

Fisheries Research 51 (2001) 35-51



www.elsevier.com/locate/fishres

### Impact of Indonesian coral reef fisheries on fish community structure and the resultant catch composition

C. Pet-Soede<sup>a,\*</sup>, W.L.T. van Densen<sup>a</sup>, J.S. Pet<sup>b</sup>, M.A.M. Machiels<sup>a</sup>

<sup>a</sup>Department of Fish Culture and Fisheries Group, Wageningen Institute of Animal Sciences, Wageningen University, P.O. Box 338, 6700 AH Wageningen, Netherlands <sup>b</sup>The Nature Conservancy, Coastal and Marine Indonesia Program, Jl. Pengembak No. 2, Sanur, Bali, Indonesia

Received 2 December 1999; received in revised form 25 April 2000; accepted 10 July 2000

#### Abstract

Species and size composition of fish community structures were studied with underwater visual census (UVC), on Indonesian coral reefs subjected to different levels of fishing intensity. Comparisons were made between reefs within Spermonde Archipelago off SW Sulawesi, between reefs inside and outside a marine park in Komodo coastal area off West Flores, and between the reef areas of Spermonde and Komodo. In Spermonde, the species and size composition of the commercial catch at sites with high and low fishing intensity were recorded to determine how these catches reflected shifts in fish community structure. Overall fishing intensity in Spermonde was 557 boatdays  $\text{km}^{-2}$  reef  $\text{yr}^{-1}$ , eight times higher than in Komodo (65 boatdays km<sup>-2</sup> reef yr<sup>-1</sup>), but catch rates were eight times lower in Spermonde (5.6 kg per trip) than at reefs in Komodo (48 kg per trip). Total yield was similar in Spermonde (3.2 t km<sup>-2</sup> reef) and in Komodo (3.1 t km<sup>-2</sup> reef). Mean length of fish in the catch was significantly related to fishing intensity. Spatial patterns in the fish community within Spermonde as observed with UVC were not significantly related to patterns in fishing intensity. Within Komodo, total fish biomass and biomass of piscivores as observed with UVC were significantly higher inside than outside the park. Fish communities at reefs differed largely between Spermonde and Komodo, in mean individual length and in total biomass but numerical densities were similar. Our results indicate that an effect of fishing pressure on the fish community structure can be detected by UVC only when comparing sites which differ greatly in fishing intensity (Spermonde and Komodo) or when comparing sites with low and with medium fishing intensity (inside and outside a marine park). The species and size composition of commercial catches still demonstrate the differential effect of fishing intensity on fish community structures and so on the resultant catches in the on-average intensively fished reef area of Spermonde. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Indonesia; Coastal fishery; Underwater visual census; Fish community structure

#### 1. Introduction

Management of a fishery requires that reliable predictions can be made of the consequences of

fax: +31-317-483-937.

alternative exploitation strategies (Sainsbury, 1982). This implies the need for a sound knowledge of (a) the condition of fish stocks at a given time, (b) how the fish community operates, and (c) how this is influenced by exploitation (Russ, 1991). A most informative indicator for fishery-induced changes in reef fish community structures is the reduction in fish diversity via local extinction of species (Jennings and Kaiser, 1998;

<sup>\*</sup> Corresponding author. Tel.: +31-317-483-307;

E-mail address: lidapet@attglobal.net (C. Pet-Soede).

<sup>0165-7836/01/\$ –</sup> see front matter 0 2001 Elsevier Science B.V. All rights reserved. PII: S0165-7836(00)00236-8

Russ, 1991; Smith et al., 1991). Under increasing fishing pressure, the density of target fish reduces (Jennings and Polunin, 1996) as does the importance of top-predators (Russ, 1991). Also average length in the population reduces (Roberts and Polunin, 1991; Jennings and Polunin, 1996; Welcomme, 1999). Indirect effects such as increased numbers of other fish species and overgrowth of macro algae with the consequent decline of coral cover (Parrish et al., 1985; Medley et al., 1993) can also be used as indicators for fishery impact. These direct and indirect effects can be traced by comparing the structure of fish communities as observed via fishery-independent sampling over time intervals with increasing fishing effort or between areas with contrasting levels of fishing effort. The fishery impact, however, can also be traced from changing catch rates and catch compositions in the professional fishery (Gulland, 1985; Sparre et al., 1989; Jennings and Lock, 1996; Welcomme, 1999).

The aim of the present study is to assess the impact of the current level of fishing intensity in the Spermonde Archipelago off southwest Sulawesi (Fig. 1) on the species and size structure of reef fish communities and to search for indirect proof for this impact as read from the outcome of the coastal fishery. It was already shown that CpUE in kilogram per trip for a small group of hook and line fishers was significantly higher at remote locations in Spermonde with lower levels of fishing intensity than at nearby locations with high fishing intensity (Pet-Soede, 2000). To find whether these patterns in fishery output reflect differences in the composition and structure of the fish community at the reefs, fish density, length and biomass, as recorded through underwater visual census (UVC) are compared between reef areas differing in fishing intensity. First, within Spermonde Archipelago, off SW Sulawesi, where fishing intensity differed by a factor of three between the less intensively northwest and the most intensively fished southeast of this coastal shelf (Pet-Soede, 2000), second within Komodo area, off West Flores, part of which encompasses a marine park in which fishing is less intense than outside the park (Pet, 1998), and third, between Komodo and Spermonde where overall fishing effort (557 boats  $\text{km}^{-2}$ reef) was eight times higher than at Komodo (65 boats  $km^{-2}$  reef). Because an earlier study in Spermonde revealed significant correlations between fish parameters and habitat complexity (Pet-Soede, 2000) patterns in the fish community structure in Komodo are related to habitat complexity as well, in order to separate this habitat effect from a fishery effect.

#### 2. Material and methods

#### 2.1. Research area and characteristics of the fishery

Two coastal areas were compared, a coastal shelf of some 2800 km<sup>2</sup> in the Spermonde Archipelago off SW Sulawesi  $(4^{\circ}40'-5^{\circ}40'S, 118^{\circ}55'-119^{\circ}30'E)$ , and an area of some 1300 km<sup>2</sup> in Komodo National Park and its buffer zone between West Flores and East Sumbawa  $(8^{\circ}20'-8^{\circ}50'S, 119^{\circ}20'-119^{\circ}55'E)$  (Fig. 1).

