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RESEARCH ARTICLE

The ecology of Indo-Pacific grouper (Serranidae) species and the effects of a small scale no take area on grouper assemblage, abundance and size frequency distribution

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Abstract This paper used the case study of the Wakatobi Marine National Park, Indonesia to examine changes in the diversity, density and maturity of grouper species over a 5-year period following the establishment of a small-scale no-take area (NTA). This work was carried out to investigate whether "small" NTAs could be effective management strategies over a time scale that is relevant to local fishery communities and their perception of management success. Our research also documents the ecology of these species, information essential if we are to understand how management practises are to affect coral reef fish species. Designation of this "small NTA" increased the density of groupers by 30% over a 5-year period of protected status. After 5 years of protection, grouper populations within this NTA were more mature and double the density of those within the adjacent lightly fished sites and nearly five times those of a heavily fished site. During this time all other nearby fished sites underwent large declines in grouper density. The nearby lightly fished Kaledupa site decreased by up to 50% year^{-1}. Such drastic declines are considered the impact of the exponential development of ever efficient and unsustainable methods of fishing within the study region. This NTA was not of benefit to all grouper species; the reasons for which are not clear. Such questions require further detailed research about the life history, population and behavioural ecology of Indo-Pacific grouper species. Such information is critical for urgently needed fisheries management. The present study found that a small scale NTA of 500 m length was large enough to increase the population of top predatory fish. In conjunction with other socially acceptable small scale NTAs it could help maintain and increase important fish stocks over a larger area. The use of "small" NTAs within networks of reserves should become a useful tool in the management of the locally exploited coral reefs.

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Introduction

Marine protected areas (MPAs) signify areas that are tightly managed, where fisheries activity and resource extraction are prohibited, yet in practice this term is ambiguous as it can be used to represent areas that are afforded very different levels of protection. Despite MPA designation, many localities across the Indo-Pacific do not have fishery or conservation management strategies. As an alternative the present research used the term "no-take area" (NTA), defined as an area where any form of fishing or exploitation is prohibited. The use of NTAs for improving fishery yield is an increasing trend both in tropical and temperate locations (Hastings and Botsford 2003). Extensive empirical evidence (e.g. Mayapa et al. 2002) has demonstrated that large scale NTAs worldwide have led to increases in abundance, body size, biomass and reproductive output of exploited species (Gell and Roberts 2002). Removal of reserve status has also been found to reduce fish abundance and biomass (Ferraris et al. 2005). Estimates suggest that for NTAs to increase fishery yield, 20–40% of a traditional fishery area are required to be closed (Gell and Roberts 2002). Yet the minimum size required for an individual NTA remains unclear. Roberts et al. (2001) argue that networks of NTAs should vary in size from a few kilometres to a few tens of kilometres. Quantitative data on the success of small NTAs in increasing fisheries yield remains scant.

Lack of agreement and understanding as to the purpose of NTAs reduces levels of regulation compliance by fishery-based communities. It is important in areas of traditional artisanal fisheries grounds that these factors are considered. High levels of compliance are desirable as low compliance results in reduced management success. Compliance increases with increased social capital, an important factor in biodiversity management (Pretty and Smith 2004), but compliance also depends on the transparency of management outcomes as well as on the degree to which traditional practises are regulated. Consequently small NTAs are likely to result in a higher level of compliance than large NTAs that by their nature will significantly affect the socioeconomic welfare of dependant communities. A trade off is required between maximising the size of NTAs for biological reasons whilst minimising the negative economic impacts (reduced fishing grounds, greater travel costs) upon local users. Research is required on the biological success of small NTAs the size of which is agreeable to local user groups. One way in which the success of NTAs can be assessed is by examining changes in abundance of exploited species or model groups.

Groupers (Serranidae) are top predatory fish feeding on fishes, crustaceans and cephalopods; they play a major role in structuring coral reef communities. A large grouper population is therefore indicative of a thriving and productive reef community yet they are heavily exploited (Bohnsack 1994; Chiappone et al. 2000; Costa et al. 2003). The longevity and slow growth of groupers, and their tendency to aggregate, renders them vulnerable to over-fishing (Sadovy and Colin 1995; Colin 1992; Beet and Friedlander 1992; Costa et al. 2003). Appropriately located NTAs represent an effective means of protecting groupers from the pressures of over-fishing (see, Russ and Alcala 1996).

Groupers are mobile fish, species such as *Plectropomus leopardus* have a home ranges greater than 1.8 ha (Samoilys et al. 1997) and can travel distances up to 2 km (Samoilys 1987; Samoilys 1997a, b, c). Designing marine reserves requires consideration of such large movements. It must also consider reef topography as well as size, as smaller NTAs (<10 km^2) may have lower topographic variation. This is an important consideration as different reef habitats have different typical grouper assemblages (Sluka et al. 2001). Management of grouper fisheries at an artisanal level should consider large fished species such as *P. leopardus*, but the contribution of smaller grouper species such as *Cephalopholis argus* should not be underestimated. Many of these smaller species are also important food items. Smaller grouper species are thought to have more restricted home ranges (Stewart and Jones 2001) yet studies on their basic ecology are limited. Little effort has been directed toward quantitative ecological studies of Indo-Pacific species (Donaldson 2000).

Fisheries management is urgently required across Indonesia, in areas such as Sulawesi, where large areas of reefs are increasingly threatened by over-fishing or destructive fishing practices, this is particularly apparent (Hopley and Suharsono 2000). Such a need is evident within the Kaledupa region of the Wakatobi Marine National Park (MNP), Sulawesi, where marine resource dependence is very high (Cullen et al. 2006) yet the local fishery is unmanaged and overexploited (e.g. May 2003; Pet-Soede et al. 2003). Regardless of trophic level, most fish in the Kaledupa fishery are harvested before they reach sexual maturity (Operation Wallacea, unpublished data).

