

# Reef fish assemblages in north-western Sri Lanka: distribution patterns and influences of fishing practises

Marcus C. Öhman,<sup>1</sup> Arjan Rajasuriya<sup>2</sup> & Emil Ólafsson<sup>1</sup>

<sup>1</sup>*Department of Zoology, Stockholm University, 10691 Stockholm, Sweden*

<sup>2</sup>*National Aquatic Resources Agency, Crow Island, Colombo 15, Sri Lanka*

Received 11.10.1995

Accepted 4.5.1996

**Key words:** habitat structure, habitat partitioning, sandstone reef, coral reef, fish community, zonation, human disturbance

## Synopsis

The distribution and abundance of reef fishes in relation to habitat structure were studied within Bar Reef Marine Sanctuary (BRMS) and on an adjacent reef, disturbed by destructive fishing techniques, in north-western Sri Lanka, by visually censusing 135 species groups using fifty metre belt-transects. Two types of continental shelf patch-reefs are found in the study area: coral reefs and sandstone reefs, which are divided into distinct habitats, four for the coral reef (shallow reef flat, shallow patch reef, deep reef flat and *Porites* domes) and two for the sandstone reef (structured sandstone-reef and flat sandstone-reef). Fish assemblages varied in structure between reef types and among habitats within reef types. Functional aspects of habitat structure and composition, such as available food and shelter, seemed to be important factors influencing distribution patterns. The strongest separation in the organisation of fish assemblages in BRMS was between reef types: 19% of all species were confined to the coral-reef patches while 22% were restricted to the sandstone reef patches and 59% were represented on both reef types. In terms of distribution among habitats, 21% of all species were restricted to one habitat while only 1.5% were present in all. The highest density of fish was in the coral reef habitats while highest species diversity was found in the most structurally complex habitat: the structured sandstone-reef. This habitat also had the highest proportion of species with restricted distribution. Planktivores were the most abundant trophic group in BRMS, and the species composition of the group varied among habitats. The comparison of the disturbed reef with BRMS suggested that habitat alteration caused by destructive fishing methods has strongly influenced the fish community. Within the fished area the structure of the fish assemblages was more heterogeneous, fish abundance was lower by an order of magnitude and species numbers were lower than in BRMS.

## Introduction

There is, at present, a bias for certain biogeographical regions, reef types and habitats in studies on tropical reef-fish ecology. Most research has been carried out on the Great Barrier Reef and in the Caribbean (Sale 1991). Commonly studied reef types

are fringing coral reefs and barrier reefs including lagoonal patch reefs (Williams 1991). There are reasons to believe that this inclination towards these regions and habitat types has caused researchers to over-emphasise the importance of certain ecological processes in reef-fish population dynamics, e.g. little is known on the ecology and structure of reef-

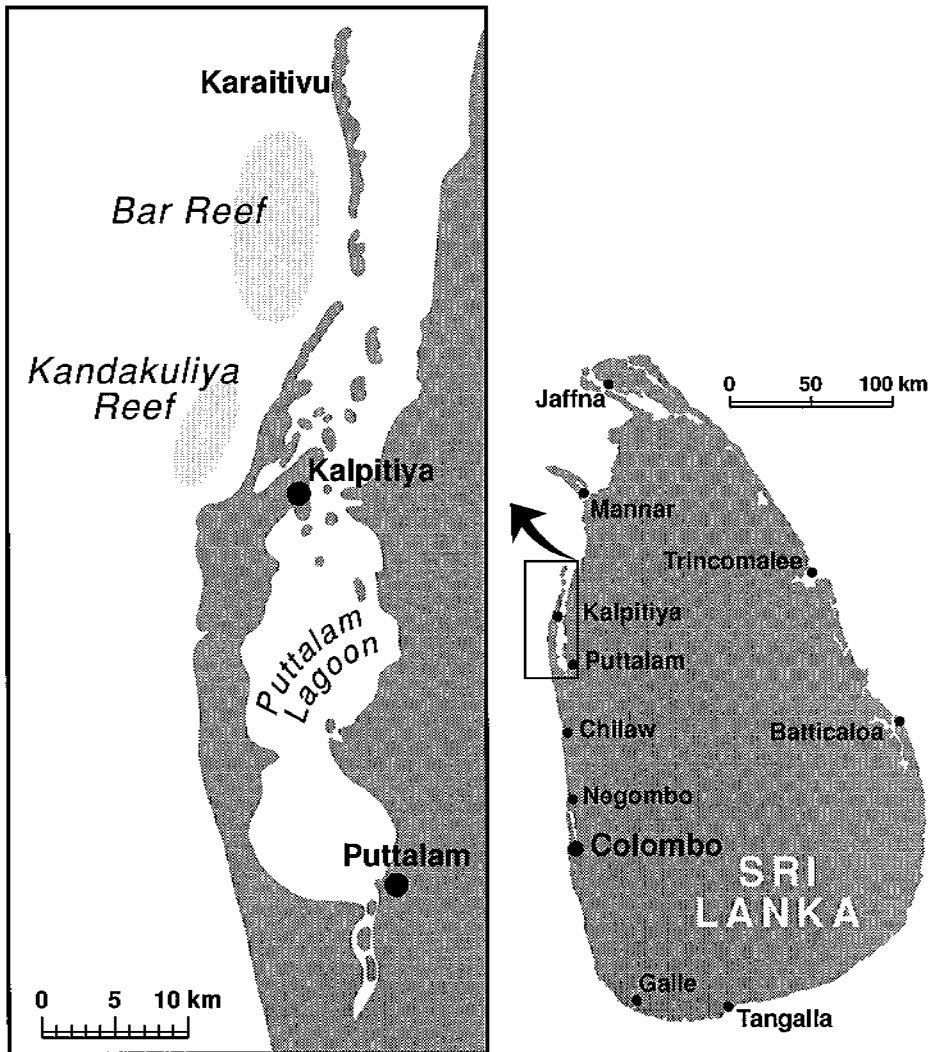


Figure 1. Map of Sri Lanka with study area indicated.

fish communities in the Indian Ocean and parts of the Pacific. Tropical reef types that have received less attention are atoll reefs, continental shelf patch-reefs, platform reefs, rocky reefs and sandstone reefs.

The first step in studying reef fish ecology in a new area should be to describe patterns in their distribution and abundance. This has been carried out on a number of reefs (Hiatt & Strasburg 1960, Gosline 1965, Chave & Eckert 1974, Goldman & Talbot 1976, Clarke 1977, Harmelin-Vivien 1977, Gladfelter & Gladfelter 1978, Bouchon-Navaro 1980, Bouchon-Navaro & Harmelin-Vivien 1981, Russ 1984b,

Russ 1989). In some of these studies it has been found that species and functional groups can have uneven distribution among habitats, with some species closely associated with certain habitats and others with widespread distribution. These patterns may be determined by varied needs in food and shelter requirements characterising different assemblages (Williams 1991). Such needs could explain correlations found in some studies between fish population numbers and specific features of the reef habitat such as structural complexity and the proportion of live coral cover (Risk 1972, Clarke 1977, Luckhurst & Luckhurst 1978, Carpenter et al.

1981, Bell & Galzin 1984, Bouchon-Navaro & Bouchon 1989, Grigg 1994). If fish assemblages are affected by variation in habitat structure, physical disturbance on the reef would then be expected to alter fish numbers. Such impact may be the result of human activities like the use of destructive fishing techniques (McManus 1988, Samoily 1988, Russ & Alcala 1989, Russ 1991, Öhman et al. 1993).

The reefs of Sri Lanka, the area of interest in this study, have been little studied. There are no earlier quantitative descriptions of the reef fish assemblages from the reefs of this region. Dominant reef types in this region are continental shelf patch-reefs. The first aim of this study was to describe patterns in the distribution and abundance of fish populations in relation to habitat structure in a reef area of north-western Sri Lanka. The second aim was to investigate how destructive fishing techniques used in these areas may influence the local reef-fish assemblages.

## Methods

### Study sites

This study was carried out in Bar Reef Marine Sanctuary (BRMS) and on Kandakuliya Reef off the Kalpitiya peninsula in the southern Gulf of Manner region, north-western Sri Lanka (Figure 1). BRMS covers an area of 306.7 km<sup>2</sup> with the closest coral patches ca. 2 km west off the north point of Kalpitiya peninsula. Although, the increased human population in the region have posed a threat to Bar Reef (Öhman et al. 1993) it is considered an undis-

turbed reef (Rajasuriya et al. 1995) which has, due to its remoteness been protected over the years. However, *Acanthaster planci* have had an impact in some section of the reef area (Rajasuriya et al. 1995). Bar Reef was declared a marine sanctuary in 1992. Kandakuliya Reef, which has been heavily disturbed by the local fishery (see Öhman et al. 1993), is situated south of Bar Reef ca. 2 km offshore of the fishing villages Kandakuliya and Kudawa.