Spermonde comprises shallow sandy bottoms at depths ranging from 2 to 60 m and about 160 submersed coral reefs, 35% of which enclose an island. The estimated total shallow reef area ( $\leq 20$  m depth) is 185 km<sup>2</sup> or 7% of the research area (Uljee et al., 1996). Shelf depth increases with distance from the mainland and four shelf zones can be identified following bathymetric lines perpendicular to the coastline and that differ in coral species composition (Moll, 1983; Hoeksema, 1990). A total of 6500 fishing families or some 30,000 inhabitants live on the 24 islands and approximately 25 coastal villages (Anonymous, 1995).

The three major islands Komodo, Rinca and Padar in the Komodo area are larger than islands in Spermonde, the others are of similar size. The estimated shallow reef area ( $\leq 20$  m depth) is approximately 100 km<sup>2</sup> or 8% of the research area (P.J. Mous, unpublished data). There are four fishing villages located inside the park and their combined number of inhabitants is 2310 (Bakar, 1996), but the majority (71%) of fishers that visited the reefs lived on islands outside the park or on the mainland of Flores and Sumbawa (Pet and Mous, 1999).

#### 2.2. Sampling the fish community by UVC

Number of fish per species and size category (cm-class) were counted underwater by one diver. Forty-five line transects at 23 different reefs were surveyed by the same observer during the dry season from June through August 1996 in Spermonde and 26 line transects at 13 different reefs were surveyed



Fig. 1. The two study areas, Spermonde and Komodo. The sampling locations for the UVC are indicated with numbers that correspond with the respective tables and bold italic numbers indicate that the reef is exposed to high fishing intensity.

during the dry season in April 1997 in Komodo. The reefs in both areas were of similar shape and size with extensive reef flats and steep slopes.

All fish observed within 2.5 m left and right of each transect line were included in the counts (English et al., 1994) and fish smaller than 1 cm that could not be identified during the underwater survey were grouped in the category 'others'. The accuracy of underwater fish length estimates was maintained by practising with fish models of known length before and throughout both assessment periods (Craik, 1981; Jennings and Polunin, 1997). Possible sources of bias such as fish behaviour (Sale and Sharp, 1983; Fowler, 1987), misidentification of species (Parker et al., 1994), the accuracy of the length estimates (Kulbicki, 1988a,b), and the effect of transect width (Sale and Sharp, 1983) were assumed similar for all sampling sites. Most of the variation that could have been caused by the selected observation method could also be disregarded because the method was similar at all sites (Craik, 1981). After the fish were counted, the same observer swam back along the transect line and estimated the relative cover (%) of seven different habitat categories in the 5 m wide belt where fish were recorded. These categories included dead coral standing, live hard coral, live soft coral, coral rubble, sand, rock and "other". The total live substrate cover (LSC) was calculated by summation of the relative cover for live hard coral, live soft coral and "other" for each transect.

# 2.3. Sampling effort and outcome of the fishery — catch assessment survey (CAS)

A monthly CAS was performed in Spermonde to study species and size composition of the catches at sea. At sea four belt transect sampling routes along the most common fishing sites were sailed and total fishing intensity was recorded. Overall annual fishing effort per unit area of coral reef in Spermonde was estimated at 557 boatdays km<sup>-2</sup> reef by dividing the annual reef fishery effort by the surface area of reefs shallower than 20 m depth.<sup>1</sup> A sub-sample of 921 boats that were observed fishing at the reefs was used

to estimate average CpUE as total catch per day-trip and catch composition for reef-related fisheries specifically. Fish were measured at sea in total length to the nearest centimetre.

Total catch biomass and individual CpUE in Komodo were assessed during a weekly fisheries monitoring program implemented in 1996 by the Indonesian Department of Forestry and Nature Conservation (PHPA) with support of The Nature Conservancy (TNC), a US-based environmental nongovernment organisation (Pet, 1998). For each of 911 reef fishing operations encountered during the patrols in 1997, total catch was recorded in kilogram. Total annual fishing effort per unit area coral reef in Komodo was estimated at 65 boatdays km<sup>-2</sup> reef by dividing the annual reef fishery effort by the estimated surface area of reefs shallower than 20 m (P.J. Mous. unpublished data). CpUE was estimated by dividing the annual fish catch by the annual fishing effort in day trips for each gear.

#### 2.4. Data processing and analysis

Data from the underwater survey were used to calculate fish biomass for each transect by converting individual length (cm) to weight (g) using lengthweight relationships published in FishBase (Froese and Pauly, 1998). The richness of the fish community was estimated by counting the number of taxonomic categories at each transect (Thresher, 1991). Mean fish density, mean fish length and mean fish biomass were estimated for the fish community as a whole, for two major fishery groups (commercial and non-commercial), for four major trophic groups (planktivores, herbivores, benthic invertebrate feeders, and piscivores), and for individual taxonomic fish categories. Fish was categorised as commercial if regularly landed at one of the auctions. Taxonomic categories were allocated to trophic groups based on knowledge of their adult feeding habits (Jennings et al., 1995; Froese and Pauly, 1998; Polunin and Jennings, 1998) (Table 1).

The habitat complexity of each of the reef transects in Spermonde and Komodo was indicated by LSC, a habitat characteristic that was highly correlated to the another commonly used habitat characteristic, reef rugosity (Pearson r = 0.84; p < 0.001, Pet-Soede, 2000). Habitat complexity was categorised as

<sup>&</sup>lt;sup>1</sup> See Pet-Soede, 2000 for further details on the sampling procedure, and Uljee et al., 1996 for details on the estimation of the reef area.

#### Table 1

Fish density (N ha<sup>-1</sup>) per taxonomic category at reefs in Spermonde and Komodo as observed during UVC. For each category, the fishery group is indicated (c: commercial, nc: non-commercial). The length–weight relation used to calculate individual fish biomass is presented (source: FishBase, Froese and Pauly, 1998). Fish categories are sorted by trophic group and by numerical density at reefs in Spermonde