In 2001 a small NTA was designated off the Island of Hoga, adjacent to Kaledupa (see Crabbe and Smith 2005). This was in partnership between Operation Wallacea and local Bajau (Sea Gypsy) communities and represented both a social and biological management experiment. It covers a 500 m long section of fringing walled reef and reef flat. Observations suggest that the area is 80–90% successful in preventing fishing activities.

This paper uses the case study of the Kaledupa region of the Wakatobi MNP, S E Sulawesi, Indonesia to examine changes in the diversity, density and maturity of grouper species over a 5-year period following the establishment of a small-scale NTA to discover whether “small” NTAs can be effective management strategies over a time scale that is relevant to the local fisheries communities and their perception of management success. Research documents the ecology of these species, information essential if we are to understand how management practises are to affect coral reef fish species.

Materials and methods

Study sites

This study was conducted during July and August 2001–2005 on the fringing reefs around the Island of Hoga, close to the Operation Wallacea Marine Research Facility within the Wakatobi MNP (Fig. 1). The Wakatobi MNP (formerly the Tukang Besi Islands) is a remote island group of about 200,000 ha, off S E Sulawesi in Indonesia (Elliot et al.

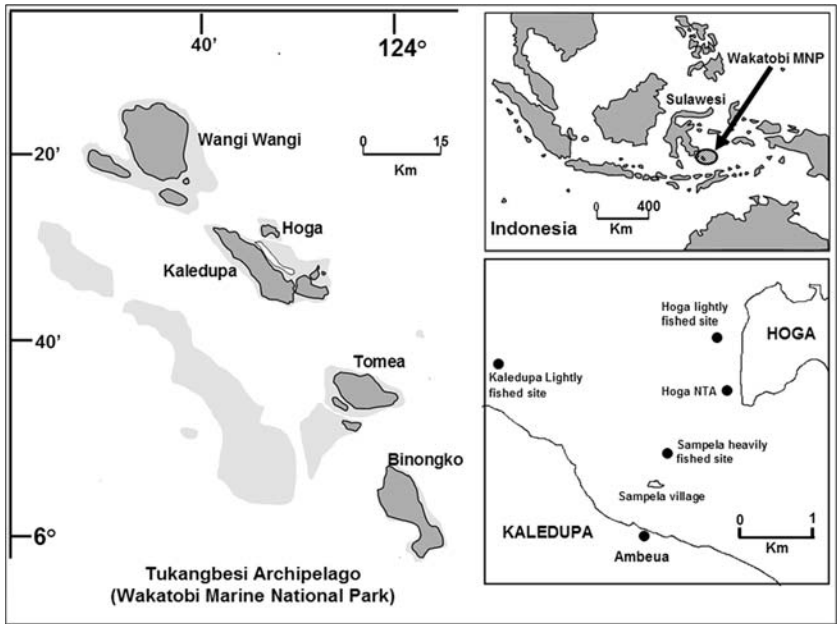

Fig. 1 Location of the four study sites (Hoga NTA, Hoga lightly fished, Kaledupa lightly fished and Sampela heavily fished) within the Wakatobi Marine National Park, Indonesia

2001). The MNP is home to approximately 90,000 people and has extensive reef and seagrass systems that are heavily exploited by local fishers (May 2005).

Grouper populations and reef habitat were evaluated at four reef locations within the Kaledupa region of the Wakatobi MNP. These sites were studied because of their varying levels of management and human impact; (1) Hoga NTA (2) Hoga lightly fished site (opposite Pak Kasim's resort) (3) Kaledupa lightly fished site (opposite Langira), and (4) Sampela heavily fished site (opposite Sampela village) (see May 2003; Crabbe and Smith 2002a, b, 2005). The two lightly fished sites are approximately 2 km from a village; however, the heavily fished site is immediately adjacent to a Bajau (sea gypsy) village where subsistence marine resource dependence is very high (Cullen et al. 2006). Most of the NTA comprises of fringing reef with a near vertical reef wall including a complex topography of variable slopes, overhangs and caves. In order to create an unbiased study the sites were carefully chosen to ensure a comparable topography but study stations were randomly chosen within each site.

Five reef habitats were surveyed; (1) the reef flat (at least 10 m away from the crest), (2) the reef crest, (3) shallow reef slope (a slope of between 30° and 75° with no overhangs or caves; at a depth of 5 m below the crest), (4) deep reef slope (as habitat 3 but at a depth of 10 m below the crest), and (5) reef wall comprising of overhangs and caves (10 m below the crest). A reef wall habitat was not present at the Sampela site.

Benthic characteristics

Benthic habitat characteristics were determined using the continual line intercept transect method of Marsh et al. (1984) described in English et al. (1997) utilising the same transect line as described for fish surveys. Rugosity (quantification of the habitat complexity), was calculated over three sections of each transect at each site using the chain method (6 m length) (see McCormick 1994; Crabbe and Smith 2003). Coral vitality is defined as the ratio of live to dead coral, and was calculated for all transects (Grigg and Dollar 1990; Gomez et al. 1994).

Grouper surveys

Two types of fish surveys were conducted; a long term monitoring survey of all fish species abundance at 12 sites incorporating 108 transect surveys each year (2001–2005, only data from the four relevant sites presented herein) and detailed grouper specific surveys (species size and abundance) carried out during July and August of 2003 and 2005 (detailed data is shown only from 2005). The detailed grouper surveys involved SCUBA or snorkelling time and a distance-restricted belt transect (30 m × 5 m) at each zone for each site with three or four repeats (see Fowler 1987; McCormick and Choat 1987; and English et al. 1997). These did not include the Kaledupa lightly fished site. The species, abundance and size of all groupers was recorded along the transect 2.5 m either side (and 5 m vertically) of a pre-laid tape measure following at least a 15 min settlement time. Prior to the study training exercises were conducted in order to accurately assess fish size underwater (see English et al. 1997). The fish monitoring transects were not directly comparable with the detailed grouper surveys as 50 m belt transects were used due to the diversity of the fish species being monitored (all fish species). Reef slope and reef crest data collected as part of the long term fish monitoring program are presented.

