

Effects of Marine Reserve Protection on Northern Red Sea Fish Populations

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Abstract. This study investigates the effects of establishment of the Ras Mohammed Marine Park on fish population structure. The park has been protected from most forms of fishing for 15 years. Cessation of fishing is expected to result in increases in abundance and average size of target species and may also lead to shifts in species composition. To determine if such effects were evident, populations of nine commercially fished families and pelagic piscivores were censused using point counts at 15m depth. Effects of protection were determined by comparison of similar sites from three fishing levels: (1) none (Ras Mohammed), (2) little-fished, and (3) fished. Data were analysed using ANOVA. The results of the study were complex. Abundance of 11 of 45 species differed significantly among fishing levels. There were greater numbers on unfished reefs for four, little-fished for three and fished for four. At the family level, surgeonfishes were significantly more common on fished reefs. Seven species increased in size significantly with decreasing fishing intensity. Biomass of 14 species differed significantly among fishing levels with higher biomass in unfished sites for five, in fished sites for four and equivocal results for five. At the family level, there were significant differences for parrotfishes and surgeonfishes with the former greatest on little-fished reefs and the latter on fished. Total biomass of all species combined (excluding the schooling surgeonfish *Naso unicornis*) did not differ significantly among fishing levels although mean biomass was 1.2 times greater on unfished than fished reefs. These results provide some support for the view that marine reserve establishment has been effective

in protecting stocks. However, fishing levels in the northern Red Sea are low and use of reserves to manage fisheries may prove most effective in regions where fishing intensities are high or use of damaging fishing methods widespread.

Introduction

Management of fisheries on coral reefs poses serious problems. Conventional approaches use methods developed primarily on the single species fisheries typical of temperate seas (Pitcher and Hart 1982) and generally require large amounts of information on catch, effort and the biology of the species concerned in order to be applied effectively. By contrast, fisheries on coral reefs are exceptionally complex due to their multi-species, multi-gear nature (Bohnsack 1990). Furthermore, the gathering of reliable fisheries statistics is made difficult due to cost constraints, the subsistence nature of many fisheries and difficulties of access to remote areas. Consequently, application of conventional management methods is impractical.

The need for management is acute with evidence of serious overexploitation widespread (Koslow et al. 1988; Norte et al. 1989; Sadovy 1989). Use of marine reserves (areas protected from fishing) has been proposed as a management approach which can overcome the above difficulties. Among the most important advantages claimed for them are: (1) protection of spawning stock biomass, (2) supply of recruits to fished areas, (3) enhancement of catches in adjacent areas through emigration, (4) insurance against stock collapse due to successive years of poor recruitment, (5) reduced data collection needs and (6) simplified enforcement (Davis

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1989, Bohnsack 1990, Roberts and Polunin 1991). Several of these advantages stem from the prediction that under zero fishing, target species will increase in abundance and average size.

Although theoretically the reserve approach seems robust, there are few data with which to test the predictions made for them (Roberts and Polunin 1991). The data which exist are suggestive, particularly from studies in the Philippines (Alcala 1981, 1988, Alcala and Russ 1990; Russ 1985, Russ and Alcala 1989; White 1987) and Florida (Clark et al. 1989; Bohnsack 1990) but fall well short of proving that reserves are effective management tools. This study seeks to test the prediction that individuals of fished species will be more abundant and larger on average within reserves than in fished areas. The study was conducted on reefs of the Sinai coast in Egypt and compared sites within the Ras Mohammed Marine Park, which has been protected from fishing for approximately fifteen years, with sites which were lightly fished (recreationally) and sites which had been fished commercially for many years.

Methods

Study sites

The study was conducted at nine sites on the Sinai coast of Egypt between Ras Mohammed and Dahab

(Fig. 1), chosen on the basis of fishing intensity. The three sites at Ras Mohammed lie within the marine park and were considered unfished. Fishing restrictions were initially established and policed by Israeli parks staff in the 1970s. In 1982 Sinai was returned to Egypt and Ras Mohammed made an Egyptian National Park in 1983. Protection from fishing was enforced by a unit of the Egyptian army stationed in the park until 1990 when management was transferred to the newly created National Parks of Egypt department.

