

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Effects of habitat characteristics and sedimentation on performance of marine reserves in St. Lucia

Julie P. Hawkins^{a,*}, Callum M. Roberts^a, Calvin Dytham^b, Chris Schelten^c,
Maggy M. Nugues^d

^aEnvironment Department, University of York, Heslington, York YO10 5DD, UK

^bDepartment of Biology, University of York, Heslington, York YO10 5DD, UK

^cFrankfurt Zoological Society, P.O. Box 14935, Arusha, Tanzania

^dCenter for Marine Science, University of North Carolina Wilmington, 5600 Marvin K. Moss Lane, Wilmington, NC 28409-5928, USA

ARTICLE INFO

Article history:

Received 18 March 2005

Received in revised form 6

September 2005

Accepted 7 September 2005

Available online 20 October 2005

Keywords:

Coral reef

Fishing

Groupers

Marine protected area

Parrotfish

ABSTRACT

This study examines factors affecting the rate and extent of biomass build-up among commercially important groupers, snappers, grunts, parrotfish and surgeonfish in a network of four marine reserves in southwest St. Lucia, Caribbean. Reserves constituted 35% of the total reef area originally available for fishing. Protection was instigated in 1995 after a baseline survey with annual or biennial censuses performed until 2002. Each survey consisted of 114 fifteen minute fish counts in reserves and 83 in fishing grounds, at depths of 5 m and 15 m in a 10 m diameter counting area. Estimates of number and size (cm) of target species were used to calculate fish family biomass. Data were analysed using three-way ANOVA in a before-after-control-impact pairs (BACIP) design. All families increased significantly in biomass over time at nearly all sites. Increases were greater in reserves than fishing grounds, except for grunts, and responses were strongest in parrotfish and surgeonfish. The combined biomass of families more than quadrupled in reserves and tripled in fishing grounds between 1995 and 2002. During this period coral cover declined by 46% in reserves and 35% in fishing grounds. Multiple regression showed that neither habitat characteristics nor habitat deterioration significantly affected rates of biomass build-up. The key factor was protection from fishing, which explained 44% of the variance in biomass growth. A further 28% of the variance was explained by sedimentation, a process known to stress reef invertebrates, significantly reducing the rate of biomass build-up. St. Lucia's reserves succeeded in producing significant gains to fish stocks despite coral cover and structural complexity falling steeply over the period of the study.

© 2005 Elsevier Ltd. All rights reserved.

1. Introduction

Throughout the world, marine reserves have been established to protect biodiversity and enhance adjacent fisheries (Gell and Roberts, 2003; Halpern, 2003). Closing areas allows ani-

mals to live longer and grow large, which is important for supporting fisheries because of the exponential relationship between fecundity and body size (Bohnsack, 1990). Large fish can also produce higher quality eggs (Berkeley et al., 2004). Recoveries of depleted stocks of sedentary species near to

* Corresponding author. Tel.: +44 1904 434073; fax: +44 1904 432998.

E-mail address: jph7@york.ac.uk (J.P. Hawkins).

0006-3207/\$ - see front matter © 2005 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2005.09.008

protected areas provide evidence that eggs and larvae from animals receiving protection are restocking fishing grounds (e.g. Roa and Bahamonde, 1993; Murawski et al., 2000; Tawake et al., 2001).

Reserves will also restock fisheries if juveniles and adults move from them into fishing grounds. The likelihood of this is believed to rise as densities of animals within reserves increase (Bohnsack, 1998). Although gaps in understanding remain (Sale et al., 2005), a wealth of evidence now shows that protection increases animal size and promotes large, rapid and sustained build-up of abundance and biomass in commercially important species (Russ and Alcala, 1996; Davidson, 2001; Lock and Newman, 2001; Côté et al., 2001; Gell and Roberts, 2003; Halpern, 2003).

Tagging studies have demonstrated movements out of protected areas into fishing grounds for a range of animals in many parts of the world (Yamasaki and Kuwahara, 1990; McClanahan and Mangi, 2000; Kelly, 2001; Rowe, 2001; Willis et al., 2001). Studies have also revealed increased point diversity (species per unit area) within protected areas (Jennings et al., 1995; Wantiez et al., 1997; Kaiser et al., 2000; Bradshaw et al., 2001). For example, areas closed to trawling on the George's Bank in the Gulf of Maine are now recovering populations of echinoderms, hydroids and seafans (NRC, 2002).

Despite these benefits, when fishers are faced with the prospect of having reserves established in their own fishing grounds they are often sceptical or even hostile towards the idea. For example, stiff opposition, mainly from fishers, resulted in proposals for a reserve in Florida's Dry Tortugas being dropped from the 1995 National Marine Sanctuary Management plan (Delaney, 2003). In this case, the reserve was eventually established, but only after another six years of consultations with the local community (Delaney, 2003).

To progress with establishing marine reserves it is tempting to place them where they will attract least opposition. Invariably this would mean avoiding more productive fishing grounds and could involve protecting areas where the habitat is poor or degraded. While reserves can improve habitats that have been transformed or degraded by fishing (Shears and Babcock, 2002; Rodwell et al., 2003), establishing them in poor quality habitat could impair their performance (Rodwell et al., 2003). For example, Heslinga et al. (1984) described how in Palau 20 years of reserve protection did not improve stocks of the snail *Trochus niloticus* or the fishery for this species. Reserves failed because they were set up in habitat that was marginal for *Trochus*. Unless reserves start producing benefits reasonably quickly support for them is likely to waver, thereby delaying or preventing critical protection for threatened habitats and species. By contrast, if reserves perform well, plans to establish more or create new ones are likely to gather support (Cocklin et al., 1998; Tawake et al., 2001).