Data analysis

Heteroscadistic data and data deviating from a normal distribution were transformed (log $n + 1$; Zar 1984) prior to statistical analyses. Data presented, as percentages were arcsine transformed for statistical analyses but back-transformed means are presented. All means presented are displayed with ± standard errors. Analysis of variance (ANOVA) was used to examine differences between multiple sample means. When one factor was tested, one-way ANOVA was used followed by a post hoc multiple comparison Tukey test to determine where significant differences existed between sample means. Uni-variate statistical testing was conducted using the statistical package Minitab™. Patterns in the distribution of grouper species were further analysed by multivariate non-metric multidimensional scaling ordination (MDS) and cluster analysis using the computer package Primer v6™ (Clarke 1993). The BIO-ENV routine within Primer™ (Clarke and Ainsworth 1993) was used to compare the biological variables and indicators against the grouper species data.

Results

Habitat characteristics

Total coral cover differed significantly between the three sites ($F_{2,26} = 23.05$, $P < 0.001$) within all habitat types, which along with the dominance of *Acropora* corals at the Hoga NTA reef flat and crest, can be attributed to the reduced cover of non *Acropora* corals at the heavily fished Sampela site, the greatest difference being on the deeper habitat of the reef slope ($P < 0.01$, post hoc Tukey test) (Table 1). The ratio of the hard coral to dead coral (coral vitality) also differed significantly between sites ($F_{2,35} = 15.39$, $P < 0.001$), and reef zones ($F_{3,35} = 14.28$, $P < 0.001$). Hoga NTA had the highest ratio, whilst Sampela was dominated by dead coral or sand. Reef structural complexity (reef rugosity) also showed a similar trend between sites ($F_{2,35} = 4.77$, $P = 0.018$). Algal coverage was patchy and varied with habitat type and reef site ($F_{2,35} = 14.91$, $P < 0.001$) and was negatively and significantly associated with total hard coral cover ($r = -0.71$, $P < 0.05$, $n = 36$). Algal cover tended to be higher within slope habitats and was greatest at the heavily fished site of Sampela within all habitat types. Soft corals did not vary between sites but differed significantly between habitats ($F_{3,36} = 22.32$, $P < 0.01$) due to higher cover at the reef crest and reef flat ($P < 0.01$, post hoc Tukey test).

The BIO-ENV procedure within PRIMER allowed the biological variables in Table 1 to be analysed in relation to the similarity matrix; this allowed any correlations between

Table 1 Benthic characteristics of the various habitat types at the three study sites located within the Wakatobi Marine National Park, Indonesia as determined during July–August 2005

Benthic descriptors	Hoga NTA				Hoga unmanaged				Sampela impacted			
	Flat	Crest	Slope	Deep	Flat	Crest	Slope	Deep	Flat	Crest	Slope	Deep
Coral cover (%)	15.8 ± 2.2	46.9 ± 3.8	42.3 ± 4.2	46.7 ± 11.7	42.1 ± 9.7	32.2 ± 8.1	28.9 ± 7.8	31.6 ± 6.0	8.2 ± 2.5	16.8 ± 4.5	16.8 ± 0.3	10.6 ± 3.3
Acropora (%)	13.3 ± 2.0	17.7 ± 13.2	10.9 ± 8.9	8.3 ± 5.3	1.8 ± 1.1	11.9 ± 11.9	4.9 ± 4.6	7.9 ± 3.0	1.2 ± 1.2	2.4 ± 1.3	1.0 ± 0.6	0.0 ± 0.0
Algae (%)	9.5 ± 1.4	9.0 ± 3.1	18.5 ± 6.4	15.4 ± 4.2	24.3 ± 4.7	12.3 ± 3.5	11.1 ± 2.4	12.3 ± 2.1	29.4 ± 3.0	27.6 ± 1.3	30.3 ± 1.1	32.1 ± 3.1
Coral vitality	0.4 ± 0.1	1.7 ± 0.3	0.9 ± 0.2	2.1 ± 1.1	1.0 ± 0.4	0.8 ± 0.2	0.8 ± 0.3	0.6 ± 0.1	0.1 ± 0.0	0.4 ± 0.2	0.2 ± 0.0	0.3 ± 0.1
Rugosity	0.9 ± 0.0	0.7 ± 0.0	0.6 ± 0.1	0.5 ± 0.1	0.7 ± 0.0	0.8 ± 0.0	0.8 ± 0.0	0.6 ± 0.0	0.6 ± 0.1	0.7 ± 0.0	0.7 ± 0.0	0.9 ± 0.0
Corallivous butterflyfish	3.3 ± 0.3	6.0 ± 1.2	4.0 ± 1.2	4.7 ± 1.3	5.0 ± 1.5	2.0 ± 0.6	1.3 ± 0.9	2.7 ± 0.7	1.7 ± 0.9	0.7 ± 0.7	0.3 ± 0.3	0.3 ± 0.3

Data expressed as a percentage of the total cover (mean ± SE, $n = 3$)

the benthic characteristics and the grouper data to be identified. The BIO-ENV routine determined that none of the parameters had any significant correlation with the distribution of groupers indicating habitat not to be the major control of grouper assemblages.

Temporal monitoring of grouper abundance (2001–2005)

At NTA designation in 2001 grouper abundance between the NTA and the two lightly fished sites was the same, whilst the heavily fished site contained 50% less grouper than the other three sites (Table 2). Since 2001, grouper abundance within the Hoga NTA (expressed as a percentage of 2001 abundance data, Fig. 2) has increased $31 \pm 10\%$ year^{-1} over the 5-year period. This was due to a much higher abundance of grouper during both 2004 and 2005 and equates to a variable mean yearly increase of $9.4 \pm 18\%$ year^{-1} resulting from initial decreasing numbers throughout the first 2 years of designation (Fig. 2). Within the lightly fished site at Hoga, abundance decreased during the first 3 years then stabilised up to 2005 recovering only once in 2004. The Kaledupa lightly fished reef had a yearly decline of $50 \pm 10.5\%$ year^{-1}. Population decline has meant that grouper abundance in 2005 at the Kaledupa lightly fished site was lower than that at the Sampela heavily fished site. Grouper abundance at the heavily fished site increased since 2001 but an overall mean decline in abundance of $14 \pm 13\%$ year^{-1} has been found. Such large proportional changes are the result of the small numbers of fish at the heavily fished site.

