Differences in recreationally targeted fishes between protected and fished areas of a coral reef marine park

Mark Westera*, Paul Lavery, Glenn Hyndes

Centre for Ecosystem Management, School of Natural Sciences, Edith Cowan University, 100 Joondalup Drive, Joondalup, WA 6027, Australia

Abstract

Many comparisons have been made between sanctuary (no-fishing) and fished areas, where fishing pressure is exerted by artisanal or commercial fishers, but few have examined the effect of recreational fishing on fish assemblages in coral reef habitats. In this study, we compared assemblages of targeted fish from coral reef habitats in sanctuary (no-fishing) and recreationally fished zones of a marine protected area (MPA). Surface visual census (SVC) transects were conducted two times, at three regions, to compare the composition of predatory fish assemblages and the abundance, biomass, and size of the most commonly targeted fish. Baited remote underwater video (BRUV) was used to make relative counts of fish between zones. We also measured benthic cover and rugosity, which may influence fish assemblages. Analysis of similarity (ANOSIM) revealed significant differences in the composition of fish families/genera targeted by fishers (Lethrinidae, Lutjanidae, Haemulidae, Serranidae, and the genus *Choerodon* of the family Labridae) in terms of biomass ($P < 0.01$) and abundance ($P < 0.05$). The most consistent trends were recorded for biomass and this was supported by clustering of replicates in nonmetric multidimensional scaling (nMDS) ordinations. Similarity percentages (SIMPER) analysis indicated that the family Lethrinidae accounted for 73% (as abundance), and up to 69% (as biomass), of the dissimilarity between zones. Three-factor ANOVA highlighted significantly greater biomass, size, and abundance of legal-sized lethrinids (the most targeted family in the region) in sanctuary zones, but no differences in other families/genera. Results of BRUV supported SVC with greater relative counts of lethrinids ($P < 0.01$) in sanctuaries, but no significant differences for other families. Cover of *Acropora* coral and hard substrate differed between zones at some regions but differences were inconsistent. There were no significant differences in algal cover or rugosity between zones. Given the inconsistency in benthic cover, the similarity of rugosity between zones, the consistently greater biomass of lethrinids in sanctuaries, and the abundance of large lethrinids in sanctuaries, the cessation of fishing in sanctuary zones appears responsible for observed differences in the populations of these fish. These results demonstrate that recreational

* Corresponding author. Tel.: +61-8-9400-5010; fax: +61-8-9400-5509.
E-mail address: m.westera@ecu.edu.au (M. Westera).

fishing pressure may be sufficient to deplete fish populations below that of adjacent protected areas and that the effect of recreational fishing in coral reef habitats may be greater than previously thought.

1. Introduction

A common objective of sanctuary or unfished zones in marine protected areas (MPAs) is to help maintain viable fisheries in adjacent areas by reducing collapses of fish stocks, increasing the density and sizes of fish, and providing centres for dispersal of individuals and larvae (Kelleher, 1999). Many studies have demonstrated a recovery of fish populations after sanctuary (no-fishing) zones have been declared (Roberts, 1995; McClanahan and Kaunda Arara, 1996; Russ and Alcala, 1996; Wantiez et al., 1997) and fished and unfished areas have been shown to differ in abundance, biomass, and numbers of species of fish (Watson and Ormond, 1994; Rakitin and Kramer, 1996; Roberts and Hawkins, 1997; Babcock et al., 1999; McClanahan et al., 1999; Chiappone et al., 2000). Differences have, however, usually been detected when fishing included: a number of methods such as spears, nets, traps, and lines that may affect a range of species; intense fishing pressure; little or no regulation; or pressure exerted by commercial or artisanal fishers. Fewer studies have compared fished and unfished coral reef areas where there are only recreational line fishers. Line fishing may have a different effect because it is selective for particular species, less intensive than netting or trapping, influenced by the abilities of the fisher, and controlled by recreational desire rather than economic necessity. Differences between areas may be smaller where line fishing is the major method.

We wanted to test whether there were differences in the populations of targeted fish between sanctuary and fished areas where: size and bag limits were applied, regulatory compliance was high, and fishing pressure was exerted by recreational line fishers only. A further aim was to test whether sanctuary areas preserved or enhanced the biomass of mature-sized fish. A suitable location for the study was Ningaloo Marine Park in Western Australia. This region had areas closed to fishing (sanctuary zones), minimum size and bag limits for predatory fish, and fishers appeared to comply with regulations. Beach netting and spearing were permitted in some small designated areas, but were generally not allowed. Recreational fishing, but not commercial fishing, was permitted in recreation zones. Hence, fishing pressure was only exerted by recreational line fishers. Fishing pressure along the reef varied (CALM, 1999; Sumner et al., 2002) due to variable access. In some locations, the coral reef is only tens of metres from shore, making it highly accessible to fishers and tourists. Under these circumstances, it was possible to compare fished and unfished areas where differences may be restricted to larger legal-sized predators that could be captured by line. The marine park was established in 1989 and sanctuary zones were implemented in 1991. Anecdotal evidence indicated that the region was heavily fished prior to this time (Weaver, 1998). There was

a reduction in bag limits for some species in 1994 that may have relieved pressure on targeted fish stocks, but there have been an increasing number of fishers coming to the region (Shaw, 2000).

We posed three hypotheses to test whether there were differences in targeted fish between sanctuary and recreationally fished areas in fringing coral reef habitats of Ningaloo Marine Park: (1) there was a difference in the composition of fish families between zones; (2) the abundance, biomass, and size of fish were greater in sanctuary zones; and (3) the abundance of legal-sized fish was greater in sanctuary zones. Habitat characteristics in sanctuary and fished zones were compared, as we were concerned that any observed differences in fish assemblages may be confounded by differences in habitat. As sanctuary zones may lead to increases in both the density and average size of individuals, we compared fish assemblages using abundance, biomass, and size measures. Measures of abundance were used to address questions of density differences, and biomass allowed a greater comparative contribution from larger individuals. We were unable to make before-vs.-after comparisons as no data had previously been collected in the sanctuary and fished zones. Given this lack of information, the study will also serve as a baseline, enabling future monitoring and performance assessment of sanctuary zones in the Ningaloo Marine Park.

2. Methods

2.1. Study areas and experimental design

Ningaloo Marine Park is in the Indian Ocean on the Northwest Cape of Western Australia (21°40′S to 23°30′S and 113°45′E) (Fig. 1). Tidal range is approximately 2 m and water temperature ranges from 22.6 °C in July to 30.7 °C in January. Much of the marine park is a shallow lagoon with deeper long-shore gutters and a fringing back reef between 200 m and 6 km offshore, with the reef flat generally less than 150 m wide (CALM, 1989).

We compared fish assemblages in sanctuary and recreation zones in the Mandu, Osprey, and Maud regions of the marine park (Fig. 1). We were restricted in the three regions we could use, as it was imperative that they each had comparable habitats between zones to reduce any confounding effects. The regions were also chosen as they were subject to a comparatively high level of fishing pressure (in recreation zones) than other parts of the marine park (CALM, 1999; Sumner et al., 2002) and would most likely be the first to show an effect of fishing. Creel survey data (Sumner et al., 2002) identified the family Lethrinidae as the most targeted in the region (Table 1).