Seasonally, commercial fishing is permitted for the emperor *Lethrinus nebulosus* when they aggregate within the park to spawn (Sheppard et al. 1992). However, this takes place well away from the areas censused.

Three sites studied between Sharm-el-Sheikh and Ras Nasrani (Ras Umm Sidd, The Tower and Ras Nasrani; Fig. 1) have been subjected only to light fishing for a similar period, predominantly recreational by hook and line. Although not formally protected, these sites are only very occasionally fished commercially by Bedouin fishermen. They lie within an area of coast used heavily for recreational SCUBA diving.

Three other sites have been continuously commercially fished by Bedouins for many years. Two of them lie close to a large Bedouin village in Dahab, while the other is adjacent to a permanent fishing camp close to the Strait of Tiran (Fig. 1).

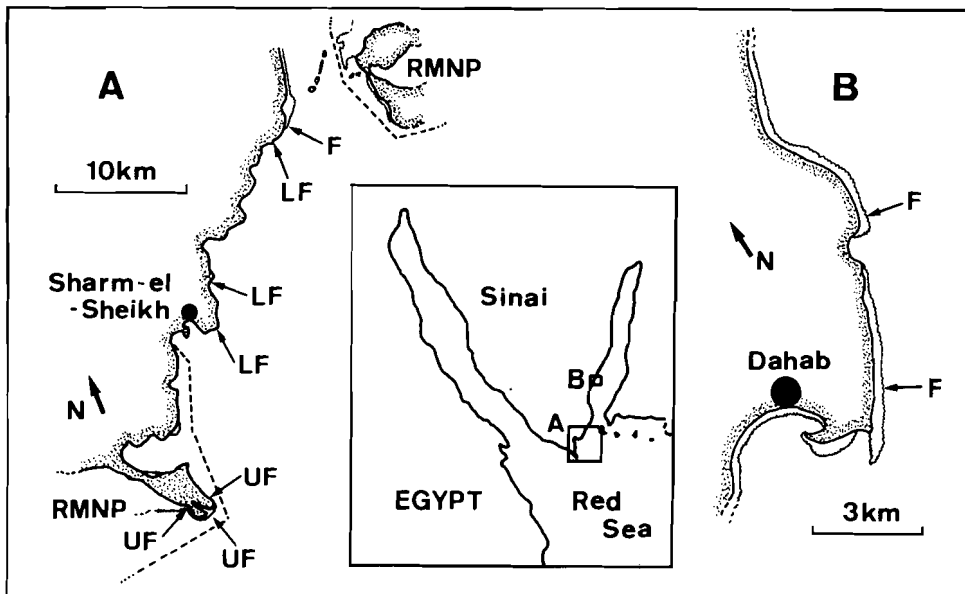


Fig. 1. Map of the study area showing location of study sites. UF = unfished, LF = little-fished and F = fished. Nine replicate counts were made at each of the sites shown. RMNP = Ras Mohammed National Park. The park is divided into two areas. The first, centred around the Ras Mohammed peninsula at the bottom left of Map A is where the fish counts were made. The second area covers Tiran Island (upper right of Map A) and was not included in the present study.

Fish census

Fishes from nine families commonly caught commercially in Sinai (Acanthuridae, Scaridae, Serranidae, Lethrinidae, Lutjanidae, Haemulidae, Sparidae, Mullidae and Kyphosidae) were censused using a modification of the stationary point count method of Bohnsack and Bannerot (1986). A SCUBA diver counted all individuals observed within a 5m radius during a fifteen minute period, and estimated their lengths to the nearest centimetre. Earlier trials had shown that length estimation was very accurate with an average error of only 3% (Polunin and Roberts 1993).

Counts were also made of roving pelagic piscivores using the method developed by Thresher and Gunn (1986). At intervals of approximately three minutes during the fifteen minute census period (five times), the observer turned 360° and counted all pelagic piscivores within a radius of 10m projecting from the reef to the surface. The mean of the five counts was used as an estimate of abundance.