Spatial variation in grouper assemblage structure, abundance and species richness

Detailed grouper surveys in 2005 found a mean number of 27.4 ± 3.34 groupers per 1,000 m^2. The Hoga NTA had significantly ($F_{2,35} = 20.68$, $P < 0.001$) higher (1.8× and 4.5×; not including reef wall data) grouper abundance than the other two sites. Lowest grouper abundance was recorded at the heavily fished site, Sampela (mean of $9.2. \pm 2.2$ per 1,000 m^2). Highest grouper abundance occurred on all reef slope and wall habitats within the Hoga NTA but no significant difference occurred between grouper abundance at the reef flat or crest between either of the two Hoga sites (Fig. 3). The reef wall environment within the Hoga NTA had the highest grouper density (77.8 ± 2.2 per 1,000 m^2). Variation (as measured by the coefficient of variation, CV; see Zar 1984) between zones was lowest for the Hoga NTA (CV of 41%) compared to the Hoga lightly fished site and the heavily fished site at Sampela (CV of 92

Table 2 Temporal change in the mean (±SE, $n = 3$) total abundance (per 1,000 m^2) of groupers at four sites of varying fishing intensity over 5 years (2001–2005) within the Wakatobi Marine National Park, Indonesia. Counts conducted using underwater visual census

Year	Sampela Heavily fished site	Hoga Lightly fished site	Kaledupa Lightly fished site	Hoga NTA
2001	14.8 ± 4.5	31.3 ± 7.0	32.5 ± 6.0	31.3 ± 6.5
2002	12.2 ± 3.9	17.8 ± 4.3	15.0 ± 5.5	20.2 ± 8.0
2003	7.2 ± 4.3	17.2 ± 7.9	17.2 ± 9.3	30.0 ± 8.4
2004	13.9 ± 2.8	33.9 ± 6.4	24.2 ± 3.3	46.0 ± 8.0
2005	17.0 ± 3.2	18.8 ± 1.9	7.5 ± 1.7	41.0 ± 5.1

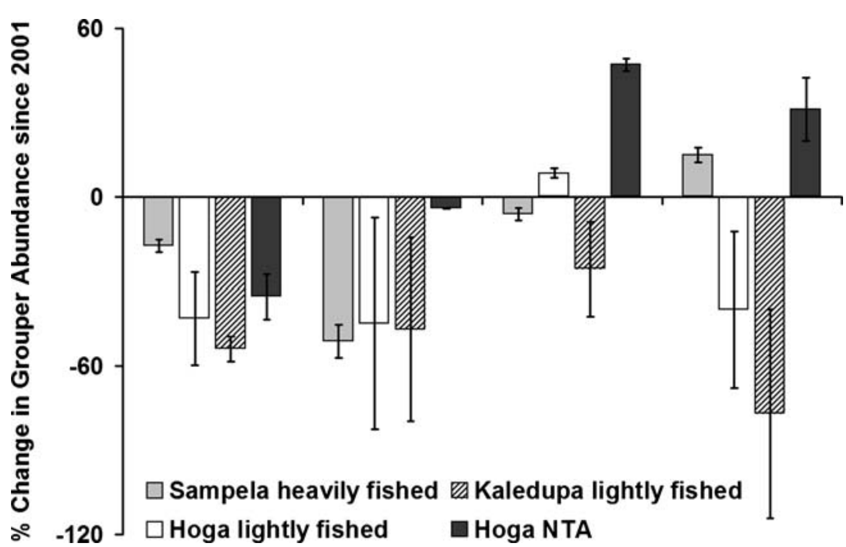

Fig. 2 Mean (±SE, $n = 6n$) percentage change in grouper abundance at four study sites [Hoga NTA (*dark bars*), Hoga lightly fished (*clear bars*), Kaledupa lightly fished site (*diagonal bars*) and Sampela heavily fished (*light bars*)] in the Wakatobi Marine National Park, Indonesia over 5 years. Data presented have been normalised against abundance data obtained during 2001 following the designation of the Hoga NTA. Data represents values averaged across reef crest and slope surveys

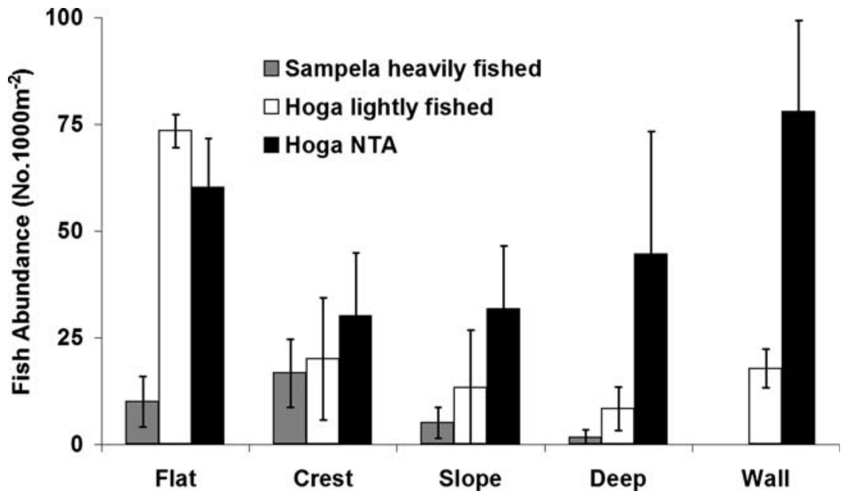

Fig. 3 Mean (±SE $n = 4$) total abundance of grouper species (nos. 1,000 m^{-2}) recorded at different reef habitats (Reef flat, crest, slope, deep slope and wall) within three different sites [Hoga NTA (*dark bars*), Hoga lightly fished (*clear bars*) and Sampela heavily fished (*light bars*)] of the Wakatobi Marine National Park, Indonesia as of August 2005. Note that there is no reef wall habitat at the Sampela site

and 60%, respectively) suggesting that within the Hoga NTA species of grouper were more evenly distributed.