Reefs in this study are continental shelf patch-reefs. The coral patches are separated by sand, rubble and sandstone and vary in size from a few square-metres to more than a hectare. There are two types of reefs within the BRMS: shallow coral reefs and deep sandstone reefs (west of the coral-reef patches). On the basis of substratum composition and depth these reefs were a priori divided into seven habitats. Six habitat forms were investigated within the BRMS. The shallow coral reef flat (SRF) contains shallow (average 3 m depth) reef-beds with patches larger than a hectare. Branching *Acropora* is by far the most dominant genus although significant stands of *Echinopora* and *Montipora* are also present. The shallow patch reef (SPR) is found on average 1–2 m deeper than SRF and consist of smaller coral patches interrupted with larger proportions of sand. The deep reef flat habitat (DRF) is, as the former two, dominated by branching *Acropora* corals, although, tabular *Acropora* is also common. This habitat type is situated deeper (depth ca. 8 m) with patches that are more continuous and cover larger areas than both the SRF and SPR. The fourth coral reef habitat, the *Porites* dome habitat (POD), occurs at ca. 10 m

Table 1. Number of censuses (transects) for each habitat and year.

Habitat	1993	1994	Σ
Disturbed Shallow Reef (DSR)	12	8	20
Shallow Reef Flat (SRF)	7	4	11
Shallow Patch Reef (SPR)	6	5	11
Deep Reef Flat (DRF)	0	6	6
Porites Dome Reef (POD)	3	8	11
Structured Sandstone Reef (SSR)	5	13	18
Flat Sandstone Reef (FSR)	0	6	6
Σ	33	50	83

Table 2. The 135 species and species groups, in 19 families, which were counted within transects. Based on published material and field observations they were divided into eight broad trophic categories determined by their preferred feeding habits including: piscivores (F; incl. F/I), invertebrate and fish feeders (I/F), invertebrate feeders (I; incl. I/P), corallivores (C; incl. C/I, C/O), planktivores (P; incl. P/O, P/H), detritivores (D; incl. D/H), herbivores (H; incl. H/D, H/O, H/C, H/I), and omnivores (O; incl. O/I). Families in alphabetic order.

<b>Acanthuridae</b>		<i>Forcipiger longirostris</i>	I	<i>S. xenochrous</i>	I
<i>Acanthurus bariene</i>	H	<i>Hemitaurchichthys zoster</i>	P	<b>Pomacanthidae</b>	
<i>A. blochii</i>	H	<i>Heniochus acuminatus</i>	O	<i>Apolemichthys xanthurus</i>	I
<i>A. dussumieri</i>	H/D	<i>H. monoceros</i>	O	<i>Centropyge multispinis</i>	H/D
<i>A. leucosternon</i>	H	<i>H. pleurotaenia</i>	O	<i>Pomacanthus annularis</i>	I
<i>A. lineatus</i>	H	<i>H. singularis</i>	O	<i>P. imperator</i>	I
<i>A. mata</i>	P	<b>Ehippidae</b>		<i>P. semicirculatus</i>	I
<i>A. tristis</i>	H	<i>Platax</i> spp.	I/P	<b>Pomacentridae</b>	
<i>A. triostegus</i>	H	<b>Haemulidae</b>		<i>Abudefduf vaigiensis</i>	P/O
<i>A. xanthopterus</i>	D/H	<i>Plectorhinchus</i> sp. 1	I	<i>Amphiprion</i> spp.	P
<i>Ctenochaetus binotatus</i>	D	<i>P.</i> sp. 2	I	<i>Chromis viridis</i>	P
<i>C. striatus</i>	D	<i>P. obscurum</i>	I	<i>Dascyllus aruanus</i>	P/O
<i>C. strigosus</i>	D	<i>P. vittatus</i>	I	<i>D. trimaculatus</i>	P/O
<i>Naso annulatus</i>	P	<i>P. schotaf</i>	I	<i>Plectroglyphidodon dickii</i>	H/O
<i>N. brevirostris</i>	P/H	<b>Kyphosidae</b>		<i>P. lacrymatus</i>	H/O
<i>N. hexacanthus</i>	P	<i>Kyphosus</i> spp.	H/O	<i>Pomacentrus chrysurus</i>	H/O
<i>N. lituratus</i>	H	<b>Labridae</b>		<i>P. similis</i>	O
<i>N. unicornis</i>	H	<i>Anampses lineatus</i>	I	<i>Stegastes</i> spp.	H/O
<i>N. vlamingii</i>	P	<i>Bodianus</i> spp.	I	<b>Scaridae</b>	
<i>Zebrasoma scopas</i>	H	<i>Cheilinus</i> spp.	I/F	<i>Chlorurus</i> sp.	H/C
<i>Z. desjardini</i>	H	<i>C. undulatus</i>	I/F	<i>Cetoscarus bicolor</i>	H
<b>Balistidae</b>		<i>Coris</i> spp.	I	<i>Scarus atrilunula</i>	H
<i>Balistapus undulatus</i>	O	<i>Epibulus insidiator</i>	I/F	<i>S. frenatus</i>	H
<i>Balistidae</i> spp.	O/I	<i>Gomphosus caeruleus</i>	I	<i>S. niger</i>	H
<i>Balistoides conspicillum</i>	O	<i>Halichoeres centriquadus</i>	I	<i>S. scaber</i>	H
<i>B. viridescens</i>	O	<i>H. marginatus</i>	I	<i>S. sordidus</i>	H
<i>Odonus niger</i>	P	<i>H. leucoxanthus</i>	I	<b>Serranidae</b>	
<b>Caesionidae</b>		<i>Hemigymnus fasciatus</i>	I	<i>Aethaloperca rogaa</i>	F/I
<i>Caesio caerulea</i>	P	<i>H. melapterus</i>	I	<i>Cephalopholis argus</i>	F/I
<i>C. cunning</i>	P	<i>Labrichthys unilineatus</i>	C	<i>C. miniata</i>	F/I
<i>Pterocaesio marri</i>	P	<i>Labroides dimidiatus</i>	I	<i>C. sonnerati</i>	F/I
<i>P. tile</i>	P	<i>Thalassoma hardwicke</i>	I	<i>Epinephelus caeruleopunct.</i>	F/I
<b>Carangidae</b>		<i>T. janseni</i>	I	<i>E. fasciatus</i>	F/I
<i>Caranx</i> spp.	F/I	<i>T. lunare</i>	I	<i>E. fuscoguttatus</i>	F/I
<b>Chaetodontidae</b>		<b>Lethrinidae</b>		<i>E. hexagonatus</i>	F/I
<i>Chaetodon auriga</i>	I	<i>Lethrinus harak</i>	I	<i>E. longispinis</i>	F/I
<i>C. collare</i>	C/I	<i>L. nebulosus</i>	I/F	<i>E. merra</i>	F/I
<i>C. decussatus</i>	O	<i>L.</i> sp.	I/F	<i>E. tukula</i>	F/I
<i>C. falcula</i>	O	<i>Monotaxis grandoculis</i>	I/F	<i>E. undulosus</i>	F/I
<i>C. gardineri</i>	O	<b>Lutjanidae</b>		<i>Pseudanthias</i> spp.	P
<i>C. guttatissimus</i>	O	<i>Lutjanus bohar</i>	F/I	<i>Plectropomus laevis</i>	F/I
<i>C. kleinii</i>	O	<i>L. decussatus</i>	I/F	<i>P. maculatus</i>	F/I
<i>C. lineolatus</i>	C/O	<i>L. fulviflamma</i>	I/F	<i>Variola louti</i>	F/I
<i>C. lunula</i>	O	<i>L. gibbus</i>	I/F	<b>Siganidae</b>	
<i>C. melannotus</i>	C	<i>L. quinque-lineatus</i>	I/F	<i>Siganus</i> sp.	H
<i>C. octofasciatus</i>	C	<i>L.</i> spp.	I/F	<i>S. stellatus</i>	H
<i>C. plebeius</i>	C	<i>Macolor niger</i>	P	<i>S. javus</i>	H
<i>C. rafflesii</i>	C/I	<b>Muraenidae</b>		<i>S. lineatus</i>	H/I
<i>C. triangulum</i>	C	<i>Gymnothorax</i> spp.	F/I	<b>Sphyraenidae</b>	
<i>C. trifascialis</i>	C	<b>Nemipteridae</b>		<i>Sphyraena</i> spp.	F
<i>C. trifasciatus</i>	C	<i>Scolopsis bimaculatus</i>	I		
<i>C. unimaculatus</i>	C	<i>S. vosmeri</i>	I		

depth and is made up of large *Porites* domes surrounded by sand and *Acropora* stands.

Two habitats were distinguished for the sandstone reef: the structured sandstone reef (SSR) and the flat sandstone reef (FSR). The SSR patches consist of rocky sandstone substrate at around 19 m depth which rise off the substratum causing a structured reef with a significant topographic relief. Patches are characterised by rocks and small hills as well as fragmented plateau-like structures with holes and crevices. The relief from the crest to the trough varies between a few dm to several metres. There are large areas west of the Kalpitiya Peninsula that could be characterised as having a flat sandstone substratum. However, the habitat typified a priori as the FSR for this study uniquely contained circular patches with depressions and holes. This habitat, which is situated at around 22 m depth, has a low coral cover and lacks prominent structures.