Estimates of biomass for each species were made by applying length-weight relationships to visual estimates of length. The relationships were obtained from both published and unpublished sources (Abdul Nabi 1980; Hashim and Shakour 1981; Wright and Richards 1985; Baddar 1987; Mathews and Samuel 1987; Samuel and Mathews 1987; Dalzell 1988; Zyadah 1989; Torres 1991).

In addition, estimates were made of the cover of dominant benthic components within each area censused. Structural complexity of the substratum was estimated on a six point scale: 0—no vertical relief, 1—low and sparse relief, 2—low but widespread relief, 3—moderately complex, 4—very complex with many caves and fissures, 5—exceptionally complex with high coral cover, many caves and overhangs.

Nine replicate counts were made at a depth of 15m at all sites. Data were analysed using one-way ANOVA. Percentage cover data were arcsin square-root transformed prior to analysis. Data from counts were tested for normality using the Kolmogorov-Smirnov one sample test. Where necessary data were transformed to approximate normality. However, in parallel tests using transformed and untransformed data, no differences in outcome were found; ANOVA is relatively robust to departures from the assumption of normality (Steel and Torrie 1980).

Results

Fishing methods and target species

Quantitative data on fishing effort and catches are not available for landings by Bedouins on the Sinai

coast. However, qualitative observations by one of us (CR) over a period of three years allow an assessment of the most important species in catches and of fishing methods used.

The great majority of finfish are caught using only two methods: hook and line and trammel nets. Fishermen use hook and line over the deeper outer-slope zone of the reef either while standing at the reef-edge, or from small wooden canoes (houris) when the weather is calm. Trammel nets are set either on the reef-flat or just to seaward of the reef-edge and capture a wide variety of species, the most important of which are the larger, more mobile species such as parrotfishes and surgeonfishes.

The following are the most important species represented in catches. Some species not included may also be subject to significant levels of fishing mortality. However, due to low population densities they do not form important components of catches.

Hook and line Groupers: *Variola louti*, *Aethaloperca rogoa*, *Cephalopholis miniata*, *C. argus*, *C. hemistiktos* (bait). Snappers: *Lutjanus bohar*. Emperors: *Lethrinus mahsena*, *L. nebulosus*. Grunts: *Plectorhynchus gaterinus*. Porgies: *Acanthopagrus bifasciatum*.

Trammel nets Parrotfishes: *Hipposcarus harid*, *Scarus sordidus*, *S. niger*, *S. ghobban*, *S. ferrugineus*, *S. frenatus*. Surgeonfishes: *Acanthurus nigricans*, *A. sohal*, *Naso unicornis*, *N. lituratus*, *N. hexacanthus*. Goatfishes: *Parupeneus cyclostomus*.

Habitat similarity among fishing levels

There was a slight but significant difference in structural complexity of the reef among fishing levels with little-fished sites marginally less complex than fished or unfished (Tab. 1). One-way ANOVAs on transformed cover data for different benthic substrata showed greater hard coral cover in fished sites and greater soft coral cover in unfished sites (Tab. 1).

A cluster analysis of benthic composition data from the 81 counts revealed four clusters (Fig. 2). Cluster membership was not related to treatment (fishing intensity) indicating that at the scale of samples and resolution of benthic composition data, habitats were relatively similar among treatments (Tab. 2).

Fish abundance

Results of one-way ANOVAs on fish abundance are shown in Table 3 for species for which there were significant effects. Analyses were run for a further

Table 1. Differences in substratum composition and complexity among fishing levels shown by one-way ANOVA (fishing effect). Values for each fishing level are mean % cover for that level except for structural complexity which was measured on a five point scale. S-N-K test is the Student-Neuman-Keuls test for differences among treatments. F = fished, LF = little-fished and UF = unfished. NS = not significant. N = 81 in all cases.

| Parameter | Fishing effect (signif., P) | Group Means | | | S-N-K Test |
|-----------------------|-----------------------------|-------------|---------------|--------|-------------|
| | | Unfished | Little fished | Fished | |
| Structural complexity | < 0.03 | 3.2 | 2.8 | 3.1 | UF = F > LF |
| Hard coral cover | < 0.0001 | 14.7 | 17.1 | 28.8 | F > LF = UF |
| Soft coral cover | < 0.002 | 32.1 | 23.2 | 19.3 | UF > LF = F |
| Sand | NS | 19.6 | 20.8 | 24.6 | |
| Rubble | < 0.0001 | 9.7 | 10.2 | 4.2 | LF = UF > F |
| Bare substratum | NS | 23.9 | 28.4 | 23.1 | |