Fish category	Common name	LW relation	Fishery group		Density in $a_{1} = 1$	Density in $V_{1} = 1$	
			c	nc	Spermonde (N ha <sup>-1</sup> )	Komodo (N ha	
Planktivores							
Abudefduf spp.	Damselfish	$0.0642L^{2.52}$		+	21928	6483	
Stolephorus spp.	Anchovy	$0.0041L^{3.33}$	+		6800	5067	
Apogon spp.	Cardinalfish	$0.0124L^{3.28}$		+	2792	133	
Caesio spp.	Fuselier	$0.0074L^{3.15}$	+		2237	3579	
Naso spp.	Unicornfish	$0.0136L^{3.13}$	+		171	1472	
Decapterus spp.	Scad	$0.0104L^3$	+		95	0	
Heniochus spp.	Bannerfish	$0.0132L^{3.37}$		+	29	43	
Pomacanthus spp.	Angelfish	$0.0371L^{2.97}$		+	25	81	
Anthias spp. <sup>a</sup>	Basslet	$0.06422L^{2.52}$		+	0	9837	
Chanos chanos	Milkfish	$0.0068L^{3.03}$	+		0	1	
Hankiyanaa							
Secure and	Domotfish	0.012673.11			764	209	
Scarus spp.	Parrouisn	0.0150L			704	308	
Acanthurus spp.	Surgeonfish	$0.01/8L^{-1}$	+		262	1368	
Siganus spp.	Rabbittish	$0.0254L^{-3.08}$	+		210	232	
Kyphosus spp.	Rudderfish	0.01216L <sup>5100</sup>	+		10	55	
Benthic invertebrate feeders		2.75					
Xyrichtys/Choerodon spp.	Wrasse	$0.0238L^{2.75}$		+	1974	2140	
Chaetodon spp.	Butterflyfish	$0.0874L^{2.18}$		+	262	352	
Parupeneus spp.	Goatfish	$0.0915L^{2.42}$	+		88	173	
Ballistoides spp.	Triggerfish	$0.0516L^{2.88}$	+		40	277	
Plectorinchus spp.	Sweetlip	$0.0827L^{2.72}$	+		37	53	
Zanclus spp.	Moorish idol	$0.01599L^{3.17}$		+	30	92	
Lethrinus spp.	Emperor	$0.0189L^{2.94}$	+		29	9	
Myripristi spp.	Squirrelfish	$0.0187L^{3.04}$		+	24	36	
Tetraodontidae	Pufferfish	$0.057L^{2.80}$		+	22	16	
Priacanthus spp.	Bigeye	$0.0392L^{2.78}$	+		1	0	
Terapon spp.	Grunter	$0.0097L^{3.14}$	+		0	1	
C. undulatus	Napoleon wrasse	$0.0132L^{3.12}$	+		0	15	
Elagatis bipinnulatus	Rainbow runner	$0.0135L^{2.92}$	+		0	1	
Piscivores							
Nemipterus spp.	Threadfinbream	$0.0149L^{3.14}$	+		340	116	
Lutjanus spp.	Snapper	$0.0153L^{3.09}$	+		290	303	
Spyraena spp.	Barracuda	$0.00986L^{2.88}$	+		227	0	
Epinephelus spp.	Seabass	$0.016L^3$	+		80	84	
Synodus spp.	Lizardfish	$0.0002L^{4.08}$	+		41	13	
Plectropomus spp.	Coral trout	$0.00923L^{3.08}$	+		24	49	
Platax spp.	Batfish	$0.045L^{2.98}$	+		10	160	
Fistularia spp.	Flutefish	$0.00005228L^{3.16}$			9	7	
Dasvatis spp.	Stingray	$0.0048L^{2.72}$	+		9	1	
Caranx spp	Jack	$0.023L^{2.94}$	+		8	45	
Cephalopholis spp	Other trout	$0.0099L^{3.21}$	+		5	35	
Rastrelliger kanagurta	Indian mackerel	$0.0014L^{3.38}$	+		5	220	
Rastrelliger son	Other mackerel	$0.006138I^{3.22}$	+		4	59	
Aprion spp.	Iohfish	$0.013L^{2.93}$	+		2	0	
Scomberomorus commerson	Spanish mackaral	$0.006138I^{3.22}$	- -		$\frac{2}{2}$	3	
Pterois spp	Stonefish	$0.0372L^{2.89}$	L.	+	- 1	0	
·	Stonenon	J.J.J. IL		1		0	

Table 1 (Continued)

Fish category	Common name	LW relation	Fisher	y group	Density in	Density in	
			c	nc	Spermonde (N ha <sup>-1</sup> )	Komodo (N ha <sup>-1</sup> )	
Leiognathus spp.	Ponyfish	$0.0263L^{2.75}$	+		<1	0	
	Other shark	$0.0255L^{2.86}$	+		<1	1	
C. altivelis	Barramundi cod	$0.016L^3$	+		0	3	
Tylosurus spp.	Houndsfish	$0.0005415L^{3.17}$	+		0	20	
Triaenodon obesus	White tip reef shark	$0.0015L^{3.38}$	+		0	4	
Carcharhinus melanopterus	Black tip reef shark	$0.0033L^{3.65}$	+		0	5	
Gymnosarda unicolor	Dogtooth tuna	$0.01505L^{3.07}$	+		0	4	

<sup>a</sup> This category was not assessed separately in Spermonde and was included in category damselfish.

follows: 0-25% = low LSC, 26-50% = medium LSC, 51-75% = high LSC, 76-100% = very high LSC. Correlations between parameters describing fish community structure and fishing intensity or habitat complexity were evaluated using Pearson's correlation coefficient (Sokal and Rohlf, 1995).

The effects of fishing pressure and habitat complexity on fish density, fish category richness, mean fish length, and fish biomass were analysed using general linear modelling. Fish density, fish length and biomass data were <sup>10</sup>log-transformed to meet the conditions for parametric analysis of variance. Variance around their geometric mean was indicated by the standard deviation of the <sup>10</sup>log-transformed values. The model was

$$y_{ijk} = \mu + \text{fishing intensity}_i + \text{habitat complexity}_j + \text{fishing intensity}_i \times \text{habitat complexity}_j + \varepsilon_{ijk}$$
(1)

where k is the replications,  $y_{ijk}$  the density, richness, length, or biomass in the UVC samples,  $\mu$  the overall mean, fishing intensity<sub>i</sub> the effect of level of fishing intensity i (i = low, high), habitat complexity<sub>j</sub> the effect of habitat complexity j (j = low LSC, medium LSC, high LSC, very high LSC), fishing intensity<sub>i</sub> × habitat complexity<sub>j</sub> the two-way interactions between fishing intensity and habitat complexity,  $\varepsilon_{ijk}$  the random effect.

In Spermonde, catches of commercial fishers recorded at sea were used to compare catch rates, species composition and size distributions between areas differing in fishing intensity. The diversity of the catches was estimated by counting the number of taxonomic categories in each catch. Catches from fishers in the less heavily fished northwest were distinguished from those in the more intensively fished southeast on the basis of GPS-coordinates of fishing locations. The Ryan–Einot–Gabriel–Welsch (REGW) multiple range test (Sokal and Rohlf, 1995) was used to calculate differences between means of all parameters. In case of significant interaction between the class variables main group means for each combination were compared using their respective 95% confidence limits.