In 2005 nine species of grouper were sighted. Several other species were recorded in the area but they were not within the designated sampling unit. Hoga NTA had the highest richness this was on the deep slope and reef wall habitats (see Fig. 4). Generally lowest richness was found at the reef flat. No clear difference in grouper species assemblages were present as four groups at the Bray Curtis 30% similarity level were formed (multi-dimensional scaling) that comprised mixed groups of sites indicating that despite large differences in abundance species assemblages are not hugely different between the three sites (Fig. 5). Similarity clusters are more a function of habitat than site.

Spatial variation in size frequency distribution of groupers

The NTA had the largest groupers; this is the only site with individuals greater than 40 cm (Fig. 6). The maximum length of those in the lightly fished and heavily fished sites was 35–40 cm but this size class was more abundant within the lightly fished site. The size frequency histogram (Fig. 6) illustrated the NTA skewed further to the right than the other two sites indicating the population of groupers in this area were on average larger and more mature than those in the lightly fished and heavily fished sites. Using similar rationale the lightly fished site at Hoga had a more mature grouper population than the Sampela heavily fished site.

Species level habitat associations

Detailed surveys in 2005 indicated variable species distribution over different reef habitats, the data suggests species-specific habitat associations (Table 3). All nine species identified were present within the NTA; six occur within both lightly and heavily fished sites. *Cephalopholis urodeta* was most abundant within the Hoga NTA particularly on reef slope and reef wall habitats no individuals were sighted on reef flat. *Ephinephelus merra* was the most abundant grouper and dominated reef flat habitats; there was no significant difference in the abundance of *E. merra* between the two Hoga sites but abundance was reduced at the heavily fished site. *Cephalopholis cyanostigma* was also most abundant within the Hoga NTA and once again within reef

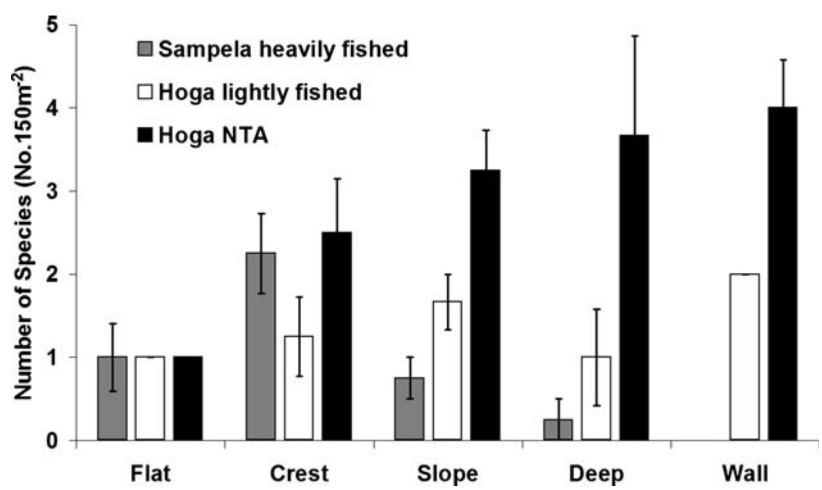

Fig. 4 Mean (±SE $n = 4$) grouper species richness (per 150 m^2 transect) recorded at different reef habitats (Reef flat, crest, slope, deep slope and wall) within three different sites [Hoga NTA (*dark bars*), Hoga lightly fished (*clear bars*) and Sampela heavily fished (*light bars*)] of the Wakatobi Marine National Park, Indonesia as of August 2005. Note that there is no reef wall habitat at the Sampela site

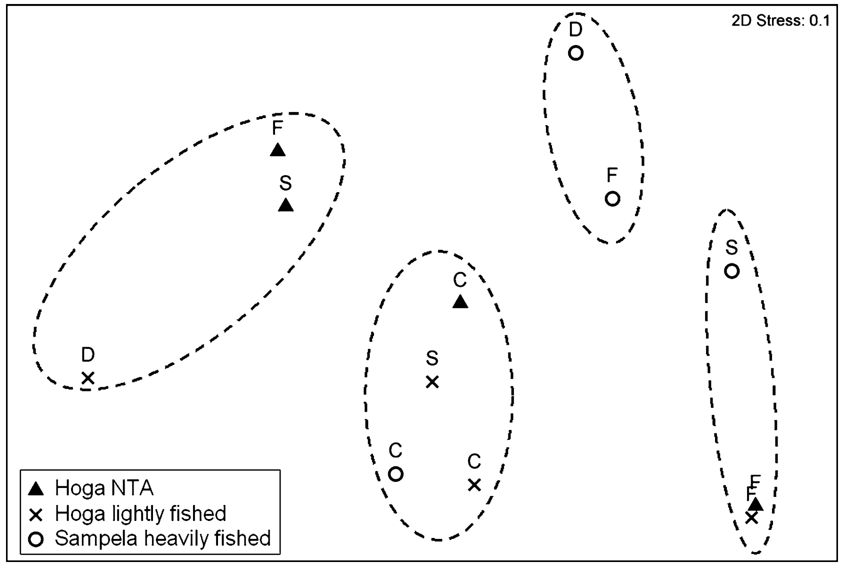

Fig. 5 Two-dimensional scaling configuration with superimposed Bray Curtis similarity clusters at the 30% level for mean grouper numbers at different reef zones (Reef flat *F*, crest *C*, slope *S*, deep slope *D* and wall *W*) of three different sites (Hoga NTA, *dark triangles*; Hoga lightly fished, *crosses* and Sampela heavily fished, *circles*) within the Wakatobi Marine National park, Indonesia July–August 2005