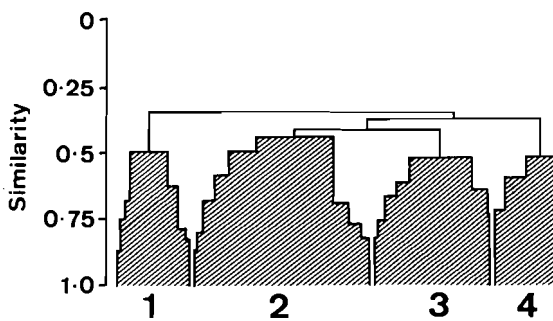


Fig. 2. Results of a cluster analysis of benthic composition data from the sites of the 81 counts. The average linkage method was used with the Bray-Curtis similarity index. The four main clusters defined have been blocked in for clarity and so individual sites within clusters are not shown. Numbers of sites from each fishing level contained within each cluster are given in Table 2 (cluster numbers are as in Table 2).

Table 2. Site composition of clusters shown in Figure 2 showing number of sites from each from each fishing level within each cluster. Cluster numbers are the same as in Figure 2.

| Cluster | Number of sites | | |
|---------|-----------------|---------------|----------|
| | Fished | Little-fished | Unfished |
| 1 | 5 | 4 | 5 |
| 2 | 10 | 13 | 10 |
| 3 | 7 | 7 | 8 |
| 4 | 5 | 3 | 4 |

34, the abundance of which did not differ significantly among fishing levels. Failure to detect differences for these species may have been due to small sample sizes in many cases, as 21 of them were uncommon (present in < 10 counts).

Significant differences in abundance were found for 11 species. Of them, four were most abundant in unfished areas, two equally with little-fished sites.

A further three species were more abundant in little-fished than either unfished or fished sites. The grouper *Cephalopholis miniata*, one of the most heavily-exploited species in the area, was three times more abundant on unfished and little-fished compared to fished reefs. A similar effect was observed for the commercially-important parrotfish *Scarus ferrugineus*. However, *Hipposcarus harid* is also widely caught but was more abundant on reefs subject to fishing. Three other species, including the commonly-caught grouper *Epinephelus fasciatus*, were more common on fished than unfished reefs.

Several common species which constitute important components of catches did not differ in abundance among fishing levels, including the snapper *Lutjanus bohar*, and grouper *Variola louti*.

Data for emperors are unlikely to have given an accurate representation of true abundance since species of this family were very wary and would not usually approach the diver close enough to be included in counts.

Mean number of pelagic fishes was greatest on unfished reefs.

At the family level, only the surgeonfishes differed significantly in abundance among fishing levels, with highest numbers on fished reefs. However, a trend was apparent for the groupers towards higher abundance on unfished and little-fished reefs.

Mean length

There were significant differences in mean length among fishing levels for seven species (Tab. 4). For three grouper species, individuals were larger on average on unfished reefs than sites subject to fishing. For two species of parrotfish, individuals on little-fished reefs tended to be larger than on other reefs, whilst for two surgeonfishes, individuals on

Table 3. Differences in abundance (number.count⁻¹) of species and families among fishing levels shown by one-way ANOVA (fishing effect). For species, only significant effects are shown. Figures show the mean value of each parameter within each fishing level. (C) indicates species which are important in catches. Abbreviations as in Table 1. N = 81 in all cases.