The sampling sites at zones within each region were comparable in terms of general habitat type (i.e., coral lagoon), depth, distance from shore, and proximity to channels. Depth at the study sites was 1.5–2 m. Sampling was repeated in January and July 2000 to test whether patterns in fish assemblages between zones were consistent over time. Zones within each region were sampled 1 day apart and at the same time of the day to minimise any confounding effects from changes in tide, lunar phase, or weather. The locations were not common dive sites where fish may have become tolerant of divers. Comparisons of
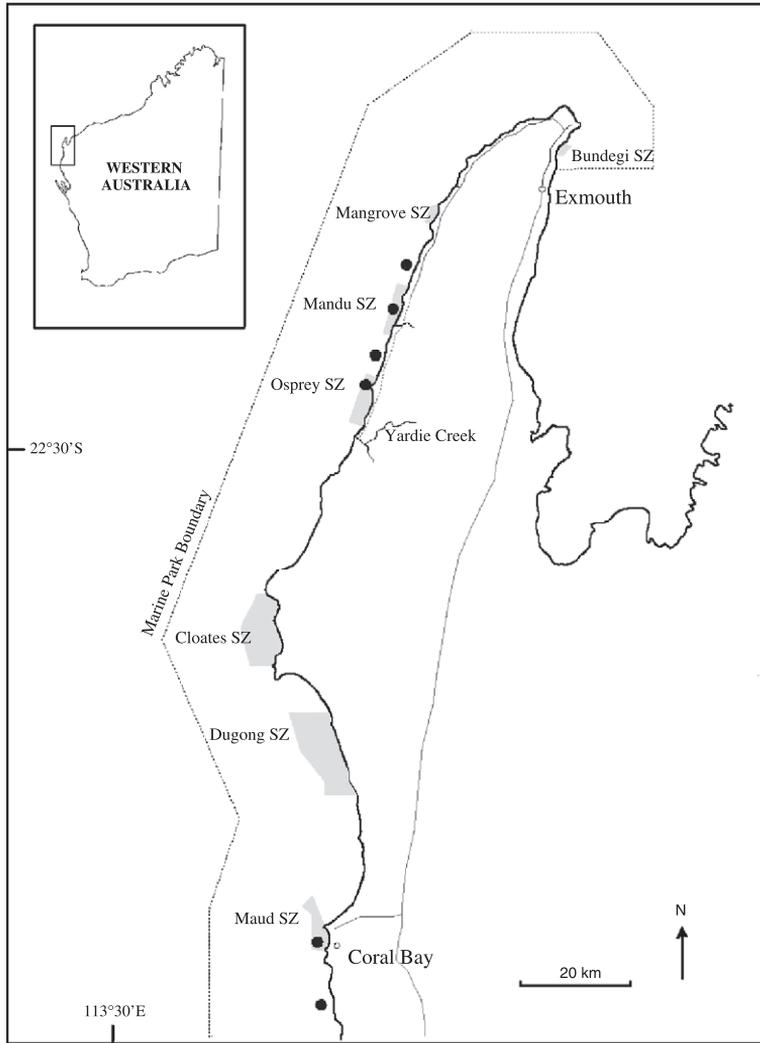
Fig. 1. Location of study sites (circles) in the Ningaloo Marine Park, Western Australia. Note the Mandu, Osprey, and Maud sanctuary zones. Shaded areas represent other sanctuary zones in the region.

fish were made at the family or genus level as we had noted that fishers would keep any individual species from a particular family or genus they were targeting.

2.2. Census of the fish community

2.2.1. Surface visual census (SVC)

Predatory fish were censused by swimming on the surface along four haphazardly located transects of 250×10 m in each zone and region. Orientation of transects

Table 1
Fish families targeted, within the Ningaloo region, and caught from locations at or near (<2 km from) the study sites (from Sumner et al., 2002)

Targeted families	Percentage of overall catch	
	Targeted	Caught
Lethrinidae	43	37
Serranidae	2	34
Lutjanidae	1	2
Haemulidae	0.2	4
Choerodon spp.	0.2	0
Others	54.6	23

"Others" include species not common at study sites (Carangidae, Scombridae, and Platycephalidae) that may frequent sand or deeper waters beyond the reef crest.

was determined using randomly generated compass bearings. Fish were counted, identified to species level, and their size was estimated to within 10 cm. We tested the accuracy of size estimates using objects of known length. SVC was used to reduce any effects of fish interacting with SCUBA divers, as larger predatory fish were wary of SCUBA during pilot trials. The width and length of transects were determined by using markers and global positioning system. To minimise bias, the same observer (M. Westera) conducted all fish censuses. Plots of species abundance against area sampled indicated that 90% of all species were recorded in the first two (of four) transects.

We compared underwater visual census (UVC) and SVC methods for the most common serranid in the region, *Epinephelus rivulatus*. As this species hides under ledges and coral plates, we suspected that SVC might underestimate its abundance. However, there was no significant difference between methods (*t* test, $P>0.05$, $n=4$) and SVC was considered suitable.

We calculated the mean size of the dominant fish family to determine whether fish were smaller in areas where fishing was permitted. The mean size was calculated for each transect ($n=4$), using the equation: Σ(midpoint of each size class × number of fish in that size class)/Σ(total number fish in each size class).

The abundance of under-sized and legal-sized lethrinids (those that can and cannot be legally taken by fishers) was compared between zones. Length at maturity corresponded with legal size for *Lethrinus lentjan* (Lacepède, 1802), *Lethrinus atkinsonii* (Seale, 1910), and *Lethrinus laticaudis* (Alleyne and Macleay, 1877) (i.e., 28 cm). *Lethrinus nebulosus* (Forsskål, 1775) matures at 38 cm but the legal size is 41 cm (Moran et al., 1993; Agbayani, 2002). We split the abundances of fish in size classes that corresponded to the legal size. For *L. lentjan*, *L. atkinsonii*, and *L. laticaudis*, 80% of the 20–30 cm size class was added to the under-sized fish and 20% was added to the legal-sized fish (i.e., 20–28 cm fish were under-sized fish and 28–30 cm were legal-sized fish). Similarly, for *L. nebulosus*, 10% of the 40–50 cm size class was added to the under-sized fish and 90% was added to the legal-sized fish. We assumed that there was an even distribution of fish within the size classes that were split.

2.2.2. Baited remote underwater video (BRUV)

Video cameras were placed on the seabed in haphazardly chosen locations, similar to other studies (Bortone et al., 1991; Cappo and Brown, 1996; Babcock et al., 1999; Willis et al., 2000). A bag containing bait was placed in front of the camera and the activity of fish was recorded for 30 min at 12 replicate locations in each zone. During filming, divers and the boat vacated the area. Footage was viewed on a television screen and the number of fish that entered the field of view was counted. Lengths of fish were estimated by placing the bait bag 1.5 m from the camera and calibrating the focal width at that distance. BRUV provided relative counts of fish between zones, overcame any observer biases or interactions with fish, and validated the findings of SVC. There was the potential to make duplicate counts of fish using BRUV, but we assumed that behavioural patterns of each species did not differ between zones. BRUV was not conducted at Osprey on either trip or Mandu in July due to time and weather constraints.

Spatial comparisons of abundances of fish may be confounded by short-term temporal variations in weather, time of day, tidal, or lunar effects. To account for such effects, short-term variability was measured by repeating the BRUV survey at the Mandu recreation zone, 3 days apart. There was no significant difference in the counts of any of the five major fish families/genera (Lethrinidae, Lutjanidae, Haemulidae, Serranidae, or *Choerodon* spp.) between days (*t* test, $P>0.05$), indicating that short-term variability was

Table 2

Fish families and species (in order of dominance) recorded in surface visual census and baited remote underwater video, January and July 2000

| Family	Species	Common name	Method
Lethrinidae	*Lethrinus nebulosus* (Forsskål, 1775)	Spangled emperor	SVC, BRUV
	Lethrinus lentjan (Lacepède, 1802)	Pinkear emperor	SVC, BRUV
	Lethrinus atkinsonii (Seale, 1910)	Yellow-tailed emperor	SVC, BRUV
	Lethrinus laticaudis (Alleyne and Macleay, 1877)	Blue-lined emperor	SVC, BRUV
Lutjanidae	*Lutjanus fulviflamma* (Forsskål, 1775)	Blackspot snapper	SVC, BRUV
	Lutjanus carponotatus (Richardson, 1842)	Stripey seaperch	SVC, BRUV
	Lutjanus lemniscatus (Valenciennes, 1839)	Dark-tailed seaperch	SVC, BRUV
	Symphorus nematophorus (Bleeker, 1860)	Chinaman fish	SVC
Haemulidae	*Plectorhincus chaetodontoides* (Lacepède, 1800)	Many-spotted sweetlips	SVC, BRUV
	Diagramma labiosum (MacLeay, 1883)	Painted sweetlips	SVC, BRUV
	Diagramma pictum (Thunberg, 1792)	Yellowdot sweetlips	SVC
	Plectorhincus chrysotaenia (Bleeker, 1855)	Celebes sweetlips	SVC
	Plectorhincus flavomaculatus (Cuvier, 1830)	Gold-spotted sweetlips	SVC
	Plectorhincus multivittatum (MacLeay, 1878)	Many-lined sweetlips	SVC
	Plectorhincus schotaf (Forsskål, 1775)	Minstrel sweetlips	SVC
Serranidae	*Epinephelus rivulatus* (Valenciennes, 1830)	Chinaman cod	SVC, BRUV
	Epinephelus fasciatus (Forsskål, 1775)	Black-tipped cod	SVC, BRUV
	Epinephelus bilobatus (Randall and Allen, 1987)	Frostback cod	SVC
	Epinephelus polyphekadion (Bleeker, 1849)	Small-toothed cod	BRUV
Labridae (genus	*Choerodon schoenlenii* (Valenciennes, 1839)	Blackspot tuskfish	SVC, BRUV
Choeorodon)	*Choerodon rubescens* (Gunther, 1862)	Baldchin groper	SVC, BRUV
	Choerodon anchorago (Bloch, 1791)	Anchor tuskfish	BRUV
	Choerodon cephalotes (Castelnau, 1875)	Purple tuskfish	BRUV
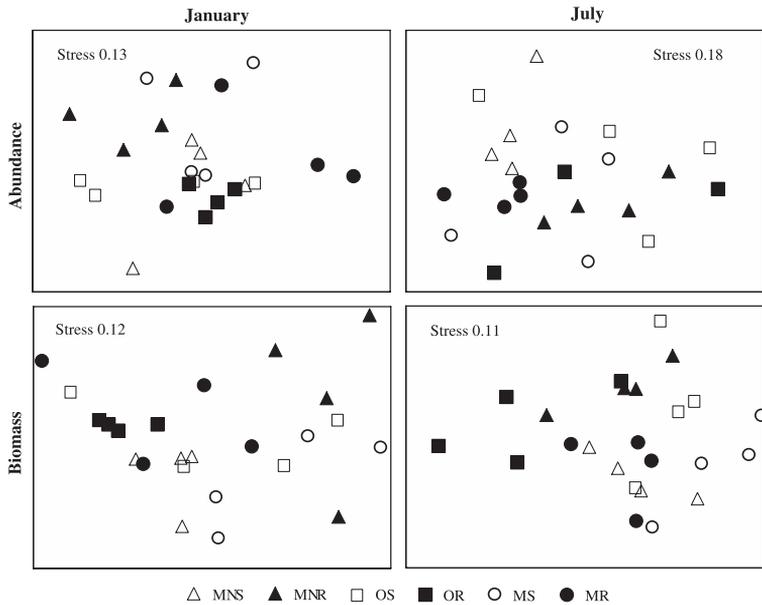
Fig. 2. NMDS ordinations of the abundance and biomass of targeted fish (SVC) from sanctuary zones (open symbols) and recreation zones (black symbols) at all regions (January and July 2000) ($n = 4$). MNS—Mandu sanctuary zone; MNR—Mandu recreation zone; OS—Osprey sanctuary zone; OR—Osprey recreation zone; MS—Maud sanctuary zone; and MR—Maud recreation zone.