#### 3. Results

#### 3.1. Fish community structures and fishing intensity - UVC

Within Spermonde, ANOVA shows no significant difference in reef fish density, mean length or biomass in total or per trophic group, that could be explained from contrasts in fishing intensity. So patterns in fish distributions at a large spatial scale must rather be explained by an effect of shelf zone, with much lower fish stock biomass in the inner, coastal zone (1) (see Pet-Soede, 2000) and which effect seems not related to fishing intensity. Excluding the observations in zone 1 from the data used for ANOVA, however, did not reveal any fishery effect either (Table 2).

Within Komodo, the habitat complexity was significantly lower at shallow transects (LSC = 55%, S.D. = 20%) than at deep transects (LSC = 72%, S.D. = 18%), but did not differ between reefs outside the park and inside the park (LSC = 64%). Only the difference in fishing pressure seemed to have an effect on total fish biomass, on biomass of planktivores and on mean length and biomass of piscivores (Table 3).

Table 2

ANOVA for the effect of fishing intensity f, and habitat complexity LSC on fish density (n m<sup>-2</sup>), fish length (cm) and fish biomass (g m<sup>-2</sup>) in zones 2, 3 and 4 combined in Spermonde. Mean sum of squares for each effect is presented

	Fish density $(n m^{-2})$			Fish length (cm)			Fish biomass (g m <sup>-2</sup> )		
	MS f	MS LSC	MS error	MS f	MS LSC	MS error	MS f	MS LSC	MS error
Total	_	_	_	_	_	_	_	_	_
Planktivores	_	_	_	_	_	-	_	$0.57^{**}$	_
Herbivores	_	_	_	_	$0.05^{***}$	0.003	_	$0.54^{**}$	0.07
Benthic invertebrate feeders	_	_	_	_	_	-	_	_	_
Piscivores	_	_	_	_	0.03**	0.005	_	$1.55^{*}$	0.38
Commercial	-	_	-	-	_	_	-	0.36*	0.10
d.f.	1	3	26	1	3	26	1	3	26

$$p^* < 0.05.$$

$$p^{**} < 0.01.$$

\*\*\*\* p < 0.001.

The overall mean fish biomass per transect differed significantly (p < 0.05) between reefs inside  $(GM = 530 \text{ g m}^{-2})$  and outside  $(GM = 227 \text{ g m}^{-2})$ , as did piscivore biomass (inside  $GM = 129 \text{ g m}^{-2}$  and outside  $GM = 27 \text{ g m}^{-2}$ ) (p < 0.05), due to the significantly (p < 0.05) higher mean length inside the park (35 cm) than outside the park (27 cm).

Spermonde and Komodo differed greatly in total fish biomass (REGW p < 0.001), which was more than four times higher in Komodo (382 g m<sup>-2</sup>) than in Spermonde (86 g m<sup>-2</sup>). These areas also differed in biomass per trophic group which was also larger for each trophic group in Komodo than in Spermonde (Fig. 2) (REGW p < 0.001). The relative importance per trophic group differed for herbivores that contributed more to total biomass in Spermonde (23%) than

in Komodo (16%), which was opposite to that for piscivores which contributed less to total biomass in Spermonde (27%) than in Komodo (37%). As overall mean fish abundance per transect did not differ between Spermonde (2.82 fish  $m^{-2}$ ) and Komodo (2.52 fish  $m^{-2}$ ), not even per trophic group, the differences in biomass were mostly due to larger mean lengths of fish in Komodo (Fig. 2). Overall mean fish size was twice as large in Komodo (14 cm) as in Spermonde (7 cm).

Mean habitat complexity, as indexed with live coral cover, was on average slightly higher in Komodo than in Spermonde (Fig. 3). Total fish biomass showed no significant correlation with LSC in Komodo (p = 0.057) or in Spermonde in zones 2, 3, and 4 (p = 0.48) (see Pet-Soede, 2000). Overall mean fish

Table 3

ANOVA for the effect of fishing intensity f, and habitat complexity LSC on fish density (n m<sup>-2</sup>), fish length (cm) and fish biomass (g m<sup>-2</sup>) in Komodo. Mean sum of squares for each effect is presented

	Fish density $(n m^{-2})$			Fish length (cm)			Fish biomass (g m <sup>-2</sup> )		
	MS f	MS LSC	MS error	MS f	MS LSC	MS error	MS f	MS LSC	MS error
Total	_	_	_	_	_	_	$0.84^{*}$	_	0.18
Planktivores	_	_	_	_	_	_	$1.78^{*}$	_	0.35
Herbivores	-	_	_	_	_	_	_	_	-
Benthic invertebrate feeders	_	_	_	_	_	_	_	_	-
Piscivores	-	_	_	$0.10^{*}$	_	0.02	$2.81^{*}$	_	0.49
Commercial	-	-	-	$0.09^*$	-	0.02	-	-	-
d.f.	1	2	24	1	2	24	1	2	24

 $p^* < 0.05$ .



Fig. 2. Mean fish biomass (g m<sup>-2</sup>) and length (cm) per trophic group as observed during UVC in Spermonde and in Komodo.

biomass inside Komodo Park (530 g m<sup>-2</sup>) was ca. 2.3 times higher than outside (227 g m<sup>-2</sup>). Mean biomass in Spermonde in zones 2, 3, and 4 was 86 g m<sup>-2</sup>. Fish biomass was significantly correlated with LSC in zone

1 in Spermonde (p = 0.002) and was 38 g m<sup>-2</sup> where there was 50% live coral cover (Fig. 3).

Comparison of biomass size distributions using 10 cm categories summarises the most important



Fig. 3. Total fish biomass (g m<sup>-2</sup>) in Spermonde at sites in zone 1 (n = 13), in zones 2, 3, and 4 combined (n = 34) and outside (n = 10) and inside Komodo National Park (n = 13) plotted on LSC (%) calculated per 100 m transect. Dotted lines indicate means per area.



Fig. 4. Absolute  $(g m^{-2})$  and relative biomass (%) per trophic group and 10 cm size category as observed during UVC at intensively fished reefs and less intensively fished reefs in Spermonde and at reefs outside and inside the marine park in Komodo.

observations related to the effect of fishing on the structure and composition of reef fish communities. Although no effect of fishing intensity in Spermonde was proven for total biomass or biomass per trophic group, biomass size distributions are still given here for sites with low and high fishing intensity, because effects were still expected for the largest, mostly piscivorous fish. Biomass density of fish <20 cm, mainly planktivores, was ca. 1.5 times higher at the intensively fished reefs in Spermonde than at reefs inside Komodo Park. Biomass density of fish >40 cm was ca. 17 times higher inside Komodo Park (72% of total fish biomass) than at intensively fished reefs in Spermonde (23% of total fish biomass) (Fig. 4).

