic habitat and zone ecosystem as a function of distance from the marine environment. One of the major considerations for this study was to try and understand how the marine influence affected assemblage

variability. I approached this by considering, as a continuous variable, 'distance' being the effective distance of each sampling station from the ocean. By comparing the marginal tests for distance and zone (Table 3) the contribution to assemblage variance, with each variable being considered alone, was 11.0% and 11.6% respectively. This suggested that the partitioning chosen for the three zones reasonably represented this distance effect.

There were significant differences among zones for species richness but not abundance. Contribution to species variability with zone is sourced from the aggregate of the influence of depth and the variables correlated to zone: salinity, visibility and temperature, plus other variables not analyzed in this study such as wave and current exposure and other abiotic variables unique to each zone. Habitat may have some influence on zone variability given some, although not significant ($P = 0.08$), interaction existed between zone and habitat. This may be attributable to the dominance of seagrass in the embayment zone. Similarly depth may have some influence on relative abundance notwithstanding a significant interaction with habitat. Depth explained, on average, 1.4% of variability in assemblage structure. Travers & Potter (2002), with their inner gulf Shark Bay study, found that fish assemblage was influenced most by habitat type (vegetated versus unvegetated) followed by depth.

Temporal changes in assemblage structure were not analyzed in this study but appear to be considerable in Shark Bay. Significant changes to assemblage and overall abundance between seasons has been previously observed with highest abundance being observed during February – March and declining to June – July (Kangas et al. 2007). Abundance of elasmobranch species as well is known to be significantly greater during the warmer water periods (Heithaus 2001, White & Potter 2004, Vaudo & Heithaus 2009). Seasonal change was also found to be the most influential factor on ichthyofaunal composition on seagrass and sand habitats (Travers & Potter 2002). This survey was carried out in the second half of September when the South Passage water is at its coolest. The current survey results, particularly mean total abundance for the embayment zone, may indicate the lower end of annual abundance variation for a number of species.

Fishing pressure on targeted and larger high-trophic level species can alter assemblage composition (Pauly et al. 2002). It is difficult to understand the impact commercial and recreational fishers have had on the study area as no specific catch records are available. Commercial fishing in the study area is confined to low level beach seine and mesh netting. This activity has been carried out adjacent to the shorelines of Shark Bay over the last 90 years and catches of three key species *Sillago schomburgkii*, *Sillago analis* and *Mugil cephalus* have remained consistent over the last decade (Fletcher & Santoro 2010). One or two commercial vessels, from a total of seven currently operating, fish from time to time in the study area and it is possible that there has been some impact on fish assemblage adjacent to the South Passage – Blind Strait shorelines. It is also possible that the small

scale of the activity, occurring in a similar fashion over many decades, has resulted in a trophic structure now in equilibrium along these shoreline locations. Recreational fishers in the study area predominantly fish from small boats. Between 2004 and 2008, approximately 40% of Shark Bay's recreational catch from boats, by number of fish, were recorded at the Denham boat-launching ramp which is the closest boat-launching ramp for larger vessels – up to 10m – to the study area (Dept of Fisheries unpubl data). It is likely only a small portion of this Denham recreational catch could be attributed to the study area as the distance from Denham to the closest point of the study area is approximately 30 km. Another complication in assessing fishing pressure is accounting for recreational fishers that launch small vessels – up to 6m – from the southern beaches of South Passage. These fishers are likely to have caused some diminishment of the abundance of some targeted species due to fishing effort in the study area. Different sampling methods utilized by the 1979 (Hutchins 1990) and the 2009 surveys and the possible seasonal effect on assemblages prevent a quantitative comparison with respect to changes in relative abundance over the 30 year period between surveys. Comparing the surveys by rank showed that two recreationally targeted species, *Choerodon rubescens* and *Lethrinus nebulosus*, were relatively abundant in 1979 and virtually absent in 2009. It is not possible to be conclusive about the impact of fishing pressure on species abundance as there is no historical catch data for the study area

Within the Shark Bay region the South Passage – Blind Strait area appears particularly species-rich. The 1979 and 2009 surveys, when combined, suggest that the South Passage – Blind Strait marine ecosystem may be more species-rich than the official record, based on the 1979 survey, of 323 fish species (Department of Environment and Conservation, www.sharkbay.org). There are a number of reasons for this. Firstly the region's geographical isolation and this particular marine setting, lying within the Shark Bay World Heritage Area, have provided a significant measure of protection (Wirsing et al. 2006, Vaudo & Heithaus 2009). Secondly, the different sampling method employed by the two surveys has likely resulted in some families and species being identified by one sampling approach and different species being identified by the other sampling technique. Numerous studies have compared differing sampling methods. Underwater visual census was seen to be better at detecting higher abundance and species richness than diver operated video (Pelletier et al. 2011). Stereo-BRUVs, used in the current study, have been seen to sample greater species richness and greater levels of relative biomass of carnivores without decreasing abundances of herbivores and omnivores than diver operated videos (Harvey et al. 2007, Langlois et al. 2010). Watson et al. (2005) found diver operated video enables access to caves and overhangs where smaller species can be identified that are not as easily recorded by remote video techniques. However, species of Labridae and rarer, large predatory fish were better

identified by stereo-BRUVs. Neither diver operated video nor stereo-BRUVs were suited to sample small cryptic families such as Gobiidae and Blenniidae. Uncommon fish families identified by the 1979 survey and not observed during the 2009 survey are generally not targeted by fishers. As a consequence these families are likely to remain present particularly as the area has been substantially 'reserved' with World Heritage Property status and other Government reserves since the earlier survey.

The results of both surveys suggest this species-rich marine area could shelter more than 90 families and over 400 species of fish, however to be more accurate on total species count a sampling approach using diver-operated stereo-video coupled with a contemporaneous stereo-BRUVs survey would be required (Watson et al 2005).

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