The disturbed shallow reef (DSR) within the Kandakuliya Reef area is made up of shallow reef patches covered by coral rubble at the same depth range as SRF and SPR. This area has been heavily affected by intensive fishing where destructive fishing techniques (bottom-set nylon-nets; see Öhman et al. 1993) and anchor damage caused habitat deformation. There are also unconfirmed reports of dynamite fishing. Earlier this area resembled the shallow reef flat and the shallow patch reef of the sanctuary with high proportions of live branching *Acropora* (Rajasuriya & DeSilva 1988).

### Field methods

This study was carried out during February and March in 1993 and 1994 as part of a larger project studying the ecology of the reefs in north-western Sri Lanka (NARA-Sida SAREC Marine Science Programme; see Rajasuriya et al. 1995). A total of 83 transects were censused within the Bar and Kandakuliya reef areas. Thirty-three transects were censused in 1993 followed by 50 in 1994 (Table 1). Each transect (50 m long) was taken by randomly laying a stretched fibre-glass measuring tape within a given habitat.

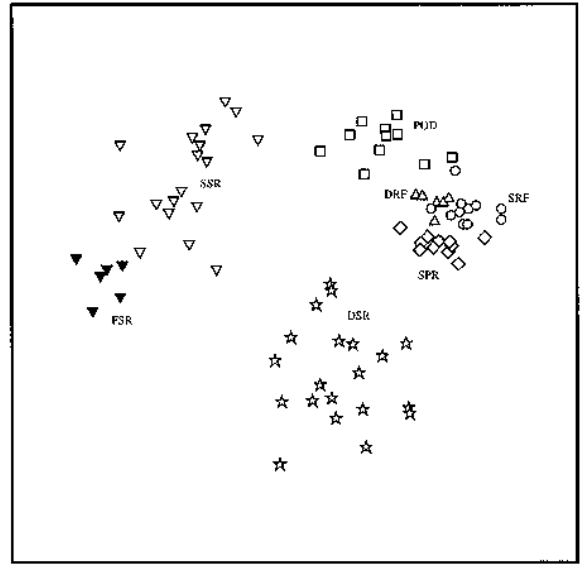


Figure 2. Multidimensional scaling ordination of Bray-Curtis similarity matrix of  $\sqrt{\sqrt{}}$  transformed abundance data (number of individuals for all species per transect). Different symbols represent different habitats indicated in the figure: DSR = Disturbed Shallow Reef, SRF = Shallow Reef Flat, SPR = Shallow Patch Reef, DRF = Deep Reef Flat, POD = *Porites* Dome, SSR = Structured Sandstone Reef, FSR = Flat Sandstone Reef.

Fish counts were carried out during mid-day using the belt transect method (Fowler 1987, McCormick & Choat 1987, English et al. 1994). To minimise divers impact each fish census commenced 5 to 10 minutes after the tape had been laid out. The fish were recorded by swimming along the transect within a 50 x 10 m corridor (500 m<sup>2</sup>).

Most fish were identified to species level, although some of the less common or taxonomically difficult were only identified to a higher taxonomic level. To verify species identification specimens were collected and investigated by the Swedish Museum of Natural History (NRM). Cryptic species and those regarded as rare were excluded from the study. Altogether, 135 species groups belonging to 19 families were included in the survey (Table 2). The abundance of common species that occurred in high numbers was estimated within nine abundance categories (Williams 1982, Russ 1984 a, b) in a log<sub>3</sub> scale (1, 2–3, 4–9, 10–27, 28–81, 82–243, etc.). Common species included *Pseudanthias* spp., *Odonus niger*, *Labrichthys unilineatus*, and *Sphyaena* spp. as well as all species belonging to the families Acan-

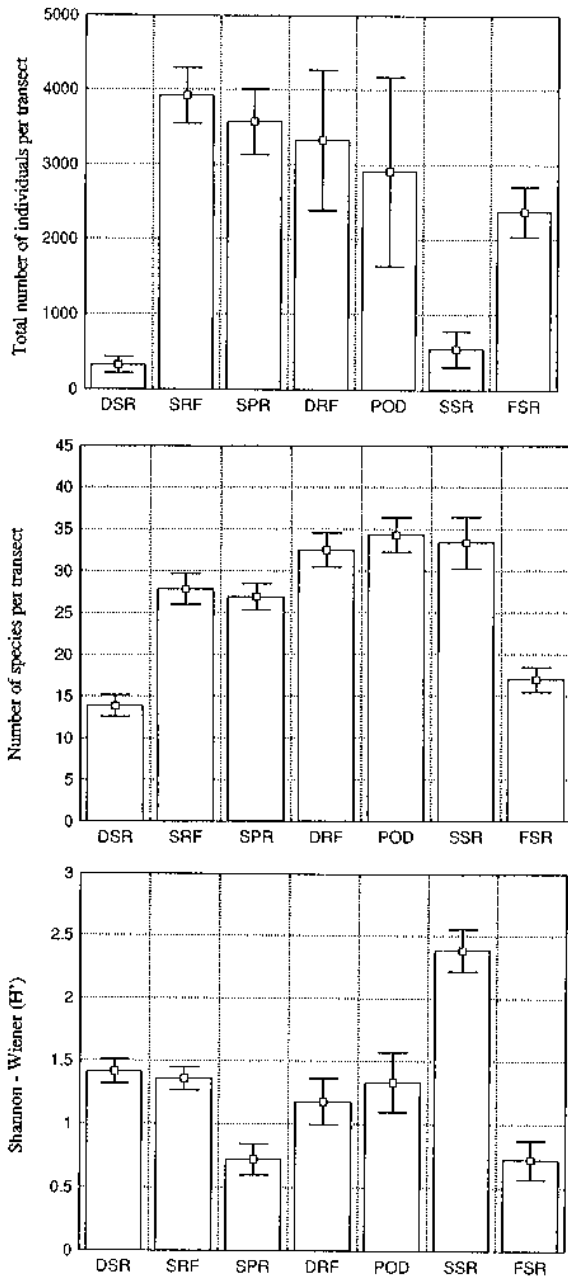


Figure 3. Mean and standard error of total fish abundance, species numbers, and Shannon-Weiner diversity index in the 7 reef habitats.

thuridae, Caesionidae and Pomacentridae. Species were classified into feeding categories based on published material (Allen 1985, 1991, Russ 1984 a, 1989, Myers 1989, Randall et al. 1990) and field observations. The effects of fishing activities in the

area was investigated by comparing fish numbers in the disturbed Kandakuliya Reef with the BRMS. The original design was to compare with more replicate reef-areas in the region, unfortunately this was hindered by civil unrest in the area. Prior to the extensive use of damaging fishing methods in the end of the 1980s the shallows of Kandakuliya Reef had a similar structure to the SRF and SPR on Bar Reef (Rajasuriya & DeSilva 1988). Since such habitat characteristics found on Bar Reef were no longer distinguishable for Kandakuliya Reef the shallow part was treated as one unit (DSR) and compared with the shallow habitats of Bar Reef (SRF, SPR). All fish censusing was done by the same person (M.C.Ö.).

### Statistical analyses

Differences in density estimates among reef habitats were investigated by means of Kruskal-Wallis rank tests and Mann-Whitney U tests (Sokal & Rohlf 1995). Species diversity was assessed by using the Shannon-Wiener information function ( $H'$ ) using  $\log_2$  (Shannon & Weaver 1949). Fish species abundance data (i.e. number of individuals or midpoint of abundance categories) were double square-root transformed and subjected to multidimensional scaling ordination (MDS) using Bray-Curtis similarity index. The ANOSIM randomisation test (Analysis of Similarities) was used to test for differences in fish assemblage structure (Warwick et al. 1990 a, b, Clarke 1993).

## Results

### Multivariate analysis

The multivariate analysis demonstrates clearly that the structure of reef fish assemblages varied among habitats (Figure 2). The MDS shows that transects taken within the pre-defined habitats aggregate, with significant differences between all pairs of habitats (ANOSIM,  $p < 0.05$ ). Tighter clusters indicate more similarities between transects. Hence, the fish assemblages within the *Acropora* dominat-

Table 3. Average number of fish per transect, standard deviation (SD), percentage of total and abundance rank of the ten most common fish species from 7 reef habitats (DSR = Disturbed shallow reef, SRF = Shallow reef flat, SPR = Shallow patch reef, DRF = Deep reef flat, POD = Porites dome, FSR = Flat sandstone reef). The results of Kruskal-Wallis tests comparing fish abundance among the 7 habitats are indicated with \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ , NS = Not significant, N = number of transects. Families in alphabetic order.