In Spermonde, the biomass of fish >40 cm is seemingly higher at less intensively fished sites than at intensively fished sites (zones 2, 3 and 4), but ANOVA for the effect of effort and LSC, or reef rugosity R, did not reveal a significant effect of fishing intensity ( $p_{LSC} = 0.12$ ;  $p_R = 0.17$ ), not even for piscivores only ( $p_{LSC} = 0.30$ ;  $p_R = 0.34$ ).

Finally, also the taxonomic composition of the fish community differed between reefs in Spermonde where 38 taxonomic fish groups were observed, and the reefs in Komodo where 44 taxonomic groups were observed. The 10 fish categories with the highest biomass differed, and reefs in Komodo were inhabited by more piscivores and more categories with high commercial value than those in Spermonde (Fig. 5). The most striking difference was that the highly valued sharks, barramundi cod (*Cromileptus altivelis*) and Napoleon wrasse (*Cheilinus undulatus*) were observed only in Komodo, and that the density of groupers (especially *Epinephelus* spp. and *Plectropomus* spp.) was higher in Komodo (Table 1). Planktivorous damselfish (*Chromis* spp.), herbivorous parrotfish (*Scarus* spp.) and piscivorous threadfinbream (*Nemipterus* spp.) were significantly more abundant in Spermonde (Table 1).

## 3.2. Catch rates, composition and fishing intensity — CAS in Spermonde

In Spermonde, catch rates for the most important reef fishery gear, hook and line, have already been shown to be significantly different between areas, characterised by shelf zone, latitude and water depth and between seasons (Pet-Soede, 2000). To assess an effect of fishing intensity on catch rate unbiased by the previously observed effect of shelf zone on fish biomass (Pet-Soede, 2000), observations were compared between the intensively fished southeast parts and the less intensively fished northwest parts of zones 2, 3 and 4 combined. Here, catch rates for hook and line were significantly lower (AM = 2.45 kg per trip) at high fishing effort than at low fishing effort (AM = 3.30 kg)per trip) (REGW p < 0.01) (Table 4). Such differences were also found for catch rates of gill nets (Table 4). Catch rates for most gears were low in zone 1, but not significantly different from



Fig. 5. The percentage contribution (%) of the 10 taxonomic categories with the highest contributions to total fish biomass at reefs in Spermonde and Komodo. Categories are sorted according to their importance in Spermonde.

#### Table 4

Mean CpUE (AM, kg per trip) including zero-catches and mean length (AM, cm) in catches per gear category for *n* boats that are significantly different between areas with high and low fishing effort *f* within zones 2, 3, and 4 combined in Spermonde (*p* for REGW multiple range test). Percentage zero catches in zones 2,3, and 4 combined and values for zone 1 are also given

Gear category	Percentage zero catches in zones 2,3, and 4		CpUE in zones 2,3, and 4 (kg per trip)		р	CpUE in zone 1 (kg per trip)	Mean length in zones 2,3, and 4 (cm)		р	Mean length in zone 1 (cm)
	$\operatorname{High} f$	Low f	High f	Low f			High f	$\operatorname{Low} f$		
Blast fishing	3	33	47.29 (29)	21.81 (24)	0.29		22.77 (19)	22.42 (8)	0.93	
Gill net	12	9	4.34 (49)	24.05 (11)	0.001	4.00 (7)	24.52 (4)	47.80 (1)	0.39	21.31 (7)
Cyanide	33	25	0.92 (5)	2.50 (8)	0.22		34.95 (5)	42.33 (1)	0.34	
Hook and line	14	10	2.45 (293)	3.30 (268)	0.002	2.94 (44)	21.93 (221)	28.83 (23)	0.03	20.25 (44)
Hook and line grouper	12	37	2.05 (28)	1.72 (118)	0.66	0.28 (1)	29.30 (26)	39.96 (24)	0.002	24.40 (1)
Hook and line mackerel	60	40	2.70 (5)	3.77 (30)	0.88		55.30 (3)	69.64 (16)	0.60	
Long line	25	0	10.21 (4)	30.18 (19)	0.75		21.97 (4)	42.77 (2)	0.05	
Spear gun	60	36	1.50 (6)	5.00 (11)	0.39		65.18 (6)	33.75 (2)	0.26	
Traps	0	44	4.50 (4)	10.00 (9)	0.31	7.00 (2)	31.12	-	_	25.27 (2)



Fig. 6. Biomass composition (%) per trophic group of the reef fish community (UVC) and of the commercial catch per type of reef fishery in Spermonde. The most important taxonomic groups contributing to piscivore biomass are indicated.

catch rates in the intensively fished parts of zones 2, 3 and 4 combined.

Planktivorous damselfish, benthic invertebrate feeding wrasses and herbivorous parrotfish contributed 33% to total fish biomass observed during the UVC in Spermonde, but were not targeted by the reef fishery in this area. Instead, catch biomass still included mostly piscivores, especially for fishers trolling for groupers and large pelagics, long liners and spear gun fishers (>90%). Only catch biomass of gill netters and blast fishers, the latter of which is least species and size selective of all reef fishery gears, included less than 50% piscivores (Fig. 6).

Overall mean length of fish in the catch was 24.5 cm. Mean length of fish was significantly higher

in catches at sites with low fishing intensity for hook and line fishers, fishers trolling for grouper, and long liners aiming at sharks (Table 4). The geometric mean length of groupers that have high export value was significantly larger at sites with low fishing intensity and so was the mean length of barracudas that are important for the local markets (Table 5). Mean length for these categories was always smaller in catches in zone 1.

There were on average 2.6 taxonomic categories in the individual catch per boat. Catches in the intensively fished southeast of zones 2, 3, and 4 in Spermonde included more categories than in the lightly fished northwest (REGW p < 0.05), due to a larger importance of hook and line fishers in the southeast,

Table 5

Mean size (AM, cm) in the catch for n boats that are significantly different between areas with high and low fishing effort f within zones 2, 3, and 4 combined in Spermonde (p for REGW multiple range test). Values for zone 1 are also given

Fish category	Mean length (cm)		р	Mean length for zone 1 (cm)
	High f	Low f		
Epinephelus spp.	24.5 (46)	30.3 (20)	0.026	19.4 (16)
Plectropomus spp.	30.7 (24)	38.8 (23)	0.001	25.1 (5)
Spyraena spp.	35.4 (21)	77.0 (6)	0.0001	26.0 (5)

Table	6
-------	---

Gear category	CpUE (kg per day	trip)	Number of taxonomic categories in Spermonde			
	Spermonde	Komodo	Individual catch	All catches combined		
Spear gun	24.8	_	1.2	4		
Diving	16.2 <sup>a</sup>	19 <sup>b</sup>	1.9	5		
Blast fishing	15.7	_	4.2	35		
Traps	8.5	205	3.1	18		
Gill net	7.5	23	3.6	30		
Hook and line/bottom line	4.9	79	2.9	51		
Trolling large pelagic fish	3.7	72	1.7	8		
Trolling live grouper	1.7	-	1.4	14		

Catch rates (CpUE, kg per daytrip) as observed at sea (see also Section 3) for Spermonde and for Komodo and the number of taxonomic categories in the catch in Spermonde

<sup>a</sup> Only grouper with cyanide.