| ABUNDANCE (numbers.count ⁻¹) | | | | | |
|--|-----------------------------|-------------|---------------|--------|-------------|
| Group/species | Fishing effect (signif., P) | Group Means | | | S-N-K Test |
| | | Unfished | Little fished | Fished | |
| SERRANIDAE | | | | | |
| <i>Cephalopholis miniata</i> (C) | < 0.001 | 2.8 | 2.7 | 0.9 | UF = LF > F |
| <i>C. hemistiktos</i> (C) | < 0.03 | 2.1 | 3.9 | 2.7 | LF > UF = F |
| <i>Aethaloperca rogae</i> (C) | < 0.001 | 0.0 | 0.4 | 0.0 | LF > UF = F |
| <i>Epinephelus fasciatus</i> | < 0.005 | 0.1 | 0.0 | 0.5 | F > LF = UF |
| SCARIDAE | | | | | |
| <i>Hipposcarus harid</i> (C) | < 0.002 | 0.0 | 0.6 | 0.6 | F = LF > UF |
| <i>Scarus ferrugineus</i> (C) | < 0.02 | 1.1 | 1.1 | 0.4 | UF = LF > F |
| <i>S. niger</i> (C) | < 0.001 | 1.1 | 2.6 | 1.6 | LF > UF = F |
| ACANTHURIDAE | | | | | |
| <i>Zebrasoma veliferum</i> | < 0.0001 | 1.7 | 0.6 | 0.2 | UF > LF = F |
| <i>Acanthurus nigrofuscus</i> | < 0.0001 | 2.1 | 1.6 | 5.1 | F > LF = UF |
| <i>Naso lituratus</i> (C) | < 0.01 | 0.3 | 0.1 | 0.0 | UF > LF = F |
| <i>N. unicornis</i> (C) | < 0.0001 | 0.1 | 0.0 | 2.1 | F > LF = UF |
| TOTAL NUMBERS | | | | | |
| Mean no. pelagics | < 0.03 | 1.8 | 0.3 | 0.6 | UF > LF = F |
| <i>Serranidae</i> | = 0.06(NS) | 6.2 | 7.6 | 5.6 | |
| <i>Lethrinidae</i> | NS | 0.3 | 0.3 | 0.8 | |
| <i>Lutjanidae</i> | NS | 0.5 | 1.1 | 0.3 | |
| <i>Mullidae</i> | NS | 1.7 | 0.9 | 2.2 | |
| <i>Scaridae</i> | NS | 5.3 | 6.7 | 6.4 | |
| <i>Acanthuridae</i> | < 0.0001 | 8.7 | 6.4 | 11.7 | F > UF > LF |
| Overall (all species) | NS | 23.2 | 23.3 | 27.3 | |
| SPECIES RICHNESS | | | | | |
| Total species richness | NS | 44.2 | 46.5 | 47.8 | |
| Fished species richness | NS | 11.1 | 10.3 | 10.9 | |

unfished and little-fished reefs were larger than on fished reefs.

among fishing levels. However, for the additional seven species which had moderate sample sizes

Table 4. Significant differences in mean length of individuals detected by one-way ANOVA (fishing effect). Values show the mean length (cm) for individuals from each fishing level. Numbers in parentheses indicate the number of counts on which the species was observed. (C) indicates species which are important in catches. Abbreviations as for Table 1.

| MEAN LENGTH (cm) | | | | | |
|----------------------------------|-----------------------------|-------------|---------------|-----------|-------------|
| Group/species | Fishing effect (signif., P) | Group Means | | | S-N-K Test |
| | | Unfished | Little fished | Fished | |
| SERRANIDAE | | | | | |
| <i>Cephalopholis miniata</i> (C) | < 0.01 | 23.5 (22) | 20.8 (21) | 20.5 (12) | UF > LF = F |
| <i>C. hemistiktos</i> (C) | < 0.005 | 16.9 (21) | 16.2 (24) | 15.6 (22) | UF > LF = F |
| <i>Variola louti</i> (C) | < 0.01 | 50.3 (16) | 40.9 (11) | 36.0 (19) | UF > LF = F |
| SCARIDAE | | | | | |
| <i>Scarus sordidus</i> (C) | < 0.0001 | 16.0 (19) | 22.1 (19) | 15.0 (17) | LF > UF = F |
| <i>S. niger</i> (C) | < 0.05 | 19.7 (18) | 21.2 (26) | 17.0 (20) | LF > UF = F |
| ACANTHURIDAE | | | | | |
| <i>Acanthurus nigrofuscus</i> | < 0.0001 | 11.2 (25) | 11.1 (22) | 8.2 (27) | UF = LF > F |
| <i>Ctenochaetus striatus</i> | < 0.0001 | 16.4 (25) | 16.7 (25) | 14.1 (25) | UF = LF > F |

Sample sizes for most other species were too small to resolve small differences in mean length

(present in 20–40 counts) there was a trend of increase in length from fished to unfished in five. The

remaining two species showed no difference in size. One of the latter was a small, unexploited parrotfish *Calotomus viridescens*.