Family	Species	DSR (N = 20)			SRF (N = 11)			SPR (N = 11)			DRF (N = 6)			POD (N = 11)			SSR (N = 18)			FSR (N = 6)			Kruskal-Wallis								
		Aver- age	SD	%	Rank	Aver- age	SD	%	Rank	Aver- age	SD	%	Rank	Aver- age	SD	%	Rank	Aver- age	SD	%	Rank	Aver- age		SD	%						
Acanthuridae	<i>Acanthurus blochii</i>	3	12	1.0	8	22	49	0.6	9	4	7	0.1	1	1	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	***			
	<i>A. diussumeri</i>	0	0	0.0	0	0	0	0.0	0	0	0	0.0	0	0	0.0	0	0	0.0	9	14	1.6	9	3	7	0.1	0	0	0.0	***		
	<i>A. mata</i>	0	0	0.0	0	0	0	0.0	0	0	0	0.0	0	0	0.0	0	0	0.0	13	39	2.4	7	0	0	0.0	0	0	0.0	***		
	<i>Ctenochaetus striatus</i>	0	1	0.1	29	48	0.7	8	1	2	0.0	0	0	0	0.0	6	6	0.2	10	12	17	2.2	8	0	0	0.0	0	0	0.0	***	
	<i>Naso brevirostris</i>	0	0	0.0	0	0	0	0.0	0	0	0.0	0	0	0	0.0	0	0	0.0	8	13	1.5	10	0	0	0.0	0	0	0.0	***		
Ballistidae	<i>Odonus niger</i>	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0	0.0	0	0	0.0	279	1028	51.3	1	1218	588	51.3	1	0	0.0	***			
Caesionidae	<i>Caesio caerulea</i>	16	50	5.0	5	15	49	0.4	5	16	0.1	0	0	0.0	576	1336	19.8	3	4	13	0.7	0	0	0.0	0	0	0.0	NS			
	<i>C. cuning</i>	5	13	1.4	6	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	3	7	0.6	0	0	0	0.0	0	0	0.0	***			
	<i>Pterocaesio marri</i>	0	0	0.0	0	0	0	0.0	0	0	0.0	7	9	0.2	10	811	1762	27.9	2	23	41	4.3	3	54	84	2.3	3	***			
	<i>Pterocaesio tile</i>	0	0	0.0	0	0	0	0.0	5	16	0.0	10	0	0	0.0	1031	1709	35.5	1	1	4	0.2	0	0	0.0	0	0	0.0	***		
	<i>Chaetodon collar</i>	1	2	0.3	3	5	0.1	3	8	0.1	3	8	0.1	1	1	0.0	11	20	0.4	7	0	0	0.0	0	0	0.0	0	0	0.0	***	
Labridae	<i>C. trifasciatus</i>	0	0	0.0	17	12	0.4	3	2	0.1	10	3	0.3	9	2	1	0.1	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	***	
Lutjanidae	<i>Halihoeres leucoxanthus</i>	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	8	10	1.5	36	26	1.5	4	***				
	<i>Labrichthys unilineatus</i>	0	1	0.1	64	65	1.6	5	5	0.1	9	36	20	1.1	6	11	15	0.4	8	0	0	0.0	0	0	0.0	0	0	0.0	***		
	<i>Thalassoma lunare</i>	3	8	1.1	7	30	47	0.8	7	4	3	0.1	5	3	0.1	1	2	0.1	3	3	0.6	0	0	0.0	0	0	0.0	0	0.0	***	
	<i>Lutjanus quinquelineatus</i>	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0	0.0	0	0	0.0	1	0	0	0.0	26	3.7	4	0	0	0.0	0	0.0	***	
	<i>Gymnothorax</i> spp.	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0.0	0	0	0.0	0	0	0.0	11	11	0.5	7	***		
Nemipteridae	<i>Scolopsis xenochrous</i>	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0.0	1	2	0.1	6	2	0.2	8	***					
	<i>Apolemichthys xanthurus</i>	0	1	0.1	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0.0	3	2	0.5	4	3	0.2	10	***					
Pomacentridae	<i>Abudefduf vaigiensis</i>	69	147	21.5	2	164	212	4.0	4	81	142	2.3	4	10	7	0.3	8	3	5	0.1	0	0	0.0	0	0	0.0	0	0	0.0	***	
	<i>Chromis viridis</i>	0	0	0.0	1988	1180	50.7	1	3049	1523	85.5	1	2376	2192	71.5	1	311	448	10.7	4	0	0.0	0	0	0.0	0	0	0.0	0	0.0	***
	<i>Dascyllus aeneus</i>	0	0	0.0	815	637	20.8	2	16	20	0.4	10	16	20	0.5	7	16	0.2	9	0	0.0	0	0	0.0	0	0	0.0	0	0.0	***	
	<i>D. trimaculatus</i>	1	4	0.3	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	2	5	0.1	36	50	6.6	2	13	21	0.5	5	***			
	<i>Plectroglyphidodon lacrymatus</i>	0	0	0.1	6	15	0.2	16	48	0.5	8	0	0	0.0	1	2	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0.0	0	0.0	***
Scaridae	<i>Pomacentrus chrysurus</i>	17	18	5.3	4	39	63	1.0	6	102	191	2.9	3	66	49	2.0	4	0	0	0.0	0	0	0.0	0	0	0.0	0	0.0	0	0.0	***
	<i>Pomacentrus similis</i>	148	328	45.9	1	16	49	0.4	31	65	0.9	5	0	0	0.0	2	6	0.1	17	22	3.0	5	11	7	0.5	6	***				
	<i>Stegastes</i> spp.	36	112	11.1	3	594	576	15.6	3	109	146	3.1	2	378	167	11.4	2	18	24	0.6	6	0	0	0	0	0.0	0	0.0	0	0.0	***
Serranidae	<i>Scarus sordidus</i>	2	7	0.7	10	21	26	0.5	10	29	42	0.8	6	46	77	1.4	5	35	59	1.2	5	0	1	0	0	0.0	0	0.0	0	0.0	***
	<i>Pseudanthias</i> spp.	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0.0	0	0.0	***	
Siganidae	<i>Cephalopholis sommerati</i>	0	0	0.0	0	0	0.0	0	0	0.0	1	1	0.0	0	0	0.0	0	0	0.0	16	39	3.0	6	989	713	42.1	2	***			
	<i>Siganus canaliculatus</i>	3	6	1.0	9	1	3	0.0	28	49	0.8	7	0	0	0.0	0	1	0.0	0	0	0.0	0	0	0	0.0	0	0.0	0	0.0	**	
Sphyraenidae	<i>Sphyraena</i> spp.	0	0	0.0	0	0	0.0	0	0	0.0	324	251	9.8	3	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0.0	0	0.0	***	

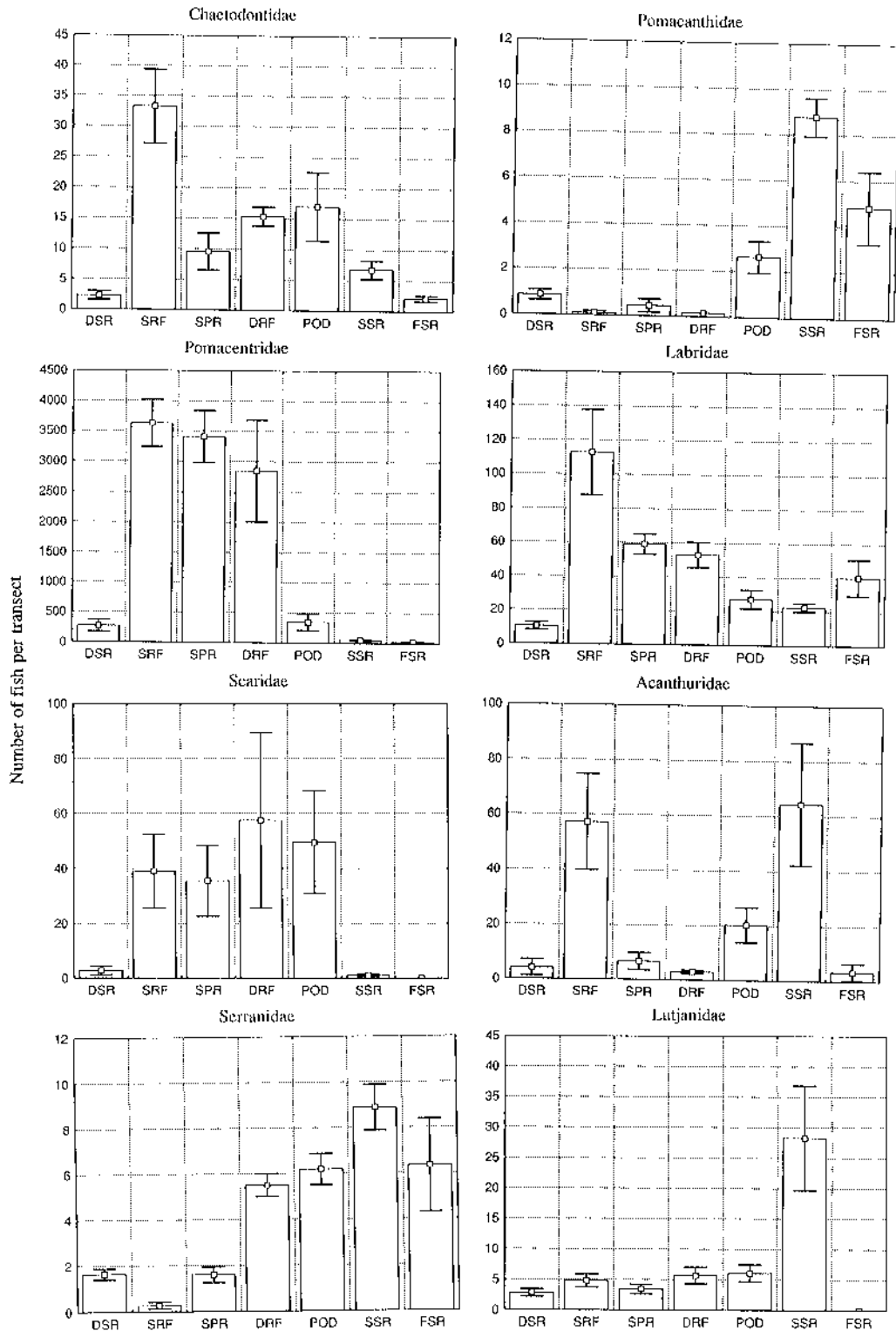


Figure 4. Mean and standard error of abundance (number of fish per transect) for different families within different habitats. The figure for Serranidae excludes *Pseudanthias* spp.