<sup>b</sup> Lobster and seacucumber.

the combined catch of which was most diverse, within a total of 51 different taxonomic categories (Table 6). Their catches were dominated by threadfin bream (*Nemipterus* spp.).

# 3.3. Catch rates from Spermonde and Komodo compared

The annual catch of the reef fishery was estimated  $3.2 \text{ t km}^{-2}$  reef in Spermonde and  $3.1 \text{ t km}^{-2}$  reef in Komodo. The mean CpUE for all reef fisheries combined was 5.8 kg per trip in Spermonde, eight times lower than for Komodo (48 kg per trip) (Table 6). Also per gear type, catch rates were much lower in Spermonde (Table 6).

#### 4. Discussion

Comparison of catch rates and catch compositions within Spermonde indicates that fishers catch more fish at less intensively fished areas and that the mean length at capture of especially piscivorous fish decreases with fishing intensity, but direct relationships between fishing intensity, fish biomass and fish length are not supported by the patterns observed underwater in Spermonde. Only when fish community structures are compared between areas with large contrasts in mean fishing intensity, such as Spermonde and Komodo, do trends appear to be directly related to fishing intensity. Fish are significantly larger and fish biomass is significantly higher at reefs in Komodo that are fished eight times less intensely than reefs in Spermonde. This trend persists throughout all levels of data aggregation, for the entire fish community, for different trophic and fishery groups, and even for many individual taxonomic fish categories. Mean fish density does not indicate a fishery influence at the level of the entire fish community or the major groups within it. However, at the level of individual taxonomic categories, numerical densities of commercially important fish were larger inside Komodo National Park than in Spermonde.

The overall high taxonomic diversity of catches per gear type illustrates the multispecies character of the fisheries in Spermonde. Therefore, even when significant, the few contrasts in mean lengths of fish throughout Spermonde that indicated a fishery impact, may be hard for the majority of the fishers to perceive. Specialists that target groupers may be able to observe a difference in mean length of these fish, but only if they go frequently to locations with high fishing intensity as well as locations with low fishing intensity. However, most small-scale reef fishers are forced to select fishing locations near their village due to the small nature of their operations (Pet-Soede, 2000). Whereas in Spermonde higher biomasses of fish >40 cm occurred in areas with low fishing effort (at a 90% confidence interval), it was nevertheless concluded that such contrasts in Spermonde were weak when compared with another reef area, Komodo, where fishing intensity was almost an order of size lower.

Most of the patterns observed through comparison of fish communities between Spermonde and Komodo

confirm the effects of fishing discussed in other studies (McManus, 1992; McClanahan, 1994; Sluka et al., 1996; Öhman et al., 1997; Rooker et al., 1997). As in many of these other studies, the results can be criticised in terms of the level of similarity between sites compared (Roberts and Polunin, 1991; Polunin et al., 1996). In general it holds, that in the absence of time series of observations on fish community structures at permanent locations, many scientists face major challenges when describing a fishery impact through spatial comparison (Jennings and Kaiser, 1998). In our case, one could argue that the comparison of fish community structures between reefs in Spermonde and Komodo is not possible, due to differences in oceanographic and geographic features. Up-welling currents in Komodo cause a lower water temperature than in Spermonde (pers. obs.), which could affect the growth of fish (Medley et al., 1993; McGhee, 1994). Colder water is associated with lower natural mortality rates and hence larger mean lengths than in warmer water (Pauly, 1980).

Reefs in both areas are characterised by a high numerical density of planktivores typical of Indo-Pacific reefs with high primary productivity (Russ, 1989), and a large piscivorous biomass. All transects were positioned in the same manner at similar depths on reefs that had extensive areas of reef flat and reef slopes (Sale and Sharp, 1983). On average, the reef habitat as described at the smallest spatial scale was more complex in Komodo, but the habitat complexity at reefs in Spermonde ranged also into the highest category of 75-100% LSC, with corresponding high rugosity (Pet-Soede, 2000). The higher relative importance of herbivores in total fish biomass in Spermonde must be explained from a proportion of reefs with the lowest category of 0-25% LSC with larger proportions of dead coral covered with algae on which many herbivores graze (Sale, 1991; Williams, 1991). The relation between fish parameters and habitat complexity appears weak in Komodo, but biomass nevertheless followed a similar increase with habitat complexity (p = 0.06 for LSC). At similar habitat complexity, biomass was much higher inside Komodo Park than in Spermonde.

We may now ask if the reef resources in Spermonde are over-fished. Annual yield in Spermonde is not particularly high when compared with literature data but neither is annual yield for Komodo. Following the

relation proposed by Arias-Gonzales et al. (1994) between the size of the resource base and yield in tropical reef fisheries, Spermonde would yield 4.9 t km<sup>-2</sup> reef rather than the current 3.2 t km<sup>-2</sup> reef. Yield in Spermonde is also lower than the  $10 \text{ km}^{-2} \text{ yr}^{-1}$  proposed by Munro and Williams (1985) as the maximum vield sustained by coral reefs. but higher however than the 1.1 t  $\text{km}^{-2}$  yr<sup>-1</sup> estimated by Munro (1977) as the potential harvest from coralline shelves in the tropical Atlantic under moderate exploitation. Annual yields are often presented to characterise a coral reef area as over-fished without mentioning the level of fishing intensity or the CpUE. Yield in Spermonde with its daily fishing intensity of 1.6 fishers  $\text{km}^{-2}$  or annual fishing duration of some  $3350 \text{ h km}^{-2}$  reef is lower than in Fiji (8.2 t km<sup>-2</sup>) where fishing intensity was similar at  $3580 \text{ h km}^{-2} \text{ yr}^{-1}$  (Polunin and Jennings, 1998). Yield in Spermonde was also lower than the 8 t  $\text{km}^{-2}$ reef in Kenya where daily fishing intensity was higher with 10 fishers  $\text{km}^{-2}$  reef (McClanahan and Kaunda-Arara, 1996). So, are fish stocks in Spermonde underor over-exploited, or are differences related to use of other gears, differences in species diversity, or primary production (Christensen, 1996)?