Biomass

Fourteen species showed significant differences in biomass among fishing levels (Tab. 5). Virtually the complete range of possible differences were present. Five species had a higher biomass in unfished areas, three equally with little-fished. Biomass of four species was highest on fished reefs, and results for a further five were equivocal, with highest biomass either in little-fished or in one case fished equal to unfished.

Trends in biomass were apparent for several commonly-fished species but were not statistically significant. Mean biomass of the groupers *Variola louti* and *Plectropomus maculatus* were respectively 1.4 and 1.2 times higher on unfished than fished

reefs. Similarly, biomass of the snapper *Lutjanus bohar* was 4.5–6.1 times higher on unfished and little-fished reefs compared to fished.

At the family level, there were significant differences in total biomass only for parrotfishes and surgeonfishes. Average surgeonfish biomass was over two times higher on fished than other reefs. However, this was almost entirely due to *Naso unicornis* with an average 4.7kg count⁻¹ on fished reefs (Tab. 5). Excluding this species, surgeonfish biomass did not differ significantly among fishing levels.

Trends were apparent for other families. For example, total biomass of groupers was between 1.4 and 1.6 times higher on unfished sites than reefs subject to fishing. By contrast, snapper biomass peaked on little-fished reefs.

Total biomass of all species combined was greatest on fished reefs, although again due to *Naso unicornis*. When excluded, differences among fishing levels were not significant, although the trend was

Table 5. Differences in biomass for species and families detected by one-way ANOVA (fishing effect). For species only significant effects are shown. Values show the mean biomass (g.count⁻¹) at each fishing level. (C) indicates species which are important in catches. Abbreviations as for Table 1. Nu = *Naso unicornis*. N = 81 in all cases.

| Group/species | Fishing effect (signif., P) | Group Means | | | S-N-K Test |
|----------------------------------|-----------------------------|-------------|---------------|--------|-------------|
| | | Unfished | Little fished | Fished | |
| SERRANIDAE | | | | | |
| <i>Cephalopholis miniata</i> (C) | < 0.0001 | 588.7 | 439.8 | 119.5 | UF = LF > F |
| <i>C. argus</i> (C) | < 0.05 | 120.3 | 6.4 | 103.0 | UF = F > LF |
| <i>C. hemistiktos</i> (C) | < 0.04 | 112.9 | 192.6 | 118.4 | LF > F = UF |
| <i>Aethaloperca rogae</i> (C) | < 0.01 | 0.0 | 162.0 | 8.4 | LF > UF = F |
| <i>Epinephelus fasciatus</i> | < 0.01 | 19.0 | 2.3 | 56.1 | F > LF = UF |
| SCARIDAE | | | | | |
| <i>Hipposcarus harid</i> (C) | < 0.005 | 0.0 | 261.9 | 277.2 | F = LF > UF |
| <i>Scarus sordidus</i> (C) | < 0.02 | 137.4 | 264.5 | 127.8 | LF > UF = F |
| <i>S. ferrugineus</i> (C) | = 0.05 | 265.7 | 231.7 | 93.1 | UF = LF > F |
| <i>S. fuscopureus</i> | = 0.05 | 16.4 | 88.4 | 120.0 | F > LF = UF |
| <i>S. niger</i> (C) | < 0.0002 | 150.6 | 444.4 | 211.4 | LF > UF = F |
| ACANTHURIDAE | | | | | |
| <i>Zebbrasoma veliferum</i> | < 0.005 | 207.0 | 77.6 | 62.0 | UF > LF = F |
| <i>Ctenochaetus striatus</i> | < 0.01 | 364.7 | 364.9 | 247.6 | UF = LF > F |
| <i>Naso lituratus</i> (C) | < 0.005 | 318.0 | 42.5 | 31.8 | UF > LF = F |
| <i>N. unicornis</i> (C) | < 0.0001 | 115.8 | 0.0 | 4676.1 | F > LF = UF |
| TOTAL BIOMASS | | | | | |
| Serranidae | NS | 2528.4 | 1598.8 | 1769.4 | |
| Lethrinidae | NS | 206.2 | 263.3 | 579.3 | |
| Lutjanidae | NS | 444.1 | 1092.1 | 125.5 | |
| Mullidae | NS | 287.8 | 110.5 | 197.7 | |
| Scaridae | < 0.03 | 5176.3 | 6368.7 | 5152.0 | LF > UF = F |
| Acanthuridae | < 0.0001 | 1752.2 | 1155.7 | 6040.7 | F > LF = UF |
| Acanthuridae (excl. Nu) | NS | 1636.3 | 1155.7 | 1364.6 | |
| Overall (all species) | < 0.02 | 6404.0 | 5896.6 | 9751.1 | F > LF = UF |
| Overall (excl. Nu) | NS | 6288.2 | 5896.6 | 5075.0 | |
| Predator biomass | NS | 3178.8 | 2954.2 | 2556.2 | |
| Herbivore biomass | < 0.001 | 2937.4 | 2831.9 | 6997.2 | F > LF = UF |
| Herbivores (excl. Nu) | NS | 2821.6 | 2831.9 | 2321.1 | |