ed habitats (SRF, SPR, DRF) were less variable than in other habitats (Figure 2). The DRF and the SSR appeared to have a more variable fish fauna. Furthermore, the aggregates were nested in 3 larger groups: (1) SRF + SPR + DRF + POD; (2) DSR; and (3) SSR + FSR. The first group includes all the coral dominated habitats, the second group represents the disturbed reef and the third aggregate includes the two habitats within the sandstone reef.

### *Univariate analysis*

The univariate data analysis showed significant variation in fish numbers among habitats (Kruskal-Wallis,  $p < 0.05$ ). Highest fish densities were found within the coral dominated habitats (SRF, SPR, DRF, POD: Figure 3). Lowest abundance was found in the DSR with an average of less than 400 adult fish per transect which is an order of magnitude lower than corresponding non-fished habitats (SRF & SPR). Also, the SSR had in comparison a low abundance of fish but, as fish individuals were generally larger than in other habitats biomass was still high. The Shannon-Wiener diversity index showed different trends from the abundance measures (Figure 3). The structurally complex SSR had the highest diversity. The DSR had a similar diversity index as the SRF on Bar Reef. Species richness (Figure 3) also varied among habitats with least number of species found in areas of low habitat complexity i.e. the FSR and the DSR.

### *Species distribution among habitats*

Habitat partitioning among the fish assemblages in BRMS was further apparent in the distribution patterns of different species. Some species (21%) seemed to be more specialised, being associated with only one habitat type, while others could be characterised as generalists showing an ubiquitous distribution. Seventeen percent of the species were present in 5 habitat types and only two species, *Labroides dimidiatus* and *Thalassoma lunare*, were found in all habitats. Most of the species with a restricted distribution (61%) were only present in the

SSR. The FSR-patches had a sparse fish fauna with only 26% of the species present. The ten most abundant species in each of the habitats are listed in Table 3. There was an apparent separation between the two reef types. Nineteen percent of all species investigated were confined to the coral-reef patches while 22% were restricted to the sandstone-reef patches (the remainder being represented on both reef types).

Families showed differences in density and species composition among habitats (Figure 4). Chaetodontidae were most abundant on the SRF, which had the highest live coral cover, and least abundant in the DSR and on the deeper FSR. The pomacanthids were found in higher numbers in the deeper habitats. Some species of this family were unevenly distributed being generally confined to one or two habitats. This included *Centropyge multispinis* which showed a preference for POD and SSR and *Apolemichthys xanthurus* which was generally restricted to the two sandstone habitats. Others such as *Pomacanthus imperator* and *P. semicirculatus* were more evenly distributed occurring in five different habitats.

Depth variation and the presence of branching coral seemed to be important factors influencing Pomacentridae. Highest abundances of the family was found in *Acropora* dominated areas (SRF, SPR, DRF) and the dominant species in these habitats was *Chromis viridis* (Table 3). Other common species were *Dascyllus aruanus*, *Stegastes* spp., and *Pomacentrus chrysurus*. *Pomacentrus similis* was found in high numbers in the disturbed area. Although different species of pomacentrids showed different habitat type preferences most species were present in most of them (4 or more). However, some were restricted in their distribution such as *Amphiprion* spp. which were only present in the sandstone areas, the only area with noticeable presence of sea anemones. Labrids were most numerous in the SRF and least abundant in the DSR. Some species were restricted in their distribution, such as *Anampses lineatus* and *Halichoeres leucanthus*, which were confined to the sandstone areas and *Thalassoma janseni* which rarely occurred outside the shallows. Four of the seven scarids investigated were present in at least four zones. The family

Table 4. Average fish abundance and species numbers per transect, standard deviation (SD) and percentage, belonging to the various trophic groups from the 7 reef habitats. N = number of transects.

Trophic groups	DSR (N = 20)			SRF (N = 11)			SPR (N = 11)			DRF (N = 6)			POD (N = 11)			SSR (N = 18)			FSR (N = 6)			
	Aver- age	SD	%	Aver- age	SD	%	Aver- age	SD	%	Aver- age	SD	%	Aver- age	SD	%	Aver- age	SD	%	Aver- age	SD	%	
Coralivores (C)	no. indiv.	2	3	0	96	68	2	14	10	0	51	21	2	26	23	1	2	3	0	0	1	0
	no. sp.	1	1	5	5	2	19	4	1	15	5	1	14	4	1	11	1	1	1	2	0	0
Herbivores (H)	no. indiv.	64	110	20	735	551	19	304	236	9	506	139	15	79	58	3	27	29	5	3	8	0
	no. sp.	3	2	22	8	3	30	7	2	26	8	1	24	8	2	23	5	3	14	1	1	1
Invertebr. feeders (I)	no. indiv.	12	10	4	47	53	1	56	19	2	17	3	1	20	7	1	40	19	7	53	26	2
	no. sp.	5	3	36	7	2	24	9	2	33	8	1	24	9	3	27	10	3	31	7	2	40
Planktivores (P)	no. indiv.	91	152	28	2982	1191	76	3155	1485	8	2409	2184	73	2743	4150	94	393	1017	72	2284	792	96
	no. sp.	1	1	6	3	1	10	3	1	11	3	1	10	4	1	10	5	2	16	3	1	17
Detritivores (D)	no. indiv.	0	1	0	32	47	1	1	2	0	1	1	0	13	18	0	16	19	3	0	0	0
	no. sp.	0	0	1	1	0	5	0	0	1	1	1	2	1	1	4	1	1	4	0	0	0
Piscivores (F)	no. indiv.	2	2	1	1	1	0	2	1	0	332	250	10	11	8	0	12	7	2	17	15	1
	no. sp.	1	1	10	0	1	1	1	1	4	5	1	15	4	1	11	4	2	13	3	1	18
Invertebrate and fish feeders (I/F)	no. indiv.	3	3	1	8	5	0	3	2	0	4	2	0	9	8	0	30	37	6	1	1	0
	no. sp.	1	1	9	2	1	8	1	1	4	2	1	6	3	1	8	2	2	2	7	0	0
Omnivores (O)	no. indiv.	149	328	46	18	51	0	32	65	1	4	2	0	6	7	0	25	21	5	17	6	1
	no. sp.	2	1	11	1	1	3	1	1	3	2	1	5	2	2	7	4	2	13	4	1	21

was most common at intermediate depths (DRF, POD). The most abundant scarid was *Scarus sordidus* being among the ten most abundant species in the coral reef habitats (Table 3).

Acanthuridae showed interesting distribution patterns with highest numbers in two very different habitats: the SRF and the SSR. However, the species composition between them was different. Some acanthurids were most abundant in the shallows (SRF, SPR) including *Acanthurus lineatus*, *A. triostegus* and *A. blochii* while others were mainly confined to the deeper sandstone reefs such as *A. bariene*, *A. dussumieri*, *A. mata*, *A. tristis* and some Nasinae. Siganidae were mostly represented on shallow reefs with between 20–30 individuals per transect.

Serranidae occurred in highest numbers on the FSR with the planktivorous *Pseudanthias* spp. occurring at around 1000 individuals per transect (Table 3). This group occurred in large schools above the circular depressions characterising this habitat. Larger carnivorous serranids were most abundant on SSR and least numerous in the shallows (Figure 4). Species which were relatively widespread (present in 4 or more habitats) included *Aethaloperca rogae*, *Cephalopholis argus*, *Epinephelus fuscoguttatus*, *E. merra* and *Plectropomus laevis*. Those serranids only noted in the sandstone habitats were *Plectropomus maculatus*, *Variola louti*, *Epinephelus longispinis*, *E. hexagonatus*, *E. undulosus* and *Pseudanthias* spp.