Our results do not allow for clear-cut conclusions on particular forms of over-fishing described by McManus (1997) as growth over-fishing, recruitment over-fishing, biological over-fishing, ecosystem overfishing, economic over-fishing and Malthusian overfishing. This leads to four considerations. First, the small length in the catch suggests growth over-fishing in Spermonde. This small length of fish indicates a lower egg and larval output per unit area than in Komodo through the relation between length and fecundity (Polunin et al., 1996; Welcomme, 1999). Yet, fish density was similar between Spermonde and Komodo, which gives ample reason to assume that recruitment over-fishing is not so much a structuring factor but rather that settlement of fish in Spermonde is at its optimum and is merely limited by competition for space and food (Polunin and Jennings, 1998).

Second, the relative density and contribution to total biomass of prey and predator fish did not differ largely between the two areas and catches in the multigear and multispecies fishery in Spermonde still included large proportions of highly valued piscivores. Therefore, there is no reason to assume ecosystem over-fishing in Spermonde, which is defined as the combination of growth and recruitment over-fishing where predator removal though fishing would lead to increased prey release so that fishers are forced to catching less valuable resources (Munro, 1982).

Third, even while the CpUE is almost an order of size lower in Spermonde than in Komodo and nearest to the lowest levels in the range published by Dalzell (1996), consumer demands are higher in Spermonde than in Komodo, however, which makes it that prices per kilogram of fish are higher in Spermonde and that the cost benefit balance remains positive.

Fourth, blast fishing is a common practice in Spermonde (Pet-Soede and Erdmann, 1998), which could indicate Malthusian over-fishing where as a result of human population growth, ecosystem over-fishing occurs and destructive fishing practices are applied with increasing frequency. Nevertheless, it must be regarded more as a traditional fishing method that has been applied in the area since the 1940s by a particular group of fishers as an easy way to make a living (Pet-Soede and Erdmann, 1998). Blast fishing was also common practice in Komodo before the frequency and intensity of patrols was increased in 1996 (Pet and Djohani, 1996).

The dilemma of whether or not fishery resources are subjected to a level of fishing intensity that threatens their subsistence calls for verification of the observed spatial patterns by monitoring changes in reef fish community structures and fishing intensity through time (Russ and Alcala, 1989). We must conclude however that within Spermonde this will not result in more clarity unless such contrasts in fishing effort would largely increase. This study indicates that if fishing efforts were decreased, the structure of the fish community in Spermonde might resemble more that of the community in Komodo, which could possibly be perceived by fishers through overall increased catch rates and greater proportions of larger and highly valued taxonomic fish categories in their catches.

#### Acknowledgements

The present study was carried out within the framework of the WOTRO/UNHAS Buginesia project on Coastal Zone Management, a co-operative project between the Indonesian counterpart Hassanuddin University (Sulawesi, Indonesia) and Wageningen University — Wageningen Institute of Animal Sciences. The Netherlands Foundation for the Advancement of Tropical Research (WOTRO) is thanked for financial support and The Nature Conservancy (TNC) — Indonesia Coastal and Marine Program for their logistic support. Peter Mous (TNC) is gratefully acknowledged for his work in mapping the different habitats in Komodo. Joep de Leeuw contributed valuable comments to the manuscript.

#### References

- Anonymous, 1995. Laporan statistik perikanan Sulawesi Selatan 1995 (Fisheries Statistics South Sulawesi Province 1995). Provicial Fisheries Service Ujung Pandang Sulawesi, 158 pp.
- Arias-Gonzales, J.E., Galzin, R., Nielson, J., Mahon, R., Aitken, K., 1994. Reference area as a factor affecting potential yield estimates of coral reef fishes. NAGA ICLARM Quart. 17 (4), 37–40.
- Bakar, A., 1996. Resource Utilization in and around Komodo National Park. The Nature Conservancy, Bali, 25 pp.
- Christensen, V., 1996. Managing fisheries involving predator and prey species. Rev. Fish Biol. Fish. 6, 417–442.
- Craik, G.J.S., 1981. Underwater survey of coral trout *Plectropomus leopardus* (Serranidae) populations in the Capricornia section of the Great Barrier Reef Marine Park. In: Proceedings of the Fourth International Coral Reef Symposium, Vol. 1, Manila, Philippines. International Society for Reef Studies, Kansas, pp. 53–58.
- Dalzell, P., 1996. Catch rates, selectivity and yields of reef fishing. In: Polunin, N.V.C., Roberts, C.M. (Eds.), Reef Fisheries. Chapman & Hall, London, pp. 161–192.
- English, C., Wilkinson, C., Baker, V., 1994. Survey Manual for Tropical Marine Resources. AIDAB, AIMS, 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.
- Froese, R., Pauly, D., 1998. FishBase 98. Concepts, Design and Data Sources. ICLARM, Manila, 293 pp.
- Gulland, J.A., 1985. Fish stock assessment. A Manual of Basic Methods. FAO Series on Food and Agriculture. Wiley, New York, 223 pp.
- Hoeksema, B.W., 1990. Systematics and ecology of mushroom corals (Scleractinia: Fungiidae). Ph.D. Thesis. State University of Leiden, Leiden, the Netherlands.
- Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. Adv. Mar. Biol. 34, 203–352.
- Jennings, S., Lock, J., 1996. Population and ecosystem effects of fishing. In: Polunin, N.V.C., Roberts, C.M. (Eds.), Reef Fisheries. Chapman & Hall, London, pp. 193–218.
- Jennings, S., Polunin, N.V.C., 1996. Impacts of fishing on tropical reef ecosystems. Ambio 25 (1), 44–49.
- Jennings, S., Polunin, N.V.C., 1997. Impacts of predator depletion

by fishing on the biomass and diversity of non-target reef fish communities. Coral Reefs 16, 71–82.