reversed with mean biomass per count 0.8–1.2kg higher in little-fished and unfished sites than fished.

Fishing in the Red Sea targets mainly predatory species although parrotfishes, surgeonfishes, chub and goatfishes are caught in trammel nets (Sheppard et al. 1992). Biomass of predators (groupers, emperors, snappers, goatfishes, grunts and bream) did not differ significantly among fishing levels although there was a trend of increasing biomass from fished to unfished sites. By contrast, herbivore biomass (parrotfishes, surgeonfishes and chub) was greatest on fished reefs. Again this was due to the presence of *Naso unicornis*. Excluding this species, biomass was lower in fished than other sites but not significantly so.

Species richness

Neither total species richness nor species richness of families subject to fishing differed significantly among fishing levels (Tab. 3).

Discussion

After 15 years of protection from fishing, the evidence from the Ras Mohammed Marine Park to support predictions of increases in abundance, average size and biomass of fished species is limited and often equivocal. The results show a diverse array of differences among fishing levels, posing substantial interpretational difficulties.

Higher abundances of several commercial species were detected within the unfished marine park sites or little-fished reefs, particularly among the groupers. However, several species showed the opposite effect, or no effect at all. The low abundance of many species clearly limits the power of the census method used to detect differences. The power of ANOVA to detect differences among sample means will be very low for species which were uncommon, especially if they were patchily distributed (e.g. species foraging in groups). Consequently, failure to detect differences among fishing levels for uncommon species does not necessarily indicate the absence of a difference.

Pooling species at the family level substantially overcomes the difficulty of low statistical power and has been successful in other studies of marine reserve efficacy (Samoilys 1988; Russ and Alcalá 1989; Polunin and Roberts 1993). There was only a significant difference in abundance for surgeonfishes with higher numbers on fished than other reefs. A trend was apparent for groupers towards higher abundance on unfished and little-fished reefs. These findings could be interpreted as a pred-

ator-prey system, and higher surgeonfish numbers on fished reefs a response to reduced predation pressure. Certainly one surgeonfish species, *Acanthurus nigrofuscus*, is a common prey species of groupers in the area (Shpigel and Fishelson 1989; Zyadah 1989). The significant increase in abundance of this species with increasing fishing pressure fits with reduced predation. However, parrotfish numbers might be expected to increase with reduced predation pressure for the same reason but did not, leaving this interpretation in doubt. Parrotfishes are also more favoured by fishermen in Sinai than surgeonfishes so the absence of an increase in their numbers should not lead to outright rejection of the predator-prey interpretation of abundances either.

Effects on mean size of fishes fitted theoretical predictions much more closely, with sizes greater on unfished or little-fished reefs for all seven species for which significant effects were detected. Some of the size differences were striking; for example, individuals of the grouper *Variola louti* were over 14cm longer on average within the marine park than on fished reefs, equivalent to a tripling in weight to 1.3kg. Trends of increase in size with decreasing fishing intensity were apparent for five of seven other species for which sample sizes were reasonable.