negligible. Due to the availability of cameras, four replicates were used for this test, whereas 12 replicates were used for between-zone comparisons.

2.2.3. Biomass of fish

Length–weight relationships were determined for Lethrinidae, Lutjanidae, Serranidae, and Haemulidae using the equation: biomass = constant × length^{exponent}. Greater than 10 individuals in each family were weighed and measured but we used length–weight relationships from Kulbicki et al. (1993) for *Choerodon* spp. due to their low abundance in the study areas. Due to the low number of fish captured, biomass estimates were also

Table 3
Two-way crossed ANOSIM R values and significance levels for targeted fish family/genera composition (in terms of abundance and biomass) (SVC)

	Time	Abundance		Biomass	
		ANOSIM R	P value	ANOSIM R	P value
Zone groups	January	0.247	0.015	0.413	0.002
	July	0.150	NS	0.533	0.002
Region groups	January	0.196	0.007	0.242	0.008
	July	0.751	0.001	0.301	0.003

Data were square root-transformed (999 permutations used).

Table 4
Results of SIMPER analysis and one-way ANOSIM (R values and significance levels) on the abundance and biomass of targeted fish families/genera from SVC for sanctuary (SZ) and recreation (RZ) zones at each region (January and July 2000)

Region	Date									
	January 2000					July 2000				
	Average abundance		Average dissimilarity	Ratio	Contribution (%)	Average abundance		Average dissimilarity	Ratio	Contribution (%)
	SZ	RZ				SZ	RZ			
Abundance										
Mandu	$R=0.292$ ($P=0.057$)					$R=0.385$ ($P=0.029$)*				
Lethrinidae	36.8	30.8	22.3	1.2	62.7	53.0	24.8	25.8	1.5	72.8
Lutjanidae	1.00	7.8	8.3	0.7	23.3	9.0	2.8	5.9	1.2	16.6
Haemulidae	0	2.2	3.5	1.6	10.0	0.2	2.5	2.9	0.9	8.1
Choerodon spp.	0.2	0.8	1.2	0.8	3.4	0	0.2	0.3	0.5	0.8
Serranidae	0	0.25	0.2	0.5	0.7	0	0.5	0.6	0.9	1.7
Osprey	$R=0.135$ ($P=0.286$)					$R=0.010$ ($P=0.514$)				
Lethrinidae	48.8	27.2	29.5	1.7	90.4	44.8	19.2	40.5	1.5	76.5
Lutjanidae	1.5	0.2	1.5	1.5	4.6	3.2	0.8	4.3	1.1	8.2
Haemulidae	1.0	0	0.9	1.0	2.8	3.5	1.2	6.2	0.9	11.6
Choerodon spp.	0.8	0	0.7	0.6	2.1	0.8	0	1.2	0.9	2.3
Serranidae	0	0	0	0	0	0.2	0.2	0.7	0.6	1.3
Maud	$R=0.031$ ($P=0.457$)					$R=0.115$ ($P=0.257$)				
Lethrinidae	18.8	14.2	31.8	1.7	74.1	42.25	35.75	10.6	1.5	64.3
Haemulidae	1.8	0.5	5.8	0.8	13.6	2.0	0	2.2	1.0	13.16
Lutjanidae	1.8	0.2	4.6	1	10.6	2.2	1.5	2.6	1.2	15.5
Choerodon spp.	0.2	0	0.7	0.5	1.7	0.2	0	0.3	0.6	1.8
Serranidae	0	0	0	0	0	1.0	0.5	0.8	1.1	5.2
Biomass										
Mandu	$R=0.729$ ($P=0.029$)*					$R=0.563$ ($P=0.029$)*				
Lethrinidae	15.1	7.24	26.4	1.2	46.0	23.6	9.5	31.1	1.7	69.0
Haemulidae	0	3.15	11.2	2.0	19.5	0.2	2.1	5.1	1.4	11.3
Lutjanidae	0.6	4.1	9.9	0.7	17.3	4.09	1.1	6.2	1.0	13.8
Choerodon spp.	0	2.8	9.5	0.8	16.6	0	0.9	2.2	0.5	4.8
Serranidae	0	0.1	0.3	0.6	0.5	0	0.2	0.5	0.8	1.2
Osprey	$R=0.302$ ($P=0.057$)					$R=0.563$ ($P=0.057$)				
Lethrinidae	11.6	6.8	29.4	4.4	73.3	16.8	5.9	35.8	1.7	59.5
Haemulidae	1.2	0	4.2	0.9	10.5	4.5	0.6	14.3	1.4	23.8
Lutjanidae	0.9	0.1	3.2	1.4	8.0	1.4	0.3	3.7	2.3	6.1
Choerodon spp.	1.0	0	3.3	0.6	8.2	1.4	0	5.6	0.8	9.3
Serranidae	0	0	0	0	0	0.1	0.1	0.8	0.7	1.3
Maud	$R=0.208$ ($P=0.086$)					$R=0.490$ ($P=0.057$)				
Lethrinidae	23.9	8.5	40.5	1.6	71.7	43.5	16.4	30.5	1.8	76.7
Haemulidae	4.3	0.5	11.9	0.9	21.0	4.3	0.3	5.5	1.1	13.8
Lutjanidae	0.9	0.1	2.1	1.2	3.7	1.1	0.8	1.9	1.1	4.7

Table 4 (*continued*)

Region	Date								
	January 2000				July 2000				
	Average abundance		Ratio	Contribution (%)	Average abundance		Ratio	Contribution (%)	
	SZ	RZ			SZ	RZ			
Biomass									
Maud	R=0.208 (P=0.086)				R=0.490 (P=0.057)				
Choerodon spp.	0.9	0	2.0	0.6	3.5	1.3	0	1.8	0.5	4.6
Serranidae	0	0	0	0	0	0	0.1	0.1	0.5	0.2

Thirty-five permutations was the maximum possible number for ANOSIM.
  * Significant differences.

calculated using the length–weight relationships of Kulbicki et al. (1993), which yielded almost identical results.

2.3. Description of habitat

Benthic cover was measured to determine whether any observed differences in fish variates were related to differences in habitat. A video camera was held 50 cm above the substrate and moved along eight replicate 50-m transects in each zone and region. Transects were haphazardly placed in the same area as the SVC transects. From the video footage of each transect, 50 randomly selected frames were analysed and substrate cover was grouped into five broad categories: *Acropora* coral cover; other coral cover; turfing algae (fine filamentous algal species); algal assemblage (all algal species except turfing such as *Sargassum*, *Turbinaria*, *Dictyota*, *Hypnea*, *Caulerpa*, and *Lobophora* species); and total hard substrate cover. Video footage was viewed on a computer screen to determine the substrate cover type under 10 points on each frame. Plots of categories against area sampled indicated that 22 frames with 10 points per frame were sufficient to capture all categories. We analysed 50 frames amounting to a total of 500 points per transect (4000 points per zone in each region). Algal and coral collections were used to verify identifications.