- Jennings, S., Grandcourt, E.M., Polunin, N.V.C., 1995. The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. Coral Reefs 14, 225–235.
- Kulbicki, M., 1988a, Patterns in the trophic structure of fish populations across the SW lagoon of New Caledonia. In: Proceedings of the Sixth International Coral Reef Symposium, Vol. 2, Townsville, Australia. International Society for Reef Studies, Kansas, pp. 89–94.
- Kulbicki, M., 1988b. Correlation between catch data from bottom longlines and fish censuses in the SW lagoon of New Caledonia. In: Proceedings of the Sixth International Coral Reef Symposium, Vol. 2, Townsville, Australia. International Society for Reef Studies, Kansas, pp. 305–312.
- McClanahan, T.R., 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. Coral Reefs 13, 231–241.
- 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 (4), 1187–1199.
- McGhee, M.A., 1994. Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. Mar. Ecol. Prog. Ser. 105, 243– 255.
- McManus, J.W., 1992. The Spratly islands a marine park alternative. NAGA ICLARM Quart. 2, 4–8.
- McManus, J., 1997. Tropical marine fisheries and the future of coral reefs: a brief review with emphasis on south east Asia. In: Proceedings of the Eighth International Coral Reef Symposium, Vol. 1, Panama. International Society for Reef Studies, Kansas, pp. 129–134.
- Medley, P.A., Gaudian, G., Wells, S., 1993. Coral reef fisheries stock assessment. Rev. Fish Biol. Fish. 3, 242–285.
- Moll, H., 1983. Zonation and diversity of scleractinia on reefs off SW Sulawesi, Indonesia. Ph.D. Thesis. State University of Leiden, Leiden, the Netherlands.
- Munro, J.L., 1977. Actual and potential production from the coralline shelves of the Caribbean Sea. FAO Fisheries Report No. 200. FAO, Rome, pp. 301–321.
- Munro, J.L., 1982. Estimation of biological and fishery parameters in coral reef fisheries. In: Pauly, D., Murphy, G.I. (Eds.), Theory and Management of Tropical Fisheries. Conference Proceedings, ICLARM, Manila, Philippines, Vol. 9, pp. 71–82.
- Munro, J.L., Williams D.McB., 1985. Assessment and management of coral reef fisheries: biological environmental and socioeconomic aspects. In: Proceedings of the Fifth International Coral Reef Symposium, Seminar C, Tahiti. International Society for Reef Studies, Kansas, 35 pp.
- Öhman, M.C., Rajasuriya, A., Ólafsson, E., 1997. Reef fish assemblages in north-western Sri Lanka: distribution patterns and influences of fishing practices. Environ. Biol. Fish 49, 45– 61.
- Parker Jr., R.O., Chester, A.J., Nelson, R.S., 1994. A video transect method for estimating reef fish abundance, composition, and habitat utilization at Gray's reef national marine sanctuary, Georgia. Fish. Bull. 92, 787–799.

- Parrish, J.D., Callahan, M.V., Norris, J.E., 1985. Fish trophic relationships that structure reef communities. In: Proceedings of the Fifth International Coral Reef Symposium, Vol. 4, Tahiti. International Society for Reef Studies, Kansas, pp. 73–78.
- Pauly, D., 1980. On the inter-relationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer. 39, 175– 192.
- Pet, J.S., 1998. Marine resource utilization in Komodo National Park. Monitoring Program 1996–1997. The Nature Conservancy, Bali, 32 pp.
- Pet, J.S., Djohani, R.H., 1996. A Framework for Management of the Marine Resources of Komodo National Park and Surrounding Fishing Grounds in Eastern Indonesia. The Nature Conservancy, Bali, 53 pp.
- Pet, J.S., Mous, P.J., 1999. Marine resource utilization in Komodo National Park. Monitoring Report 1997–1998. The Nature Conservancy, Bali, 37 pp.
- Pet-Soede, C., 2000. Options for co-management of an Indonesian coastal fishery. Ph.D. Thesis. Wageningen Agricultural University, 144 pp.
- Pet-Soede, C., Erdmann, M.V.E., 1998. Blastfishing in SW Sulawesi, Indonesia. NAGA ICLARM Quart. 2 (2), 4–9.
- Polunin, N.V.C., Jennings, S., 1998. Differential effects of smallscale fishing on predatory and prey fishes on Fijian reefs. In: Newbery, D.M., Prins, H.H.T., Brown, N. (Eds.), Dynamics of Tropical Communities, Symposia of the British Ecological Society, Vol. 37. Blackwell, Oxford, pp. 95–124.
- Polunin, N.V.C., Roberts, C.M., Pauly, D., 1996. Developments in tropical reef fisheries science and management. In: Polunin, N.V.C., Roberts, C.M. (Eds.), Reef Fisheries. Chapman & Hall, London, pp. 361–377.
- Roberts, C.M., Polunin, N.V.C., 1991. Are marine reserves effective in management of reef fisheries? Rev. Fish Biol. Fish. 1, 65–91.
- 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.
- Russ, G.R., 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. In: Sale, P.F. (Ed.), The Ecology of Fishes on Coral Reefs. Academic Press, California, pp. 601–635.
- Russ, G.R., Alcala, A.C., 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. Mar. Ecol. Prog. Ser. 56, 13–27.
- Sainsbury, K.J., 1982. The ecological basis of tropical fisheries management. In: Pauly, D., Murphy, G.I. (Eds.), Theory and Management of Tropical Fisheries. Conference Proceedings, ICLARM, Manila, Philippines, Vol. 9, pp. 167–188.
- Sale, P.F., 1991. The Ecology of Fishes on Coral Reefs, 1st Edition. Academic Press, California.
- Sale, P.F., Sharp, B.J., 1983. Correction for bias in visual transect censuses of coral reef fishes. Coral Reefs 2, 37–42.
- Sluka, R.D., Chiappone, M., Sullivan, K.M., 1996. Habitat

50

preference of groupers in the Exuma Cays. Bahamas J. Sci. 4 (1), 8–14.

- Smith, P.J., Francis, R.I.C.C., McVeagh, M., 1991. Loss of genetic diversity due to fishing pressure. Fish. Res. 10, 309–316.
- Sokal, R.R., Rohlf, F.J., 1995. Biometry: The Principles and Practice of Statistics in Biological Research, 3rd Edition. Freeman, New York, 887 pp.
- Sparre, P., Ursin, E., Venema, S.C., 1989. Introductions to tropical fish stock assessment. FAO Fisheries Technical Paper No. 306 (1 and 2). FAO, Rome.
- Thresher, R.E., 1991. Geographic variability in the ecology of coral reef fishes: evidence, evolution, and possible implications. In:

Sale, P.F. (Ed.), The Ecology of Fishes on Coral Reefs. Academic Press, California, pp. 401–436.

- Uljee, I., Engelen, G., White, R., 1996. RamCo Demo Guide. Work Document CZM-C 96.08. Coastal Zone Management Centre, National Institute for Coastal and Marine Management, The Hague, the Netherlands.
- Welcomme, R.L., 1999. A review of a model for qualitative evaluation of exploitation levels in multi-species fisheries. Fish. Mgmt. Ecol. 6, 1–19.
- Williams, D.McB., 1991. Patterns and processes in the distribution of coral reef fishes. In: Sale, P.F. (Ed.), The Ecology of Fishes on Coral Reefs. Academic Press, California, pp. 37–74.