Carangids were most common at intermediate depths (DRF, POD) or deeper above the structured sandstone patches. Lutjanidae were most common in the SSR dominated by *Lutjanus quinquelineatus* and *L. fulviflamma*. Although predominant in the shallows, *Lutjanus decussatus* and *Lutjanus* spp. were present in all habitats except the FSR. One lutjanid, *Macolor niger*, was mainly found in the Porites area. Caesionidae was by far most abundant in the Porites dome habitat (Table 3) than anywhere else (ca. 2400 individuals per transect). Haemulidae were also common in the Porites dominated areas as well as on the SSR. However, *Plectorhinchus vittatus* was more common on the coral reef. Lethrinidae occurred in low numbers in all habitats. One nemipterid, *Scolopsis bimaculatus*, was present in most

habitats while *Scolopsis xenochrous* was confined to the sandstone areas. Barracuda (Sphyraenidae), was only seen in the deeper *Acropora* areas (DRF) where they occurred in large schools. Muraenids were only noted in the characteristic depressions within the FSR (ca. 11 individuals per transect). Balistidae were very common in deeper areas (Table 3).

### Trophic groups

Fish belonging to different trophic groups distributed unevenly among habitats. Coral feeders dominated in high live-coral cover habitats (Table 4). Common coral feeders were species belonging to Chaetodontidae as well as the labrid *Labrichthys unilineatus*. Herbivores were most abundant on the shallow reef flat. They were a diverse group comprising, together with invertebrate feeders, most species in all habitats. Invertebrate feeders were abundant on the SRF, SPR, SSR and FSR. Planktivores were the most dominant trophic group making up for 72–96% of all individuals in the different habitats of Bar Reef. However, the composition of the group varied among habitats: Pomacentridae dominated the *Acropora* habitats, while Caesionidae were the most abundant family in the Porites habitat. On the sandstone reefs the planktivorous *Odonus niger* was the most numerous species. Detritivores such as *Ctenochaetus striatus*, were most abundant on the SRF. Piscivores were most abundant in the deep *Acropora* area. However, if barracuda was excluded, the highest numbers of piscivores were present on the sandstone reefs. The invertebrate-and-fish-feeders were most abundant on the SSR due to large numbers of lutjanids. On the DSR omnivores were most dominant (46%) followed by the planktivores (28%) and herbivores (20%).

## Discussion

### Fish distribution patterns

Fish assemblages on coral reefs commonly show zo-

nation patterns, with the number of zones/habitats varying between different reefs. For example five zones are common for the mid-shelf or outer shelf reefs of the Great Barrier Reef (Goldman & Talbot 1976, Russ 1984a, 1984b, Williams 1991) while four zones are evident for the fringing reefs of Moorea, French Polynesia, and Gulf of Aqaba, Red Sea (Bouchon-Navaro & Harmelin-Vivien 1981, Galzin & Legendre 1987). Harmelin-Vivien (1989) compared reefs at Tulear in the Indian Ocean with reefs at Moorea in the Pacific. She noted stronger separation in fish-assemblage structure among zones in the reef area with higher species richness (Tulear) than the reef area with fewer species (Moorea). It has been suggested that a comparison between Caribbean reefs and reefs in the Indo-Pacific would show similar patterns, with more distinct zonation among fish assemblages on Indo-Pacific reefs which generally have higher species richness (Williams 1991). If species richness increases among-habitat variation, distinct habitat partitioning of the reef-fish assemblages in Sri Lanka could be expected. The total number of reef-fish species in Sri Lanka is yet to be determined. On a global scale Harmelin-Vivien (1989) calculated a strong positive correlation between coral and fish species richness ( $y = -13.63 + 3.92x$ ,  $r = 0.97$ ,  $p < 0.01$ ). If such correlation is applicable for Sri Lankan reefs, where 183 coral species (68 genera) have been recorded (Rajasuriya et al. 1995), the total number of reef-fish species would be around 700. This would be considered a rich fish fauna taking into account the extension of Sri Lanka's reefs. Hence, reef fish assemblages of Sri Lanka would be expected to be clearly separated in composition among habitats.

In this study the multivariate analysis of the fish abundance data showed that the fish community in BRMS was divided into six distinct assemblages: two with a distribution limited to the sandstone reef and four confined to the coral reef. A high number of species with a restricted distribution (21% in one habitat) and a low number with a ubiquitous distribution (1.5% in all habitats) verify habitat partitioning even further. Similar patterns may be seen on other reefs. For example, at Moorea Galzin & Legendre (1987) and Galzin (1987) calculated that 45% of the species were confined to one habitat and

5.4% were ubiquitous. Goldman & Talbot (1976) found that 48% of the species were restricted and 6.6% widespread among five habitats on reefs at One Tree Island in the Great Barrier Reef. These workers included all species found in their study. If rare species of low abundance are included chances are that they will only be present in one habitat which would increase the proportion of restricted species.

The strongest separation overall in the fishes of this study was between the different reef types: the coral-reef patches and the sandstone-reef patches (and the disturbed Kandakuliya Reef). The division between sandstone reefs and coral reefs may be analogous to how fish assemblages associated with reef slopes separate from other zones on other reefs. Goldman & Talbot (1976) and Galzin & Legendre (1987) detected that around 15% of the fish fauna were restricted to the reef slope which could be compared to the 22% confined to the sandstone reef in this study. Reef slopes have been characterised as having a higher proportion of larger fish (Goldman & Talbot 1976, Russ 1989, Harmelin-Vivien 1989, Williams 1991) which is in accordance with our findings in the sandstone reef habitat which had high numbers of large fish.

As different taxa or trophic groups have different ecological preferences in terms of food and shelter, habitat partitioning among fish assemblages within a reef may occur. There are a number of ecological processes that may determine these among-habitat patterns including habitat selection at settlement (personal observation, Sale et al. 1984, Eckert 1985, Levin 1991, Wellington 1992, Booth 1992, Booth & Beretta 1994, Carr 1994), migration (Robertson 1988, Lirman 1994), competition (Ebersole 1985, Robertson & Gaines 1986), and predation (Hixon 1991, Caley 1993, Hixon & Beets 1993). Functional aspects of reef-fish communities are commonly correlated with shelter and food (Williams 1991). In this study the reef flat, with the largest proportion of live coral, had most corallivores, while they were practically absent on the sandstone reefs; a pattern seen in other studies where corallivorous chaetodontids have been correlated with live coral cover (Bouchon-Navaro et al. 1985, Bell et al. 1985, Bouchon-Navaro & Bouchon 1989). Herbivores, may also

distribute according to food availability (e. g. Russ 1984a, Carpenter 1990, Robertson 1991; but see Williams 1986, Hart et al. 1996). In this study they were most abundant in the coral reef habitat. Although the live coral cover was high, especially on the reef flat, turf algae were present growing within and between the branching structure of the *Acropora* colonies.

The coral reef habitats had a more abundant fish community than the sandstone reefs. This was due to the high numbers of planktivores. Planktivores are commonly most abundant along the reef edge (reef crest) near deeper water (Hobson 1991), a pattern which has been explained by increased densities of plankton as the reef edge may act as a hydrological front for up-currents. In this study the increase in depth was gradual, hence plankton density may be less variable over the continental shelf. This could explain why planktivores differed little in numbers among most habitats in this study. However, the species composition of plankton feeders varied among habitats within the coral reef area; in particular between *Porites* and *Acropora* habitats. This pattern may have been influenced by a combination of habitat structure and depth. Branching *Acropora* offer protection for more site-attached deep-bodied planktivores such as the dominant *Chromis viridis* and *Dascyllus aruanus* (Sale 1972, Sweatman 1985, 1988). However, the schooling caesionids which dominated the *Porites* dome habitat are less dependent on such structures for protection. The zoo-planktivore *Odonus niger* dominated the sandstone areas. This species is commonly associated with outer reef-slopes on other reef types (Randall et al. 1990). In this study it fed high up in the water column but depended on the sandstone reef habitat for protection using holes in the substratum.

### *Influences of fishing practises*

Increased mortality and low fish densities is an expected consequence of fishing practises (Russ 1991). Reef fisheries have been found to negatively influence larger predatory species because they are usually directly targeted (Munro 1983, Russ 1985,

Samoilys 1988, Russ & Alcala 1989, Watson & Ormond 1994). The results of this study did not show such patterns probably because the disturbed patches were situated in the shallow reef with naturally low numbers of large predatory fish species.