Rugosity was estimated by measuring the depth at the surface of the substrate, every metre along each benthic transect. A contour distance was calculated using the difference in depth at each metre along the transect. Rugosity was analysed as the straight-line distance divided by the contour distance (McClanahan and Shafir, 1990) and compared among transects and regions as an index of spatial relief.

2.4. Statistical analyses

Analyses were conducted to examine spatial trends in fish family/genera composition and benthic cover between zones and among regions, and to identify which fish, or types of benthic cover, were driving any observed differences. This approach required the use of multivariate (ANOSIM, nMDS, and SIMPER) and univariate (ANOVA and Fisher's PLSD post-hoc testing) techniques.

154

M. Westera et al. / J. Exp. Mar. Biol. Ecol. 294 (2003) 145–168

Table 5
Results of three-factor ANOVA on lethrinid measurements (overall abundance, biomass, mean size, abundance of legal-sized fish, and abundance of under-legal-sized fish) (SVC), with sampling time (January and July 2000), region (Mandu, Osprey, and Maud), and zone (sanctuary and recreation) as factors

Source	df	Mean square	F ratio	P value	Mean square	F ratio	P value	P value	F ratio	P value
		Abundance			Biomass			Size		
Time	1	623.5	0.64	NS	604.2	1.85	NS	0.001	0.08	NS
Region	2	340.3	0.41	NS	696.6	4.87	NS	0.096	27.52	0.035
Zone	1	2836.7	10.66	NS	2144	11.09	NS	0.056	585.37	0.0263
Time × Region	2	825.3	6.63	NS	143	14.17	NS	0.003	0.64	NS
Time × Zone	1	266.0	2.13	NS	193.2	19.14	0.0485	0.000	0.02	NS
Region × Zone	2	333.2	2.68	NS	196.4	19.46	0.0489	0.004	0.71	NS
Time × Region × Zone	2	124.5	0.29	NS	10.1	0.17	NS	0.005	1.47	NS
Residual	36	423.5			59.5			0.004		

Source	df	Mean square	F ratio	P value	Mean square	F ratio	P value
		Abundance of legal-sized fish			Abundance of under-legal-sized fish		
Time	1	1.05	3.29	NS	252.08	3.74	NS
Region	2	0.75	2.27	NS	1742.68	10.52	NS
Zone	1	1.07	607.9	0.0258	1104.96	15.14	NS
Time × Region	2	0.33	27.53	0.0351	165.62	0.97	NS
Time × Zone	1	0.01	0.15	NS	73.01	0.43	NS
Region × Zone	2	0.03	2.60	NS	879.41	5.13	NS
Time × Region × Zone	2	0.01	0.26	NS	171.29	0.49	NS
Residual	36	0.04			351.56		

Tests for significant interactions

Biomass						Abundance of legal-sized lethrinids		
Time × Zone	F ratio	P value	Region × Zone	F ratio	P value	Time × Region	F ratio	P value
January	52.01	0.0187	Maud	179.05	0.0055	January	3.91	NS
July	179.51	0.0055	Mandu	47.69	0.0203	July	86.11	0.0115
Sanctuary zone	73.34	0.0134	Osprey	24.55	0.0384	Maud	92.11	0.0107
Recreation zone	5.65	NS	Sanctuary zone	80.82	0.0122	Mandu	50.51	0.0192
			Recreation zone	7.63	NS	Osprey	0.23	NS

Abundance, biomass, and under-legal-size data passed Cochran's test; mean-size and legal-size data passed after transformation $\{\log_{10}(x+1)\}$. Analysis using multiple comparisons has been conducted where there were significant interactions.

2.4.1. Multivariate analyses

Multivariate analyses were conducted using the PRIMER statistical package (PRIMER-E, 2000). Nonmetric multidimensional scaling (nMDS) (Field et al., 1982) was used to examine spatial patterns. Two-way crossed analysis of similarity (ANOSIM) (Clarke and Warwick, 1994) was used to determine the significance of spatial trends (for each time sampled) in fish family composition (abundance and biomass) and benthic cover (percentage cover) between zones and among regions. The tests were based on a Bray–Curtis rank similarity matrix, calculated using square root transformed data. Time was not factored into multivariate analyses as we expected fish assemblages to change over the 6-month study period (Letourneur, 1996b; Rooker et al., 1997). We were concerned primarily with differences in fish composition between zones, not with changes between
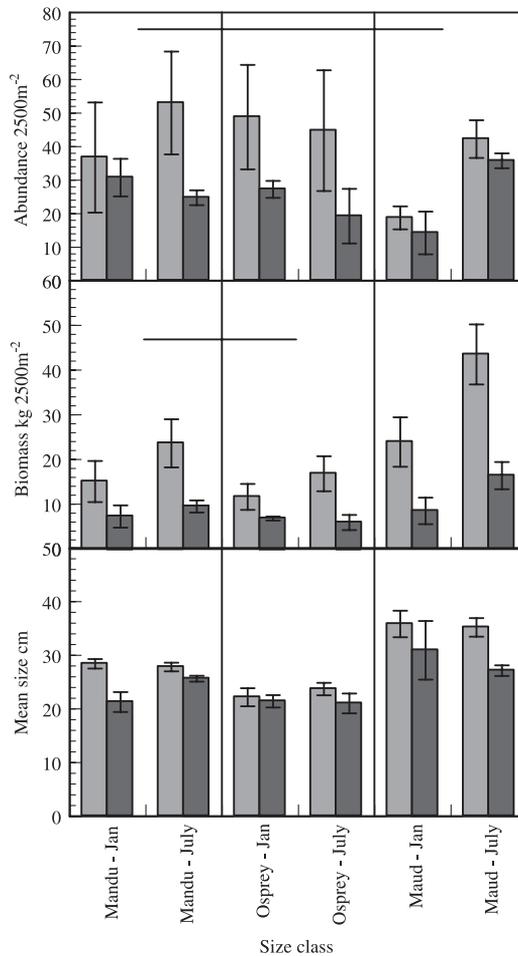
Fig. 3. The abundance, biomass, and size of lethrinids (± S.E.) (SVC) from sanctuary zones (▨) and recreation zones (▮) at all regions in January and July 2000 (*n* = 4). Horizontal bars indicate those regions that were not significantly different (Fisher's PLSD post-hoc test).

the two times sampled. One-way ANOSIM was also used to determine the significance of any clustering of replicates, within each region, in nMDS ordinations. Similarity percentages (SIMPER) (Clarke, 1993) were used to examine individual contributions to any observed differences in fish composition or benthic cover.

2.4.2. Univariate analyses

A three-factor orthogonal, mixed-model analysis of variance (ANOVA) (time, region, and zone as factors) was used to compare the abundance, biomass, and size of the dominant fish family/genera and benthic cover. Two-factor ANOVA was used to compare rugosity measurements between regions and zones for one time. Interactions between factors were analysed using multiple comparisons with the test slices function in the SAS statistical programme, JMP (SAS Institute, 2000).

Sampling time was treated as a random factor. As mentioned previously, we were restricted in the regions we could use for this study. Regions that had comparable habitats in sanctuary and adjacent recreation zones and also had a high level of fishing pressure compared with other recreation zones at Ningaloo were chosen. Zones were chosen to represent fished (recreation) and unfished (sanctuary) areas. Given that the choices of region and zone were not random, they were treated as fixed factors. BRUV data were
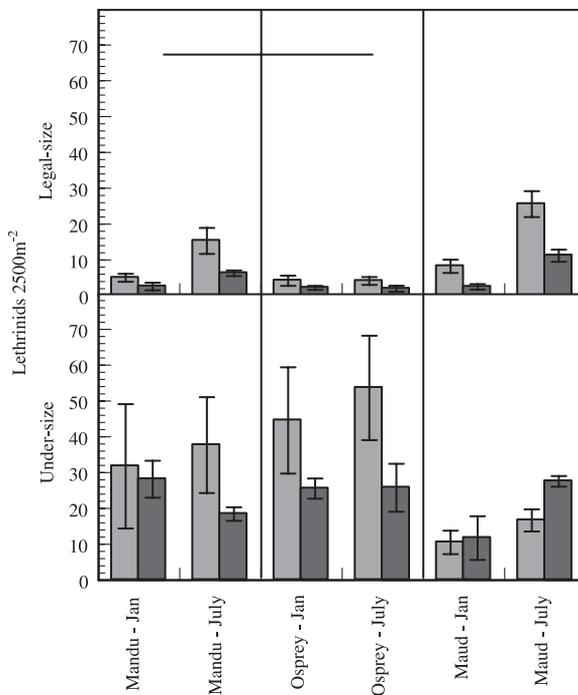

Fig. 4. Mean abundances (SVC) of legal-sized and under-sized lethrinids (± S.E.) from sanctuary (■) and recreation (■) zones, for each region and time. Horizontal lines indicate those regions that were not significantly different (Fisher's PLSD post-hoc test).

compared between zones using *t* tests. Data were tested for homogeneity of variance using Cochran's test and transformed if they were heterogeneous $\{\log_{10}(x+1)$ – fish data; arcsine and $\log_{10}(x+1)$ – benthic cover data$\}$. Fisher's PLSD post-hoc testing was used to determine which factors were driving any differences in ANOVA tests.