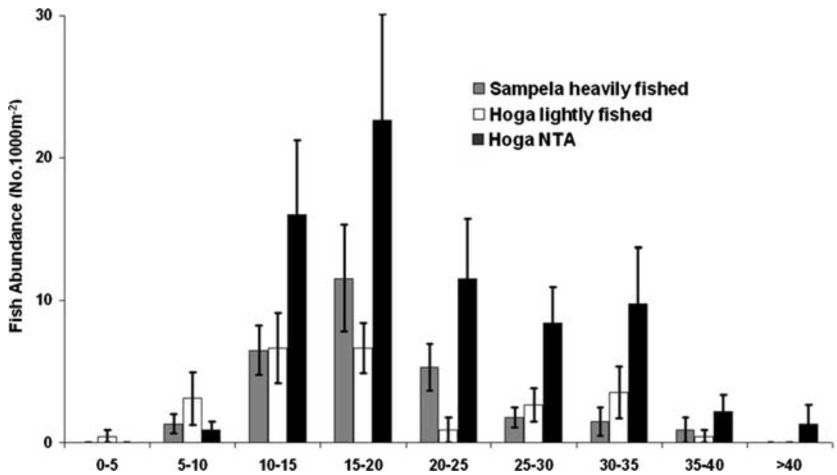

Fig. 6 Mean number (±SE, $n = 4$) of groupers (nos.1,000 m^{-2}) of each length category (cm) at three different sites (Hoga NTA, *dark bars*; Hoga lightly fished, *clear bars* and Sampela heavily fished, *light bars*) averaged over five habitats (Reef flat, crest, slope, deep slope and wall) within the Wakatobi Marine National Park, Indonesia as of August 2005. *Empty bars* represent the no take area at Hoga, *patterned bars* represent the unmanaged reef at Hoga and *Solid grey bars* represent the impacted reef at Sampela. Note that there is no reef wall habitat at the Sampela site

slope and wall habitats. *Cephalopholis spiloparea* dominated reef wall habitats and was also most abundant in the Hoga NTA. Highest abundances of *Cephalopholis argus* were recorded on the reef crest and shallow slope and this species was not recorded within any other habitat; there was minimal difference in abundance of *C. argus* between the two Hoga sites and although recorded at the heavily fished site on the crest, it was not found on shallow reef slopes. *Ephinephelus flascatus* resided on the reef slope, crest and flat and was most abundant in the Hoga NTA. *Anyperodon leucogrammicus* was once again most abundant in the Hoga NTA only residing on the reef slope and crest. *Gracilla albomarginata* and *Cephalopholis sexmaculata* were only abundant within the Hoga NTA, recorded on deep slope and wall habitats.

Most species had similar distributions throughout sites and habitat types (Fig. 7) sharing 45% Bray Curtis similarity (encircled with a continuous line). These clumped species vary differently from both *E. merra*, which appears out on its own, and the pairing of *C. argus* and *A. leucogrammicus*.

Discussion

This study presented an opportunity to evaluate whether a small scale NTA could enhance artisanal coral reef fisheries. Grouper species were used as a model group because of their trophic position and their high commodity value to the local fishers, an important fact if we are to provide local

Table 3 Abundance (per 1,000 m^2) of different grouper species within varying reef habitats and three reef sites within the Wakatobi Marine National Park, Indonesia, as of August 2005

	Cephalopholis urodeta	*Cephalopholis cyanostigma*	*Cephalopholis spiloparea*	*Cephalopholis argus*	*Cephalopholis sexmaculata*	*Ephinephelus merra*	*Ephinephelus fasciatus*	*Anyperodon leucogrammicus*	*Gracilla albomarginata*	All species
Hoga NTA										
Flat	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	60 ± 12	0 ± 0	0 ± 0	0 ± 0	60 ± 12
Crest	3.3 ± 1.9	3.3 ± 3.3	0 ± 0	8.3 ± 3.2	0 ± 0	13 ± 4.7	1.7 ± 1.7	0 ± 0	0 ± 0	30 ± 15
Slope	10 ± 6.4	8.3 ± 3.2	3.3 ± 1.9	1.7 ± 1.7	1.7 ± 1.7	0 ± 0	6.7 ± 0	0 ± 0	0 ± 0	32 ± 15
Deep	20 ± 12	2.2 ± 2.2	4.5 ± 2.2	0 ± 0	4.5 ± 4.5	0 ± 0	6.7 ± 3.9	4.5 ± 2.2	2.2 ± 2.2	45 ± 29
Wall	18 ± 4.5	4.5 ± 2.2	36 ± 8	0 ± 0	18 ± 4.5	0 ± 0	0 ± 0	0 ± 0	2.2 ± 2.2	78 ± 21
Hoga lightly fished										
Flat	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	73 ± 3.9	0 ± 0	0 ± 0	0 ± 0	73 ± 3.9
Crest	0 ± 0	0 ± 0	0 ± 0	6.7 ± 4.7	0 ± 0	12 ± 7.9	0 ± 0	1.7 ± 1.7	0 ± 0	20 ± 14
Slope	2.2 ± 2.2	0 ± 0	0 ± 0	4.5 ± 4.5	0 ± 0	2.2 ± 2.2	2.2 ± 2.2	2.2 ± 2.2	0 ± 0	13 ± 13
Deep	3.3 ± 1.9	0 ± 0	5 ± 3.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	8.3 ± 5.1
Wall	8.9 ± 2.2	0 ± 0	8.9 ± 2.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	18 ± 4.5
Sampela heavily fished										
Flat	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	8.3 ± 4.2	1.7 ± 1.7	0 ± 0	0 ± 0	10 ± 5.9
Crest	3.3±1.9	0 ± 0	0 ± 0	5 ± 1.7	0 ± 0	6.7 ± 2.7	0 ± 0	1.7 ± 1.7	0 ± 0	17 ± 8
Slope	0±0	1.7 ± 1.7	0 ± 0	0 ± 0	0 ± 0	3.3 ± 1.9	0 ± 0	0 ± 0	0 ± 0	5 ± 3.6
Deep	0±0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.7 ± 1.7	0 ± 0	0 ± 0	1.7 ± 1.7
All sites										
All habitats	4.9 ± 2.3	1.4 ± 0.9	4.1 ± 1.3	1.9 ± 1.1	1.7 ± 0.8	13 ± 2.8	1.5 ± 0.8	0.7 ± 0.6	0.3 ± 0.3	29 ± 11