Indirect effects of fishing on the fish community through habitat destruction caused by destructive fishing techniques, has also been reported in a number of studies (see Russ 1991). Bottom-set nets has been used intensively on Kandakuliya Reef. These three layer nylon nets are laid over the corals and as they are removed corals are broken which decreases live coral cover and habitat complexity (Öhman et al. 1993, Rajasuriya et al. 1995). Our findings suggest that the difference in the fish assemblage structure between the disturbed reef and the sanctuary is to a large extent the result of habitat alteration. Fishing practises in the shallows of Kandakuliya Reef has ceased since 1991 and fishermen are now mainly targeting pelagic species offshore. Hence, the fish community is not influenced directly by fish removal. Different aspects of the fish assemblages, which separated the disturbed reef from the sanctuary, seemed to be related to habitat destruction in terms of lack of food and shelter. For example, planktivorous pomacentrids which dominated the shallow non-disturbed area (*Chromis viridis* and *Dascyllus aruanus*) were completely absent on Kandakuliya Reef. With the destruction of branching corals the number of refuges available to these species declined and they may have become more vulnerable to predation. Furthermore, coral destruction appeared to have negatively influenced corallivores. Russ & Alcala (1989) studied effects of fishing pressure on fish assemblages in the Philippines and also noted a decrease of corallivores (as well as pomacentrids) which they attributed to habitat modification. Sano et al. (1984, 1987) observed that coral feeders disappeared completely on dead and rubble reefs. Coral-feeding chaetodontids may be less abundant on disturbed reefs with low live coral cover than on reefs with high coral cover (Hourigan et al. 1988). For this reason it has been suggested that their relative abundance is a measure of the degree of disturbance on coral reefs (Reese 1981, Hourigan et al. 1988). However, the value of chaetodontids as indicator species has been

criticised as some studies have not seen such correlations (e.g. Roberts & Ormond 1987, Roberts et al. 1988). Possibly the usefulness of this family as a measure of disturbance vary in different regions and on different types of reefs. In this study butterflyfishes had low abundance in areas of low coral cover. In particular the disturbed area showed low numbers (and the non-disturbed SRF showed high numbers). Hence, chaetodontids may be a useful indicator of disturbance on coral reefs in Sri Lanka.

The lower abundance of invertebrate feeders on the disturbed reef may also be attributed to lack of food: Kohn & Leviten (1976) observed that reefs with low habitat complexity supported less benthic invertebrates. A large number of invertebrates are commonly present among the branches of *Acropora* spp (Patton 1994). Omnivores were most abundant overall on the disturbed reef with *Pomacentrus similis* dominating. This group may be in a better position in a disturbed environment due to their high feeding adaptability compared to other more specialised species. The higher numbers of *Pomacentrus similis* on Kandakuliya Reef, as compared with the sanctuary, may further be an effect of destructive fishing; the preferred habitat for this species, as with the closely related *P. coelestis* (Myers 1989), is coral rubble. Hence, these species could function as indicators of human disturbance, although coral destruction is also caused by natural processes such as storms and predation. Algal grazers were less abundant on Kandakuliya Reef than on other reef habitats despite of a high algal cover (Rajasuriya et al. unpublished data). The explanation for this may be that herbivores feed mainly on turfs of filamentous algae (Williams & Hatcher 1983) and not on macroalgae (e.g. *Halimeda* and *Padina*) which were common in the disturbed reef. Also, an increase of turf algae, as a result of disturbance, does not necessarily mean that the number of herbivores will increase shortly after the impact (Williams 1986, Hart et al. unpublished).

The multivariate analysis indicated that the disturbed area had a more heterogeneous fish assemblage than the shallow undisturbed habitats. Warwick & Clarke (1993) have noted, in a number of studies on effects of environmental impact on marine fauna, that there is an increased variability

among samples within disturbed sites compared to control sites. Shepherd et al. (1992) observed the same effects in a study on the influence of coral mining on reef fish assemblages in the Maldives.

The conclusions drawn from comparing Bar Reef Marine Sanctuary and Kandakuliya Reef, in regards to the effects of fishing activities, should be taken with caution. Investigating the effects of environmental impact by comparing disturbed and undisturbed areas is based on the assumption that they only differ in the degree of disturbance. This is difficult to control for without pre-disturbance quantitative data on the fish community which is lacking in this study. However, with this in mind results do suggest that fishing practises carried out on Kandakuliya Reef has profoundly altered the fish assemblage structure.

### Acknowledgements

This study was conducted by the National Aquatic Resources Agency (NARA) of Sri Lanka in co-operation with the Department of Zoology, Stockholm University, Sweden. It was supported by the Sida-SAREC Marine Science Programme (Sida: Swedish International Development Cooperation Authority). We thank Olof Lindén and Ron Johnstone for their invaluable support in various aspects of the study. We also appreciate the support given by the Chairman and the Director General of NARA. Sture Hansson, Ian Mayer and anonymous reviewers gave valuable comments on the manuscript. Field assistance was provided by Kavish Rathnapriya, Carl-Adam Wachtmeister, Ranjith Thomas and Jens Mogensen. Figure 1 was made by B. Mayrhofer, Stockholm University.

### References cited

- Allen, G.R. 1985. Butterfly and angelfishes of the world. Mergus, Melle. 352 pp.
- Allen, G.R. 1991. Damselfishes of the world. Mergus, Melle. 271 pp.
- Anderson, C. 1996. Common reef fishes of Sri Lanka. The Wildlife Heritage Trust, Colombo. 80 pp.

- Bell, J.D. & R. Galzin. 1984. Influence of live coral cover on coral reef fish communities. *Mar. Ecol. Prog. Ser.* 15: 265–274.
- Bell, J.D., M.L. Harmelin-Vivien & R. Galzin. 1985. Large scale spatial variation in abundance of butterflyfishes (Chaetodontidae) on Polynesian reefs. *Proceedings of the Fifth International Coral Reef Symposium, Tahiti* 5: 421–426.
- Booth, D.J. 1992. Larval settlement patterns and preferences by domino damselfish *Dascyllus albisella* Gill. *J. Exp. Mar. Biol. Ecol.* 155: 85–104.
- Booth, D.J. & G.A. Beretta. 1994. Seasonal recruitment, habitat association, and survival of pomacentrid reef fish in the US Virgin Islands. *Coral Reefs* 13: 81–89.
- Bouchon-Navaro, Y. 1980. Quantitative distribution of the Chaetodontidae on a fringing reef of the Jordanian coast (Gulf of Aqaba, Red Sea). *Tethys* 9: 247–251.
- Bouchon-Navaro, Y. & C. Bouchon. 1989. Correlations between chaetodontid fishes and coral communities of the Gulf of Aqaba (Red Sea). *Env. Biol. Fish.* 25: 1–3.
- Bouchon-Navaro Y. & M.L. Harmelin-Vivien. 1981. Quantitative distribution of herbivorous reef fishes in the Gulf of Aqaba (Red Sea). *Mar. Biol.* 63: 79–86.
- Bouchon-Navaro Y, C. Bouchon & M. Harmelin-Vivien. 1985. Impact of coral degradation on a chaetodontid fish assemblage (Moorea, French Polynesia). *Proceedings of the Fifth International Coral Reef Symposium, Tahiti* 5: 427–432.
- Caley, M.J. 1993. Predation, recruitment and the dynamics of communities of coral reef fishes. *Mar. Biol.* 117: 33–43.
- Carpenter, K.E., R.I. Micalat, V.D. Albaladejo & V.T. Corpuz. 1981. The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. *Proceedings of the Fourth International Coral Reef Symposium, Manila* 2: 497–502.
- Carpenter, R.C. 1990. Mass mortality of *Diadema antillarum*. II. Effects on population densities and grazing intensity of parrotfishes and surgeonfishes. *Mar. Biol.* 104: 79–86.
- Carr, M.H. Effects of macroalgal dynamics on recruitment of a temperate reef fish. *Ecology* 75: 1320–1333.
- Chave, E.H. & D.B. Eckert. 1974. Ecological aspects of the distribution of fishes at Fanning Island. *Pacific Science* 28: 297–317.
- Clarke, R.D. 1977. Habitat distribution and species diversity of chaetodontid and pomacentrid fishes near Bimini, Bahamas. *Mar. Biol.* 40: 277–289.
- Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Austr. J. Ecol.* 18: 117–143.
- Ebersole, J.P. 1985. Niche separation of two damselfish species by aggression and differential microhabitat utilization. *Ecology* 66:14–20.
- Eckert, G.J. 1985. Settlement of coral reef fishes to different natural substrata and at different depths. *Proceedings of the Fifth International Coral Reef Symposium, Tahiti* 5: 385–390.
- English, S., C. Wilkinson & V. Baker. 1994. Survey manual for tropical marine resources. ASEAN-Australian Marine Science Project, Australian Institute of Marine Science, Townsville. 368 pp.
- Fowler, A.J. 1987. The development of sampling strategies for population studies of coral reef fishes. A case study. *Coral reefs* 6: 49–58.
- Galzin, R. 1987. Structure of fish communities of French Polynesian coral reefs, I. Spatial scales. *Mar. Ecol. Prog. Ser.* 41: 129–136.
- Galzin, R. & P. Legendre. 1987. The fish communities of a coral reef transect. *Pacific Science* 41: 158–165.
- Gladfelter W.B. & E.H. Gladfelter. 1978. Fish community structure as a function of habitat structure on West Indian patch reefs. *Revista de Biologia Tropical* 26: 65–84.
- Goldman, B & F.H. Talbot. 1976. Aspects of the ecology of coral reef fishes. pp. 125–154. *In: Jones O.A. & R. Endean (ed.) Biology and Geology of Coral Reefs*, Academic Press, New York.
- Gosline, W.A. 1965. Vertical zonation of inshore fishes in the upper layers of the Hawaiian Islands. *Ecology* 46:823–831.
- Grigg, R.W. 1994. Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. *Mar. Ecol. Prog. Ser.* 103: 25–34.
- Harmelin-Vivien, L. 1977. Ecological distributions of fishes on the outer slope of Tulear Reef (Madagascar). *Proceedings of the Third International Coral Reef Symposium, Miami* 1: 289–296.
- Harmelin-Vivien, M.L. 1989. Reef fish community structure: an Indo-Pacific comparison. *Ecol. Stud.* 69: 21–60.
- Hiatt, R.W. & D.W. Strasburg. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr* 30: 65–127.
- Hixon, M.A. 1991. Predation as process structuring coral reef fish communities. pp. 475–508. *In: P.F. Sale (ed.) The Ecology of Fishes on Coral Reefs*, Academic Press, San Diego.
- Hixon, M.A. & J.P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol. Monogr.* 63: 77–101.
- Hobson, E.S. 1991. Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. pp. 69–95. *In: P.F. Sale (ed.) The Ecology of Fishes on Coral Reefs*, Academic Press, San Diego.
- Hourigan, T.F., T.C. Tricas & E.S. Reese. 1988. Coral reef fishes as indicators of environmental stress in coral reefs. pp. 107–136. *In: D.F. Soule & G.S. Keppel (ed.) Marine Organisms as Indicators*, Springer-Verlag, New York.
- Kohn A.J. & P.J. Leviten. 1976. Effects of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. *Oecologia* 25:199–210.
- Lirman, D. 1994. Ontogenic shifts in habitat preferences in the three-spot damselfish, *Stegastes planifrons* (Cuvier), in Roatan Islands, Honduras. *J. Exp. Mar. Biol. Ecol.* 180: 71–81.
- Levin, P.S. 1991. Effects of microhabitat on recruitment variation in a Gulf of Maine reef fish. *Mar. Ecol. Prog. Ser.* 75: 183–189.
- Luckhurst, B.E. & K. Luckhurst. 1978. Analysis of the influence of the substrate variables on coral reef fish communities. *Mar. Biol.* 49: 317–323.
- McCormick, M.I. & J.H. Choat. 1987. Estimating total abundance of a large temperate-reef fish using visual strip-transects. *Mar. Biol.* 96: 469–478.
- McManus, J.W., R.I. Micalat & V.P. Palaganas. 1981. Coral and