3. Results

Twenty-three species of recreationally targeted fish were recorded in the SVC and BRUV (Table 2), the most common being *L. nebulosus*, *L. lentjan*, *L. atkinsonii*, *Lutjanus fulviflamma* (Forsskål, 1775), *Plectorhincus chaetodontoides* (Lacepède, 1800), and *Choerodon schoenlenii* (Valenciennes, 1839).

3.1. Surface visual census

3.1.1. Multivariate analyses

Replicate samples for fish composition (Lethrinidae, Lutjanidae, Haemulidae, Serranidae, and *Choerodon* spp.) from sanctuary and recreation zones did not appear to separate
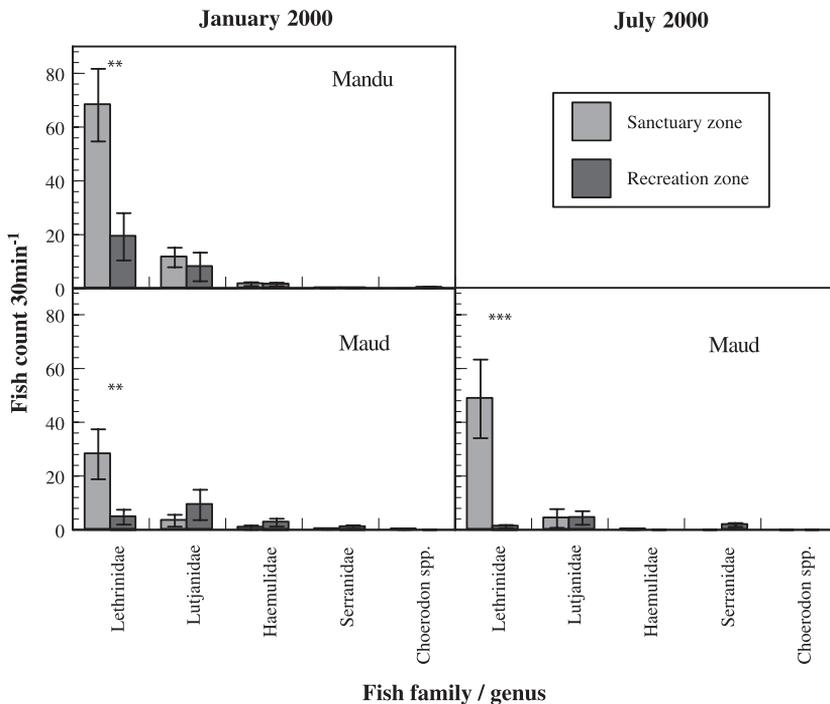

Fig. 5. Mean counts (BRUV) of targeted predatory fish ($\pm$ S.E.) recorded at sanctuary and recreation zones in the Mandu and Maud regions. Data were transformed $\{\log_{10}(x+1)\}$. Note significant differences (*t* test). **$P < 0.01$, ***$P < 0.001$ ($n = 12$).

Table 6
Two-way crossed ANOSIM *R* values and significance levels for benthic cover (%)

| | Benthic cover | | |
	Time	ANOSIM *R*	*P* value
Zone groups	January	0.352	0.001
	July	0.278	0.001
Region groups	January	0.359	0.001
	July	0.210	0.001

Data were square root-transformed (999 permutations used).

in nMDS ordinations when all regions were considered. However, there was a separation within regions based on abundance and biomass data for Mandu, and on biomass data for Osprey and Maud (Fig. 2). Two-way crossed ANOSIM highlighted significant differences between zones for abundance data in January and biomass data in January and July (Table 3). There were also significant differences between regions.

Table 7
Results of SIMPER and one-way ANOSIM (*R* values and significance) for benthic cover (%) for sanctuary (SZ) and recreation (RZ) zones at each region (January and July 2000)

Region	Date								
	January 2000					July 2000			
	Average abundance		Average dissimilarity	Ratio	Contribution (%)	Average abundance		Average dissimilarity	Ratio	Contribution (%)
	SZ	RZ				SZ	RZ			
Mandu	*R*=0.075 (*P*=0.155)					*R*=0.214 (*P*=0.014)*				
Hard substrate	70.0	58.0	7.6	1.1	45.6	72.9	63.1	6.7	1.3	38.6
Acropora	28.2	28.6	5.0	1.5	30.1	31.2	31.8	5.7	1.4	33.0
Turf algae	9.8	13.0	2.1	1.3	12.5	8.8	5.6	2.0	1.6	11.8
Algal assemblage	9.6	4.4	1.3	1.1	7.9	9.5	4.7	2.4	1.7	13.6
Other coral	1.4	1.0	0.7	1.0	4.0	1.4	0.8	0.5	1.2	3.0
Osprey	*R*=0.282 (*P*=0.005)*					*R*=0.042 (*P*=0.625)				
Acropora	7.7	25.4	7.3	1.5	43.2	16.6	22.6	5.5	1.3	33.2
Hard substrate	77.0	76.0	5.1	1.3	30.2	71.7	66.8	6.5	1.4	39.4
Turf algae	16.3	16.2	2.5	1.3	14.5	9.9	10.0	2.4	1.4	14.4
Algal assemblage	3.9	7.0	1.6	1.1	9.2	3.9	3.3	1.2	1.3	7.5
Other coral	1.4	0.7	0.5	1.2	2.9	2.4	1.0	0.9	1.0	5.4
Maud	*R*=0.679 (*P*=0.001)*					*R*=0.642 (*P*=0.001)*				
Hard substrate	50.2	88.4	15.8	1.9	40.8	52.5	77.4	14.2	1.4	40.4
Acropora	13.3	45.7	13.6	1.5	35.3	7.6	39.6	14.4	1.8	40.9
Algal assemblage	3.5	14.4	4.9	1.2	12.7	3.3	5.0	1.3	1.2	3.7
Turf algae	15.1	17.7	3.1	1.6	8.0	11.5	12.4	3.0	1.2	8.7
Other coral	3.4	0.4	1.2	1.8	3.2	5.1	0.3	2.2	1.7	6.4

A total of 999 permutations were used.
 * Significant differences.

Fish composition was analysed using one-way ANOSIM to determine which regions were driving differences observed in two-way crossed ANOSIM. There were significant differences between the Mandu sanctuary and recreation zones for abundance data in July, and for biomass data at both times ($P < 0.05$) (Fig. 2, Table 4). Despite separation of replicates at Osprey and Maud using biomass data (Fig. 2), one-way ANOSIM values were weaker ($P = 0.057$ and 0.086; Table 4). There were, however, only 35 permutations available for this test. SIMPER demonstrated that significant composition differences where being driven by the family Lethrinidae (Table 4).

3.1.2. Univariate analysis

ANOVA yielded interactions between factors using biomass data (time × zone and region × zone). Analysis of the interactions showed that there was a greater biomass of lethrinids in sanctuary zones, than in recreation zones, in January ($P < 0.05$) and July ($P < 0.01$) and that differences were significant for each individual region (Table 5, Fig. 3). There was also a difference between sanctuary zones in the regions with greater biomass at Maud than at Mandu or Osprey ($P < 0.05$) (Fig. 3) (see Table 4 for relative abundance and biomass values). There were no significant differences in the overall abundance of lethrinids or the abundance or biomass of other taxa of fish.

The mean size of lethrinids was greater in sanctuary zones than recreation zones and there was a significant difference among regions (both $P < 0.05$), with the greatest mean size at Maud, followed by Mandu and Osprey (Table 5, Fig. 3). The abundance of legal-sized lethrinids was significantly greater in sanctuary zones (Table 5, Fig. 4) and there was
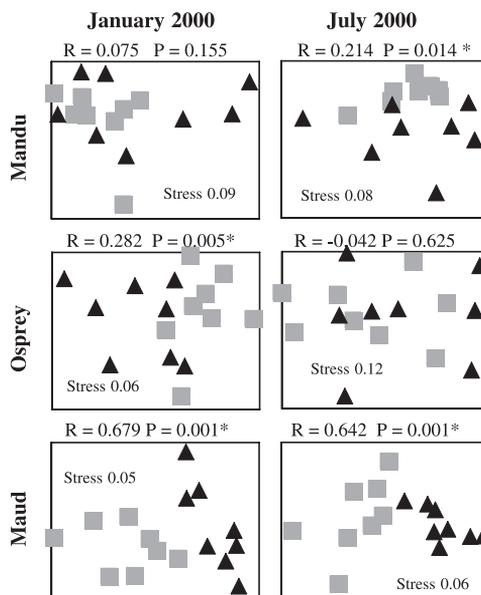

Fig. 6. Benthic cover (%) nMDS plots from sanctuary (■) and recreation (▲) zones for each region in January and July 2000 ($n = 8$). Note ANOSIM R values and significance levels. *Significant differences.

an interaction between time and region. Subsequent analysis revealed a significant difference between regions in July, and between times at Mandu and Maud. There were no significant differences in the abundance of under-sized lethrinids.