Means ± SE, n = 3 or 4

Note that there is no reef wall habitat at the Sampela site

Counts conducted using underwater visual census

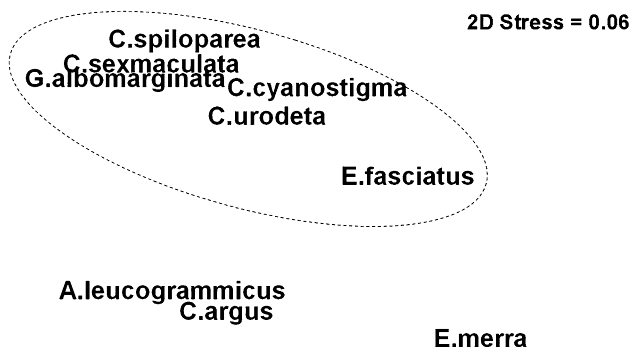

Fig. 7 Two-dimensional scaling configuration with a superimposed Bray Curtis similarity cluster at the 40% level for mean numbers of different grouper species recorded at different reef sites (Hoga NTA, Hoga lightly fished and Sampela heavily fished) and habitats (Reef flat, crest, slope, deep slope and wall) during July–August 2005 within the Wakatobi Marine National Park, Indonesia

user groups with transparent feedback demonstrating the potential of NTAs. Small areas of strictly protected reef are beneficial in terms of the degree of local compliance and the reduced costs (from a social and economic standpoint) of enforcement, the main question is whether or not such small areas can be effective in protecting important species. Present research found groupers to increase in density over a 5-year period within a small NTA whilst adjacent reefs suffered large population declines.

Fishery pressure or habitat: local influences on grouper assemblages

Benthic features of coral reefs are known to be important in structuring reef fish communities (Chabanet et al. 1997; Sluka et al. 2001) whilst species specific relationships exist between reef habitat and grouper abundance (Sluka et al. 2001). The present study found no relationship between grouper abundance and benthic habitat. Additionally, prior to NTA designation and despite inter-site habitat differences, little difference in grouper abundance was observed. This suggests that, although species such as grouper will be affected by habitat quality and complexity, in the case of this study, other variables influenced grouper populations to a greater extent. May (2003) found fishing to be an important cause of reductions in numbers of piscivore and commercially fished species around the study sites. Based upon the data presented herein and that of May (2003) it seems most likely that a major variable separating these reefs is the extent of fishing pressure, the inter-site influence of habitat upon our data is minimal.

Are small-scale NTAs effective?

Designation of a “small NTA” increased the density and species richness of groupers over a 5-year period of protected status. After 5 years of protection, grouper populations within this NTA were double those within the adjacent lightly fished sites and nearly five times those of the heavily fished site. Numbers of groupers within the NTA were 30% greater in 2005 than in 2001, however, numbers fluctuated highly. During this time grouper populations in nearby sites declined. The small NTA does, however, fail to increase abundance of three of the nine species recorded within this survey. A number of reasons have been proposed as to why these species have not increased in numbers relative to the lightly and heavily fished sites. Fluctuations may have been natural but may have also been the result of increased NTA poaching. To answer such questions with any certainty it is important that further information about the behavioural and population ecology of individual species is acquired and that longer-term population trends are determined through continued monitoring. Initial grouper declines (2001–2002) observed in the present research are supported by findings within the Sumilon Non-Reserve where fishing for groupers was prohibited (Russ and Alcala 1998b). After the initial decrease, numbers increased, agreeing with the findings of the meta-analysis of data from over 80 reserves (Halpern and Warner 2002) suggesting that fish abundance stabilises after 3 years.

The NTA contained a more mature grouper population than either the lightly or heavily fished sites. A more mature and denser assemblage of grouper within the NTA indicates increased adult fish survivorship and represents higher grouper biomass within the protected area. Despite this most of the populations observed were not mature. Russ and Alcala (1996) found that mean densities of large predatory fish were still increasing after 9 and 11 years of protection. These factors suggest that in time, and if fully protected, this NTA may see further increases in grouper biomass. This study outlined that the characteristics of grouper assemblages seem to be sensitive enough to demonstrate the success of small scale NTA over a time period that is appropriate to local fishing communities.

Declining grouper populations

All sites apart from the NTA have undergone large decreases in grouper density over the 5-years 2001–2005. This study documented the alarming decline of the grouper populations within the lightly fished Kaledupa site where populations decreased by 50% per year resulting in a population in 2005 lower than that at the heavily fished site. The heavily fished site also experienced a steady and near constant decline in grouper (14% per year). Similar trends have been observed in other areas of the Park (May 2003; Pet-Soede et al. 2003). These declines are most likely the result of continued over-fishing of immature fish and exponential increases in the use of large “Fyke Net” fisheries (tidal fish fences) placed across the reef flat. This is cause for concern in a region where the use of such highly efficient fishing methods is increasing.