- fish community structure of Sombrero Island, Batangas, Philippines. Proceedings of the Fourth International Coral Reef Symposium, Manila 2: 271–280.
- Munro, J.L. 1983. Caribbean coral reef fishery resources. ICLARM Stud. Rev. 7: 1–276.
- Myers, R.F. 1989. Micronesian reef fishes. Coral Graphics, Guam. 298 pp.
- Öhman, M.C., O. Linden & A. Rajasuriya. 1993. Human disturbances on coral reefs in Sri Lanka: a case study. *Ambio* 22: 474–480.
- Patton, W.K. 1994. Distribution and ecology of animals associated with branching corals (*Acropora* spp.) from the Great Barrier Reef, Australia. *Bull. Mar. Sci.* 55: 193–211.
- Rajasuriya, A & M.W.R.N. De Silva. 1988. Stony corals of the fringing reefs of the western south-western and southern coasts of Sri Lanka. Proceedings of the Sixth International Coral Reef Symposium, Townsville 3: 287–296.
- Rajasuriya, A., M.W.R.N. De Silva & M.C. Öhman. 1995. Coral reefs of Sri Lanka: human disturbance and management issues. *Ambio* 24: 428–437.
- Randall, J.E., G.R. Allen & R.C. Steene. 1990. Fishes of the Great Barrier Reef and Coral Sea. Crawford House Press, Bathurst, 507 pp.
- Reese, E.S. 1981. Predation on coral by fishes of the family Chaetodontidae: implications for conservation and management of coral reef ecosystems. *Bull. Mar. Sci.* 31: 594–604.
- Risk, M.J. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Res. Bull.* 153: 1–6.
- Roberts, C.M. & R.F.G. Ormond. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar. Ecol. Prog. Ser.* 41: 1–8.
- Roberts, C.M., R.F.G. Ormond & A.R.D. Shepherd. 1988. The usefulness of butterflyfishes as environmental indicators on coral reefs. Proceedings of the Sixth International Coral Reef Symposium. Townsville 2: 331–336.
- Robertson, D.R. 1988. Abundances of surgeonfishes on patch-reefs in Caribbean Panamá: due to settlement, or post-settlement events? *Mar. Biol.* 97: 495–501.
- Robertson, D.R. 1991. Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panama indicate food limitation. *Mar. Biol.* 111: 437–444.
- Robertson, D.R. & S.D. Gaines. 1986. Interference competition structure habitat use in local assemblage of coral reef surgeonfishes. *Ecology* 67: 1372–1383.
- Russ, G. 1984a. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Mar. Ecol. Prog. Ser.* 20: 23–34.
- Russ, G. 1984b. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Patterns of zonation of mid-shelf and outershelf reefs. *Mar. Ecol. Prog. Ser.* 20: 35–44.
- Russ, G.R. 1985. Effects protective management on coral reef fishes in the central Philippines. Proceedings of the Fifth International Coral Reef Symposium, Tahiti 4: 219–224.
- Russ, G. 1989. Distribution and abundance of coral reef fishes in the Sumilon Island Reserve, central Philippines, after nine years of protection from fishing. *Asian Mar. Biol.* 6: 59–71.
- Russ, G.R. 1991. Coral reef fisheries: effects and yields. pp. 601–635. *In*: P. F. Sale (ed.) *The Ecology of Fishes on Coral Reefs*, Academic Press, San Diego.
- Russ, G.R. & A.C. Alcalá. 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. *Mar. Ecol. Prog. Ser.* 56: 13–27.
- Sale, P.F. 1972. Influence of corals in the dispersion of the pomacentrid fish, *Dascyllus aruanus*. *Ecology* 53: 741–744.
- Sale, P.F. 1991. Reef fish communities: open nonequilibrium systems. pp. 564–598. *In*: P. F. Sale (ed.) *The Ecology of Fishes on Coral Reefs*, Academic Press, San Diego.
- Sale, P.F., W.A. Douglas & P.J. Doherty. 1984. Choice of microhabitats by coral reef fishes at settlement. *Coral Reefs* 3: 91–99.
- Samoilys, M.A. 1988. Abundance and species richness of coral reef fish on the Kenyan coast: the effects of protective management and fishing. Proceedings of the Sixth International Coral Reef Symposium, Townsville: 2: 261–266.
- Sano, M., M. Shimizu & Y. Nose. 1984. Changes in structure of coral reef fish communities by destruction of hermatypic corals: observational and experimental views. *Pac. Sci.* 38: 51–79.
- Sano, M., M. Shimizu & Y. Nose. 1987. Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan. *Mar. Ecol. Prog. Ser.* 37: 191–199.
- Shannon, C. & W. Weaver. 1949. *The mathematical theory of communication*. University of Illinois Press, Urbana. 117 pp.
- Shepherd, A.R.D., R.M. Warwick, K.R. Clarke & B.E. Brown. 1992. An analysis of fish community responses to coral mining in the Maldives. *Env. Biol. Fish.* 33: 367–380.
- Sokal, R.R. & F.J. Rohlf. 1995. *Biometry*. Freeman, New York. 887 pp.
- Sweatman, H.P.A. 1985. The influence of adults of some coral reef fishes on larval recruitment. *Ecol. Monogr.* 55: 469–485.
- Sweatman, H.P.A. 1988. Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. *J. Exp. Mar. Biol. Ecol.* 124: 163–174.
- Warwick, R.M. & K.R. Clarke. 1993. Increased variability as a symptom of stress in marine communities. *J. Exp. Mar. Biol. Ecol.* 172: 215–226.
- Warwick, R.M., K.R. Clarke & G.M. Gee. 1990a. The effect of disturbance by soldier crabs *Mictyris platycheles* H. Milne Edwards on meiobenthic community structure. *J. Exp. Mar. Biol. Ecol.* 135: 19–33.
- Warwick, R.M., H.M. Platt, K.R. Clarke, J. Agard & J. Gobin. 1990b. Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda. *J. Exp. Mar. Biol. Ecol.* 138: 119–142.
- Watson, M. & R.F.G. Ormond. 1994. Effect of an artisanal fishery on the fish and urchin populations of a Kenyan coral reef. *Mar. Ecol. Prog. Ser.* 109: 115–129.
- Wellington, G.M. 1992. Habitat selection and juvenile persistence control the distribution of two closely related Caribbean damselfishes. *Oecologia* 90: 500–508.

- Williams, D.M. 1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. *Coral Reefs* 1: 35-43.
- Williams, D.M. 1986. Temporal variation in the structure of reef slope fish communities (central Great Barrier Reef): short-term effects of *Acanthaster planci* infestation. *Mar. Ecol. Prog. Ser.* 28: 157-164.
- Williams, D.M. 1991. Patterns and Processes in the distribution of coral reef fishes. pp. 437-474. *In* P.F. Sale (ed.) *The Ecology of Fishes on Coral Reefs*, Academic Press, San Diego.
- Williams, D.M. & A.I. Hatcher. 1983. Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 10: 239-250.