3.2. Baited remote underwater video

Differences in lethrinid populations recorded using SVC were confirmed with BRUV. *t* tests highlighted greater counts of lethrinids in the Mandu and Maud sanctuary zones ($P < 0.01$) (Fig. 5). There were no significant differences in the counts of other targeted fish.

Table 8
Results of ANOVA on benthic cover (%) variables with time (January and July 2000), region (Mandu, Osprey, and Maud), and zone (sanctuary and recreation) as factors

Source	df	Mean square	F ratio	P value	Mean square	F ratio	P value	Mean square	F ratio	P value
		Acropora coral			Other coral			Hard substrate		
Time	1	0.001	0.01	NS	0.0001	1.03	NS	0.047	0.55	NS
Region	2	0.016	5.53	NS	0.001	7.08	NS	0.083	1.34	NS
Zone	1	0.067	58.19	NS	0.008	18.40	NS	0.179	3.11	NS
Time × Region	2	0.003	2.14	NS	0.000	1.15	NS	0.062	1.77	NS
Time × Zone	1	0.001	0.89	NS	0.0001	2.98	NS	0.057	1.64	NS
Region × Zone	2	0.026	19.96	0.0477	0.002	17.97	NS	0.783	22.29	0.0429
Time × Region × Zone	2	0.001	0.58	NS	0.0001	0.65	NS	0.035	1.11	NS
Residual	84	0.002			0.0002			0.031		

	df	Mean square	F ratio	P value	Mean square	F ratio	P value
		Algal assemblage			Turf algae		
Time	1	0.001	0.03	NS	0.061	18.98	NS
Region	2	0.003	0.18	NS	0.021	19.72	0.0482
Zone	1	0.006	0.28	NS	0.001	0.19	NS
Time × Region	2	0.019	11.05	NS	0.001	0.46	NS
Time × Zone	1	0.021	12.16	NS	0.004	1.90	NS
Region × Zone	2	0.017	9.93	NS	0.001	0.40	NS
Time × Region × Zone	2	0.002	1.27	NS	0.002	0.91	NS
Residual	84	0.001			0.002		

Tests for significant interactions

Region × Zone	F ratio	P value	F ratio	P value
	Acropora coral		Hard substrate measurements	
Maud	79.68	0.0123	44.57	0.0217
Mandu	0.01	NS	4.79	NS
Osprey	11.82	NS	0.32	NS
Sanctuary zone	19.13	0.0496	11.52	NS
Recreation zone	12.71	NS	13.13	NS

Data were transformed {arcsine and $\log_{10}(x+1)$}. $\alpha = 0.01$ for "other coral" cover as variances were heterogeneous after transformation.

3.3. Habitat measurements

3.3.1. Multivariate analysis

Two-way crossed ANOSIM highlighted a significant difference in the benthic cover between zones and among regions in both January and July (Table 6). NMDS ordinations, used to examine trends within each region and time, showed variable patterns. At Mandu
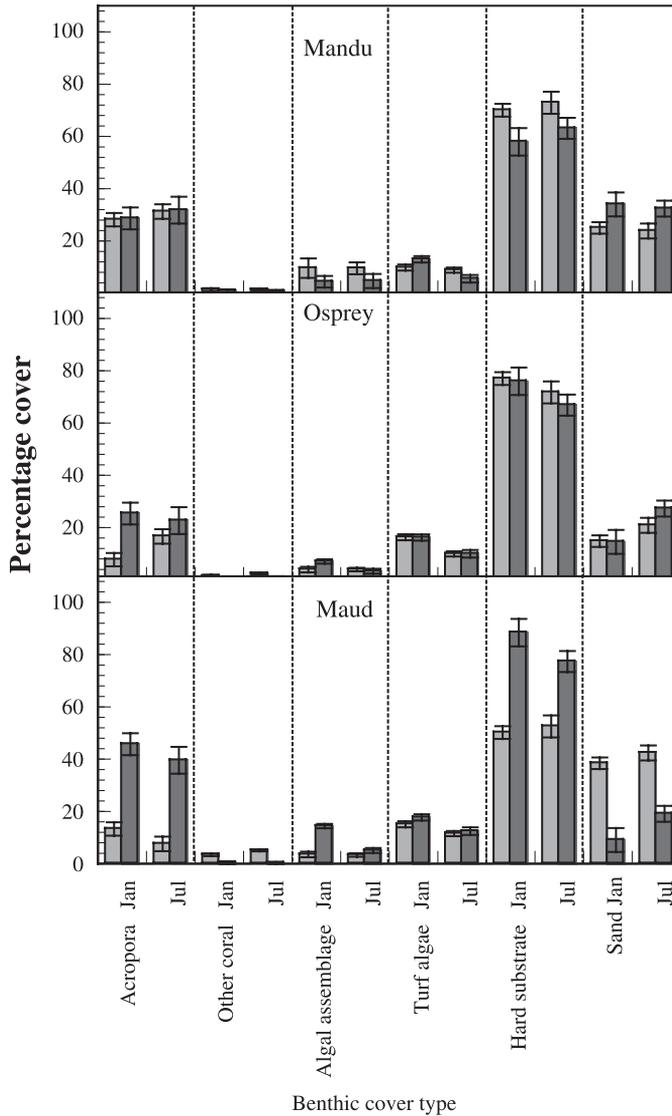

Fig. 7. Mean benthic cover (% ± S.E.) for sanctuary (■) and recreation (■) zones from each region in January and July 2000 ($n = 8$).

and Osprey, there were significant patterns using one-way ANOSIM in July and January, respectively (Table 7, Fig. 6). Trends at Maud were consistent over time with a clear separation between zones. SIMPER analysis (Table 7) indicated that *Acropora* coral and total hard substrate cover were primarily responsible for dissimilarity between zones. Contributions from algal assemblage, turf algae, and other coral types were generally much lower.

3.3.2. Univariate analysis

ANOVA revealed a significant difference between regions for turf algae and significant interactions between region and zone for *Acropora* coral cover, and total hard substrate cover (Table 8, Fig. 7) (see Table 7 for relative cover values). Analysis of interactions showed a significantly greater cover of *Acropora* coral and total hard substrate at the Maud recreation zone than at the sanctuary zone, and a significant difference in *Acropora* coral cover between sanctuary zones at each region. Analysis of rugosity measurements showed a significant difference between regions ($P < 0.01$), with Mandu and Maud being more rugose than Osprey (Fisher's PLSD post-hoc: $P < 0.01$) but there was no significant difference between zones.

4. Discussion

4.1. Species composition and family level differences

This study has provided a rare comparison of targeted fish assemblages in sanctuary and fished areas, where recreational line fishing is the only pressure exerted on fish stocks. Under these circumstances, we have shown that the sanctuary zones studied at Ningaloo Marine Park support a different composition of targeted fish families/genera to adjacent recreation zones. Differences in fish composition between fished and unfished zones have been demonstrated in other coral reef MPA comparisons (Jennings et al., 1996b; Rakitin and Kramer, 1996; Roberts and Hawkins, 1997; Wantiez et al., 1997; Chiappone and Sealey, 2000), but where fishing pressure was exerted by commercial or artisanal fishers. Our study has shown that recreational line fishing alone may, in some cases, be sufficient to alter the composition of targeted fish.

Trends for fish family/genera composition in terms of biomass were stronger than those using abundance data. Mandu showed the greatest difference between zones of the three regions. Although not significant, there was a separation in nMDS ordinations between zones for biomass at Osprey and Maud. Differences in assemblages were driven by lethrinids, which constituted approximately 78% of all fish censused and differed between zones in terms of biomass, mean size, and abundance of legal-sized fish. We recorded no differences in other families/genera (Lutjanidae, Haemulidae, Serranidae, and *Choerodon* spp.) between zones. However, these families combined formed less than 22% of fish censused. The mean size of lethrinids was smaller in the fished zones, which may be the result of recreational fishers removing the larger legal-sized fish. This was supported by the fact that legal-sized lethrinids were significantly more abundant in the sanctuary zones (i.e., where there was no fishing pressure). There was also a greater abundance of legal-

sized lethrinids at the Maud region, than at Mandu or Osprey (Fig. 4). Differences in the abundance of under-sized lethrinids were not significant, but they tended to be more abundant at the Mandu and Osprey regions, than at Maud. A number of factors may have influenced these findings, including the duration of protection and the level of fishing pressure. These factors varied between the regions we sampled but were not controlled in the design of our study.