Species distribution

The NTA had a variable effect upon different grouper species. *C. urodeta*, *C. cyanostigma*, *C. spiloparea*, *E. fasciatus*, *G. albomarginata* and *C. sexmaculata* all benefited from the small NTA management strategy, whilst *E. merra*, *C. argus* and *A. leucogrammicus* did not (over the time scale of this study). Of the six species that were found in the Hoga NTA, two species *G. albomarginata* and *C. sexmaculata*, were only found inside the protected area boundaries. This suggests that the NTA did not seed or help to maintain populations of these species on adjacent reefs. Potentially large home ranges of these species may mean that such a small NTA might have been too small allowing the survival of a few individuals, yet not significantly enough to increase adult survivorship and have any chance of spilling over to adjacent reefs. This study could also be too soon to show any additional effect upon *G. albomarginata* and *C. sexmaculata* populations. Alternatively, fisheries pressure outside the NTA may be masking increases in biomass of these two species (fishermen are regularly seen fishing right up to the boundaries of the NTA). A further hypothesis for the absences of *G. albomarginata* and *C. sexmaculata* is the large minimum population doubling time (4.5–14 years) for these species (Heemstar and Randall 1993).

Ephinephelus merra was the most abundant species recorded; this is surprising as it is commonly seen within Chinese and Japanese live fish markets obtaining a relatively high export value (Lee and Sadovy 1998) and there is live fish trade occuring within the Wakatobi MNP. Our results agree with Heemstar and Randall (1993) who suggest that individuals of *E. merra* are common in shallow lagoons and semi-protected seaward reefs; and that juveniles are common in thickets of staghorn *Acropora* corals. A total of 90% of the population of *E. merra* were below 20 cm in length, with 70% below 15 cm (half maximum size, Froese and Pauly 2005), indicating immature populations at all sites. Immature *E. merra* are likely to inhabit the reef flat for shelter within the dense stands of *Acropora* corals in the case of the NTA or within the complex reef flat topography of the lightly fished reef flat. The lower minimum population doubling time of *E. merra* (1.4–4.4 years compared to 4.4–14 years; Froese and Pauly 2005), suggests its population within the NTA may have increased sufficiently to be benefiting the neighbouring population within the adjacent lightly fished site because of high spillover of individuals.

Cephalopholis argus and *A. leucogrammicus* have similar densities inside and outside of the NTA, it is not clear why. *A. leucogrammicus* was only found on the reef crest and slope and had low abundance across all sites. High variability suggests a patchy distribution and any differences within such a small population are unlikely to have been detected by our survey method. The larger *C. argus* was only recorded on the slope and crest, this is a conspicuous brightly coloured fish and individuals sighted were mostly over 20 cm long, with some up to 40 cm in length, hence this species presents a more obvious target for the large artisanal spear fishery. Diver observations whilst not sampling on transects detected even larger (>50 cm in length) individuals of *C. argus* within the NTA but not at other sites. *C. argus* is also utilised by the live fish trade (Lee and Sadovy 1998). The minimal effect of the NTA upon *C. argus* and *A. leucogrammicus* may also be a result of the slow recovery time of mature adults as the lower numbers of both these species may act to reduce their reproductive output. Reserves have not always been found to be immediately successful; Ferreira and Russ (1995) found that after 4 years of no-take protection in a reserve within the Great Barrier Reef, there was no significant difference in the age and structure of *Plectropomus leopardus.*

Fisheries management

Strategic fisheries management is required to halt the declining fisheries surrounding the islands of Kaledupa and Hoga (May 2003; Pet-Soede et al. 2003). The large declines in grouper populations illustrated by the present study suggest such management is an urgent requirement. Small scale NTAs such as the Hoga NTA are acceptable to local fishers, this is particularly important in locations where cultural challenges such as working with local people from different cultural backgrounds (Kaledupans and Bajau peoples’) are significant. The present study demonstrates the biological success of such a strategy. Small NTAs have the ability to reduce conflict between conservation management strategies and local user group requirements particularly in densely populated areas where fisheries are the main source of protein and an important source of income for many people. Jennings et al. (1996) considers small reserves to be advantageous for managers as they can operate without depriving locals of all their fishing ground and are more easily regulated. Although desirable for conservation, large NTAs are not possible, without massive socioeconomic disruption. The lack of compliance by local communities would undoubtedly make such schemes nearly impossible to implement and maintain. Community led NTAs could be an important tool for conservation managers working in exploited areas. If such NTAs were to be used as a fishery management scheme within the Kaledupa sub-region of the Wakatobi MNP it is proposed that a minimum of 46 such small NTAs would be required to designate 30% of the fishery as closed. Larval dispersal and availability of nursery grounds were never priorities in citing the Hoga NTA. If small NTAs were to be considered for an area such as Kaledupa, currents and larval flow as well as availability of potential fish nursery grounds should be important. Habitat connectivity (Mumby et al. 2004; Dorenbosch et al. 2005) and larval dispersal (Forester 1999; Palumbi 2003) are now widely recognised factors influencing reef fish. Understanding of the life-history and habitat usage of immature Indo-Pacific groupers is sadly lacking, such information is vital for the further planning of fisheries management throughout a region so dependent upon its declining marine resources.

Many of the larger groupers such as *Plectropomus leopardus*, which utilise spawning aggregations, will not be protected by a small isolated NTA. Marine reserves may need to be extremely large in size in order to be self-sustaining for large grouper species. A network of smaller specifically located NTA reserves, which allows movement from one reserve to another whilst including specific locations such as spawning sites is a powerful tool for the management of "working" coral reef systems.

Conclusions

This research demonstrated that a "small" NTA has the ability to significantly increase grouper populations over a 5-year period. The study also documented a large decline in the grouper populations of all nearby reefs. This NTA was not of benefit to all grouper species; the reasons for this are not clear. Further detailed research is required into the life history, population and behavioural ecology of Indo-Pacific grouper species. Such information is critical for urgently needed fisheries management. The NTA in the present study was a social community self management experiment that demonstrated small scale NTAs are capable of stabilising top predatory fish species and in conjunction with other socially acceptable small scale NTAs could help maintain and increase important fish stocks over a larger area. The use of "small" NTAs within networks of reserves could be useful tools in the management of coral reef fisheries and an important strategy in the future management of the Wakatobi Marine National Park.

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