A prediction of higher biomass of commercial species on unfished reefs was supported for only five species. Several showed the opposite effect or results were equivocal. At the family level there were significant differences among fishing levels only for surgeonfish and parrotfish, although for the former this was only true when *Naso unicornis* were included. This large species forms schools over the fore-reef and was common in fished but not other sites. Exclusion of *N. unicornis* led to a trend of decreasing surgeonfish biomass with increasing fishing intensity, a pattern matched by groupers. By contrast, parrotfish biomass peaked on little-fished reefs with almost equal biomass in unfished and fished sites. A similar trend was evident for snappers. Goatfish, although common on reefs of the area, constitute a very small element of catches. Biomass of this family was similar among fishing levels.

The trend of decreasing biomass from unfished to fished was also supported for higher level groupings of species (excluding *N. unicornis*): herbivores, predators and all species combined. However, the differences among fishing levels were small and none significant. For all species combined the difference in mean biomass between fished and unfished was only 1.2kg count⁻¹, 1.2 times the biomass on unfished reefs.

A key problem faced by comparative studies is that of knowing whether any differences detected are due to the factor of interest, or to other variables not held constant across levels of that factor. This difficulty has plagued studies of marine reserve function and of effects of fishing in general (Roberts and Polunin 1991). Comparisons of sites, reserves or otherwise, can rarely match habitat characteristics precisely across fishing levels. The present study is no exception. At the scale of counts there were small but potentially important differences in hard and soft coral cover among fishing levels. Cluster analysis suggested that there was no systematic basis to these differences and that sites were relatively similar. Differences in structural complexity were minor and unlikely to cause systematic differences in abundance among fishing levels. However, Figure 1 shows that sites from the three fishing levels were located along a geographical gradient from the tip of the Sinai Peninsula northward into the Gulf of Aqaba. That various differences exist across this gradient is undeniable (Sheppard et al. 1992). The question is, do they affect interpretation of the study?

Some of the differences we detected probably owe more to habitat differences than fishing. For example, the higher abundance of pelagic piscivores within the marine park is unsurprising. Ras Mohammed has long been renowned for the abundance of such fish but this has been attributed to the proximity of deep water and accident of location at the convergence of markedly different water bodies. Indeed, anecdotal reports suggest that pelagic piscivores are now less abundant than prior to protective management (Anonymous 1989).

That the results of this study exhibit a remarkable complexity is not unexpected. Complexity is an integral property of the coral reef ecosystem. The effects of a perturbation are thus likely to cover a spectrum of responses, both direct and indirect. The potential for indirect effects of fishing is great. Removal of certain species may have widespread effects within assemblages through processes such as competitive release and reduced predation. The much greater biomass of *Naso unicornis* in fished sites might, for example, be a response to lower numbers of other herbivorous species, although other explanations may be equally possible.

Fishing intensity in the Red Sea generally is low compared with many other regions (Norte et al. 1989; Sadovy 1989; Sheppard et al. 1992). Hence direct effects of fishing are likely to be small and indirect effects large by comparison. The differences we detected in abundance, mean size and biomass of commercial species were relatively small except

in a few cases. This should not lead to the conclusion that marine reserves are ineffective in protecting stocks. The converse is probably more true; that we were able to detect effects apparently due to fishing in the northern Red Sea suggests that even a low fishing intensity can have a pronounced influence and that this can be readily counteracted by protective management.

Protective management of reef fisheries would be unwarranted in Sinai where present catches appear to be below sustainable levels. In regions where intensity of exploitation is much greater, or destructive fishing methods widespread, protective management may be one of the few means available to control fishing and protect stocks. It has now been relatively well established that reserve protection can result in increases in abundance, mean size and biomass of fish populations (Roberts and Polunin 1991). The critical questions now are how much can stocks within reserves contribute to recruitment into fishing grounds and to enhanced catches in adjacent areas through emigration of fish? Although comparative studies still hold some potential to provide answers to these questions, adoption of experimental approaches is likely to prove much more productive.

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