Other researchers have noted the vulnerability of lethrinids to overfishing, with significant differences in abundances between fished and unfished zones (Letourneur, 1996c; Russ and Alcala, 1998). Watson and Ormond (1994) recorded mean abundances of *Lethrinus* spp. within an unfished marine park that were over 500 times higher than on an apparently identical reef that was fished artisanally. Our results indicate that recreational fishing has reduced the biomass, mean size, and abundance of legal-sized lethrinids in the fished zones of the study areas.

4.2. Habitat structure

In our study, there was a possibility that the differences we observed in fish assemblages between zones were a consequence of factors other than fishing pressure such as the influence of benthic cover (Galzin et al., 1994; Jennings et al., 1996a) and topographic complexity (Ohman et al., 1997; Connell and Kingsford, 1998) on fish assemblages. These factors are discussed below.

In multivariate analyses of benthic cover, *Acropora* coral appeared to be influencing between-zone differences and tended to be greater in the recreation zones at Osprey and Maud, and very similar between zones at Mandu. Significant differences in overall hard substrate cover were also inconsistent and there was no difference in rugosity between zones within any region in our study. Greater abundance, biomass, and species richness of coral reef fishes have been associated with more topographically complex habitats (Letourneur, 1996a; Friedlander and Parrish, 1998) and greater coral cover (Chabanet et al., 1997). Other researchers have shown no such relationship between these variables (Roberts, 1995; Roberts and Ormond, 1987), but still recorded greater abundance and biomass of fish in no-fishing zones. Ayling and Ayling (1987) noted that *L. nebulosus* at Ningaloo were most common in areas where sandy substratum was associated with coral patches. This sand and coral habitat was typical of all locations in our study. The inconsistent differences we recorded in habitat and the similarity of rugosity measures do not explain the differences in fish assemblages between zones.

Algal cover may provide a structural habitat (Sala, 1997) or food source (De Ridder and Lawrence, 1982; Babcock et al., 1999) for invertebrates, which are in turn preyed on by fish (Hiatt and Strasbourg, 1960; Hobson, 1974). Thus, differences in algal cover may have influenced predatory fish populations. There were no significant differences in algal assemblage cover between zones, but it tended to be higher in the recreation zone at Maud (driven by *Dictyota* and *Lobophora* spp.) and the sanctuary zone at Mandu in July (driven by extensive seasonal growth of *Turbinaria ornata*). Cover of algal turf did not differ significantly between zones. Other researchers have noted relationships between the cover of algal turf and the abundance of herbivorous fish (Polunin and Klumpp, 1992) and invertebrates (Morrison, 1988), the potential prey of the targeted predatory fish we

censused (Randall, 1967; Jones et al., 1991). However, there were no similar patterns between algal cover and the targeted fish populations in the regions we studied.

It was possible that observed differences between zones were an artefact of habitats or fish assemblages prior to implementation of sanctuary zones. A criterion for determining sanctuary zones in the Ningaloo Marine Park stated that, "Representative areas of high biological and structural diversity have priority" (CALM, 1989). We chose comparative zones in each region that were similar in terms of bathymetry, proximity to channel areas, and distance from shore, and the aforementioned benthic cover results confirm that there were no consistent differences between zones. It therefore seems unlikely that presanctuary zoning effects influenced the targeted fish assemblages in our study.

The aforementioned differences in habitat structure are unlikely to explain the different composition of fish families and the greater biomass, size, and abundance of legal-sized lethrinids in sanctuary zones. The consistent findings from our census of targeted fish across three regions of the Ningaloo Marine Park suggest that the cessation of fishing in these sanctuary zones exerts an overriding influence on targeted fish assemblages and particularly lethrinids.

4.3. Sanctuaries for the protection of targeted fish

The sanctuary zones we examined at Ningaloo have, to some extent, met the management objective of preserving higher numbers of mature-sized fish, and thus potential spawning stock. For a sanctuary to have achieved this, the proportion of spawning age/size fish should be greater than adjacent fished areas, as was the case at the regions we studied. Theoretically, larval export from the Maud sanctuary should be greater than the Mandu or Osprey sanctuaries, given the greater abundance of large lethrinids. However, this was not reflected in high numbers of juvenile fish in the Maud recreation zone, perhaps due to eggs and larvae being transported to other areas or density-dependent effects on recruitment.

Sanctuary zones at Ningaloo may be preserving higher numbers of potential spawning fish, but we do not know whether the spawning fish were sufficient to replenish fished areas, whether they actually spawn within the sanctuary zones, or how and where eggs and larvae are dispersed. D'Adamo and Simpson (2001) reported that circulation within the lagoons at Ningaloo is driven by a wave-pumping effect, with water coming over the reef crest and flowing out via channels in the back reef. Consequently, some eggs and larvae may be dispersed in the lagoons, but lagoon flushing times are rapid (6 h to 5 days depending on wave, tide, and wind conditions) and eggs and larvae may also be dispersed by passing oceanic currents. D'Adamo and Simpson (2001) suggest that Ningaloo may act as a source of eggs and larvae to reefs in the Monte Bello Islands and Dampier Archipelago (proposed marine reserves 250 and 400 km to the north of Ningaloo, respectively) during summer, with their transport facilitated by the north-flowing Ningaloo current. However, there is debate in the literature on the mobility of fish larvae and oceanographic transport mechanisms. Some authors have rejected the assumption that settlement stage reef fish larvae are passive (Leis and Carson-Ewart, 2001). But larval mobility increases with age (Fisher et al., 2000) and, during earlier developmental stages

(presettlement), larval dispersal may depend more on oceanographic conditions than swimming. Recent studies have demonstrated both passive and active dispersal among different fish species (Tilney et al., 1996; Smith, 2000).

5. Conclusion

This study is unique in that it has highlighted differences between fished and unfished areas of a fringing coral reef marine park that is subject only to recreational line fishing. We have demonstrated differences in predatory fish assemblages between sanctuary and recreation zones in three regions of the Ningaloo Marine Park. Differences appeared to be due to the removal of fishing pressure from the sanctuary areas and could not be explained by habitat variables. Our data suggest that fishing of legal-sized lethrinids in recreation zones has depleted their numbers to levels below that in sanctuary zones. The greater abundance of lethrinids in the sanctuary zone at Maud (compared with Mandu and Osprey) may be due to its size or the duration of protection, but these factors need to be investigated.

Our findings highlight the need for managers to understand that recreational fishing may significantly affect populations of targeted fish. The study has implications for the management of marine parks and recreational fishing, and assessment of the importance of sanctuary areas for protecting fish stocks. These findings may be of particular relevance in developed countries where recreational fishing is popular and MPAs are being established for fisheries management and conservation purposes. Western Australia has a population of 1.9 million and coastline of 12,500 km. Despite this sparse population, the potential effects of recreational fishing on targeted fish seemed apparent. A greater effect could be expected in more densely populated regions.

Future studies that would be universally applicable to marine parks should investigate larval transport and spillover of mature fish from sanctuary zones, under a recreational fishing regime. The effect of removing predatory fish on other reef biota has been shown elsewhere (McClanahan, 1997; Rosado Solorzano and del Proo, 1998; Babcock et al., 1999), but generally under a commercial or artisanal fishing regime. Potential trophic effects that may arise from recreational fishing should therefore also be investigated.

Acknowledgements

References

Agbayani, E., 2002. Fishbase: estimation of life-history key facts. www.fishbase.org.

Ayling, A.M., Ayling, A.L., 1987. Ningaloo Marine Park: Preliminary Fish Density Assessment and Habitat Survey. Sea Research, Daintree, Queensland, Australia.

Babcock, R.C., Kelly, S., Shears, N.T., Walker, J.W., Willis, T.J., 1999. Changes in community structure in temperate marine reserves. Mar. Ecol. Prog. Ser. 189, 125–134.

Bortone, S.A., Martin, T., Bundrick, C.M., 1991. Visual census of reef fish assemblages: a comparison of slate, audio, and video recording devices. Northeast Gulf Sci. 12, 17–23.

CALM, 1989. Ningaloo Marine Park (State Waters) Management Plan 1989–1999. Department of Conservation and Land Management, Perth, Western Australia.

CALM, 1999. Parks of the coral coast resource use database: aerial survey results. Camping, Vehicles and Vessels 1995–1997. Department of Conservation and Land Management-Exmouth, Exmouth, Western Australia.

Cappo, M., Brown, I.W., 1996. Evaluation of Sampling Methods for Reef Fish Populations of Commercial and Recreational Interest. CRC Reef Research Centre, Townsville, Queensland, Australia.

Chabanet, P., Ralambondrainy, H., Amanieu, M., Faure, G., Galzin, R., 1997. Relationships between coral reef substrata and fish. Coral Reefs 16, 93–102.

Chiappone, M., Sealey, K.M.S., 2000. Marine reserve design criteria and measures of success: lessons learned from the Exuma Cays Land and Sea Park, Bahamas. Bull. Mar. Sci. 66, 691–705.

Chiappone, M., Sluka, R., Sealey, K.S., 2000. Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. Mar. Ecol. Prog. Ser. 198, 261–272.

Clarke, K.R., 1993. Non parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.

Clarke, K.R., Warwick, R.M., 1994. Changes in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth Marine Laboratory, UK.

Connell, S.D., Kingsford, M.J., 1998. Spatial, temporal and habitat related variation in the abundance of large predatory fish at One Tree Reef, Australia. Coral Reefs 17, 49–57.

D'Adamo, N., Simpson, C.J., 2001. Review of the Oceanography of Ningaloo Reef and Adjacent Waters. Marine Conservation Branch, Department of Conservation and Land Management, Perth, Western Australia.

De Ridder, C., Lawrence, J.M., 1982. Food and feeding mechanisms: Echinoidea. In: Jangoux, M., Lawrence, J.M. (Eds.), Echinoderm Nutrition. A.A. Balkema, Rotterdam.

Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8, 37–52.

Fisher, R., Bellwood, D.R., Job, S.D., 2000. Development of swimming abilities in reef fish larvae. Mar. Ecol. Prog. Ser. 202, 163–173.

Friedlander, A.M., Parrish, J.D., 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J. Exp. Mar. Biol. Ecol. 224, 1–30.

Galzin, R., Planes, S., Dufour, V., Salvat, B., 1994. Variation in diversity of coral reef fish between French Polynesian atolls. Coral Reefs 13, 175–180.

Hiatt, R.W., Strasbourg, D.W., 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30, 65–127.

Hobson, E.S., 1974. Feeding relationships of Teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull. 72, 915–1031.

Jennings, S., Boulle, D.P., Polunin, N.V.C., 1996a. Habitat correlates of the distribution and biomass of Seychelles' reef fishes. Environ. Biol. Fisches 46, 15–25.

Jennings, S., Marshall, S.S., Polunin, N.V.C., 1996b. Seychelles' marine protected areas: comparative structure and status of reef fish communities. Biol. Conserv. 75, 201–209.

Jones, G.P., Ferrell, D.J., Sale, P.F., 1991. Fish predation and its impacts on the invertebrates of coral reefs and adjacent sediments. In: Sale, P.F. (Ed.), The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, CA, USA, pp. 156–179.

Kelleher, G., 1999. Guidelines for Marine Protected Areas. IUCN, Gland, Switzerland.

Kulbicki, M., Moutham, G., Thollet, P., Wantiez, L., 1993. Length–weight relationships of fish from the lagoon of New Caledonia. NAGA, ICLARM Q., 26–33.

Leis, J.M., Carson-Ewart, B.M., 2001. Behaviour of pelagic larvae of four coral-reef fish species in the ocean and an atoll lagoon. Coral Reefs 19, 247–257.

Letourneur, Y., 1996a. Dynamics of fish communities on Reunion fringing reefs, Indian Ocean: 1. Patterns of spatial distribution. J. Exp. Mar. Biol. Ecol. 195, 1–30.

Letourneur, Y., 1996b. Dynamics of fish communities of Reunion fringing reefs, Indian Ocean: 2. Patterns of temporal fluctuations. J. Exp. Mar. Biol. Ecol. 195, 31–52.

Letourneur, Y., 1996c. Fish populations after establishment of a marine reserved at Mayotte: I. Western Indian Ocean. Ecoscience 3, 442–450.

McClanahan, T.R., 1997. Primary succession of coral-reef algae: differing patterns on fished versus unfished reefs. J. Exp. Mar. Biol. Ecol. 218, 77–102.

McClanahan, T.R., Kaunda Arara, B., 1996. Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. Conserv. Biol. 10, 1187–1199.

McClanahan, T.R., Shafir, S.H., 1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. Oecologia 83, 362–370.

McClanahan, T.R., Muthiga, N.A., Kamukuru, A.T., Machano, H., Kiambo, R.W., 1999. The effects of marine parks and fishing on coral reefs of northern Tanzania. Biol. Conserv. 89, 161–182.

Moran, M., Edmonds, J., Jenke, J., Cassells, G., Burton, C., 1993. Fisheries Biology of Emperors (Lethrinidae) in North-west Australian Coastal Waters. Western Australian Marine Research Laboratories, Fisheries Western Australia, Perth.

Morrison, D., 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. Ecology 69, 1367–1382.

Ohman, M.C., Rajasuriya, A., Olafsson, E., 1997. Reef fish assemblages in north-western Sri Lanka: distribution patterns and influences of fishing practices. Environ. Biol. Fisches 49, 45–61.

Polunin, N.V.C., Klumpp, D.W., 1992. Algal food supply and grazer demand in a very productive coral-reef zone. J. Exp. Mar. Biol. Ecol. 164, 1–15.

PRIMER-E, 2000. Plymouth routines in multivariate ecological research. PRIMER 5 for Windows version 5.1.1. Plymouth, UK.

Rakitin, A., Kramer, D.L., 1996. Effect of a marine reserve on the distribution of coral reef fishes in Barbados. Mar. Ecol. Prog. Ser. 131, 97–113.

Randall, J.E., 1967. Food habits of the reef fish of the West Indies. Stud. Trop. Oceanogr. 5, 665–847.

Roberts, C.M., 1995. Rapid build up of fish biomass in a Caribbean marine reserve. Conserv. Biol. 9, 815–826.

Roberts, C.M., Hawkins, J.P., 1997. How small can a marine reserve be and still be effective? Coral Reefs 16, 150.

Roberts, C.M., Ormond, R.F.G., 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Mar. Ecol. Prog. Ser. 41, 1–8.

Rooker, J.R., Dokken, Q.R., Pattengill, C.V., Holt, G.J., 1997. Fish assemblages on artificial and natural reefs in the Flower Garden Banks National Marine Sanctuary, USA. Coral Reefs 16, 83–92.

Rosado Solorzano, R., del Proo, S.A.G., 1998. Preliminary trophic structure model for Tampamachoco lagoon, Veracruz, Mexico. Ecol. Model. 109, 141–154.

Russ, G.R., Alcala, A.C., 1996. Marine reserves: rates and patterns of recovery and decline of large predatory fish. Ecol. Appl. 6, 947–961.

Russ, G.R., Alcala, A.C., 1998. Natural fishing experiments in marine reserves 1983–1993: roles of life history and fishing intensity in family responses. Coral Reefs 17, 399–416.

Sala, E., 1997. The role of fishes in the organization of a Mediterranean sublittoral community: II. Epifaunal communities. J. Exp. Mar. Biol. Ecol. 212, 45–60.

SAS Institute, 2000. JMP Version 4.0.2. Cary, NC, USA.

Shaw, J., 2000. Fisheries environmental management review. Gascoyne. Fisheries Western Australia, Perth, p. 229.

Smith, K.A., 2000. Active and passive dispersal of *Centroberyx affinis* (Berycidae) and *Gonorynchus greyi* (Gonorynchidae) larvae on the Sydney shelf. Mar. Freshw. Res. 51, 229–234.

Sumner, N.R., Williamson, P.C., Malseed, B.E., 2002. A 12-Month Survey of Recreational Fishing in the Gascoyne Bioregion of Western Australia During 1998–99. WA Marine Research Laboratories, Department of Fisheries, Perth, Western Australia.

Tilney, R.L., Nelson, G., Radloff, S.E., Buxton, C.D., 1996. Ichthyoplankton distribution and dispersal in the Tsitsikamma Coastal National Park marine reserve, South Africa. S. Afr. J. Mar. Sci./S. Afr. Tydskr. Suiweltegnol. 17, 1–14.

Wantiez, L., Thollot, P., Kulbicki, M., 1997. Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. Coral Reefs 16, 215–224.

Watson, M., Ormond, R.F.G., 1994. Effect of an artisanal fishery on the fish and urchin populations of a Kenyan Coral reef. Mar. Ecol. Prog. Ser. 109, 115–129.

Weaver, P.R., 1998. An oral history of Ningaloo Reef. Edith Cowan University, Perth, Western Australia.

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