Evidence for the importance of habitat characteristics on recruitment, survival and growth of marine organisms is increasing. In a study of Atlantic cod (*Gadus morhua*), Ratz and Lloret (2003) examined 10 stocks from the north Atlantic and found that fish from colder waters had poorer body condition than those from warmer areas and that poor body condition reduced fish growth and reproductive potential. Anderson and Sabado (1995) found that growth rates of juvenile kelp perch (*Brachyistius frenatus*) among sites in kelp

forests in California increased with abundance of their prey. A study of the damselfish *Pomacentrus amboinensis* in Japan, found that rates of recruitment were significantly greater in more structurally complex habitats (Kawasaki et al., 2003). For the damselfish *Acanthochromis polyacanthus*, Connell (1998) highlighted the importance of spatial variation in predation pressure as a limitation to population growth. In this species, mortality rates were greater in habitats with greater densities of predators.

The above examples illustrate that population processes vary with habitat characteristics, implying that marine reserve performance will also be affected by habitat. However, few studies have evaluated reserve effects in relation to habitat. Roberts (2000) compared the Hol Chan Marine reserve in Belize with a reserve in the Saba Marine Park in the Netherlands Antilles. Reefs in the Hol Chan reserve received daily inputs of nutrients, detritus and plankton via tidal flushing from nearby lagoon and offshore habitats, while the Saba reserve did not. After four years of protection, the build-up of fish biomass within the Hol Chan reserve was six times greater than in Saba. Unsurprisingly, the Hol Chan reserve had previously been a highly productive fishing area before it became over-exploited.

To determine whether protection from fishing influenced the body condition of white seabream (*Diplodus sargus*) for a given type of habitat, Lloret and Planes (2003) compared fish in rocky and sandy coastlines, inside and outside a Mediterranean reserve. They found no effect of protection on the reproductive potential of fish, or on their ability to feed as measured by digestive tract weight. However, after fish had spawned those occurring in rocky areas inside reserves were in better condition than those in rocky areas that were not protected. Amongst juvenile fish within reserves, body condition (higher weight to length ratio) was better in rocky rather than in sandy areas.

In this study we examine how coral cover and structural complexity, influence the rate and extent of recovery in fish communities following the creation of a network of four marine reserves in St. Lucia, West Indies. These two factors are considered to be important influences on reef fish assemblages (Roberts and Ormond, 1987; Jones, 1991) and are widely used to guide the placement of marine reserves, areas with high coral cover and complexity being favoured (Roberts, 2000). We also consider whether levels of sediment input, a form of pollution from land-based sources, influences reserve performance. If coral cover and structural complexity affect reserve performance, then sediment input could undermine it by degrading habitat. We are unaware of any other study that has tried to evaluate the impact of a form of pollution on marine reserves.

2. Methods

The Soufrière Marine Management Area (SMMA) covers an 11 km stretch of coastline in the south west of St. Lucia (Fig. 1). It was established in 1995 with a management plan developed during three years of consultation with local stakeholders (including government agencies, fishers, water taxi operators, hoteliers, dive centres, yachters, local people). One of its principal aims was to rebuild severely overexploited

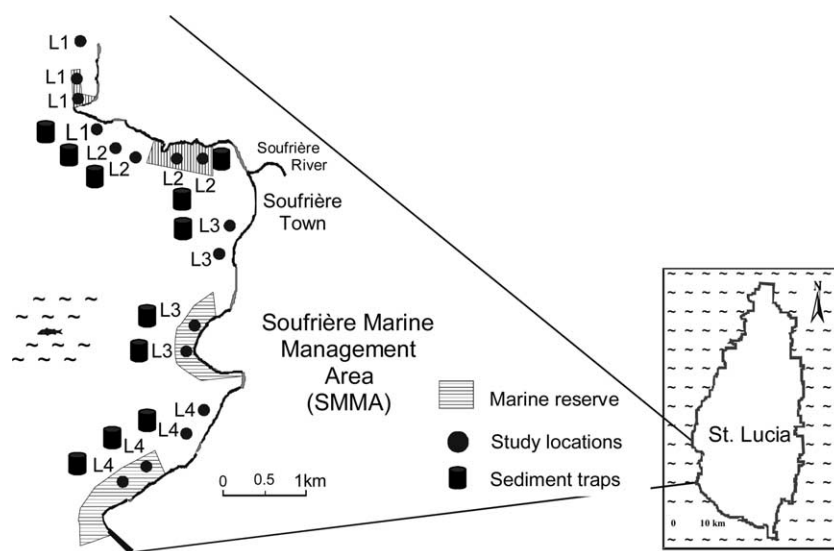


Fig. 1 – Map of St. Lucia's Soufrière Marine Management Area showing marine reserves and sample sites within each of four reserve-fishing grounds. Paired reserve-fishing ground comparisons are indicated by sites labelled L1, L2, etc.

fish stocks and recover fishery productivity. This was to be achieved by protecting 35% of the coral reef habitat in a network of four marine reserves that were off limits to all fishing. Reserves were interspersed between fishing grounds and their boundaries marked with signs on land and buoys in the sea. Wardens patrol the area daily, and compliance with reserves has been good throughout the study (Roberts et al., 2001). At the time of establishment, fishing pressure was redirected from reserves to adjacent areas and has remained approximately constant over the period of the study (Roberts et al., 2001).

In December 1994 and January 1995, six months before the planned reserves were closed to fishing we censused fish populations within the SMMA. In August and September 1996, we performed a second census after the reserves had received just over one year of protection. From then until 2002, we monitored the SMMA annually, except for in 1999. Each year we made 114 fish counts in reserves and 83 in fishing grounds using an adaptation of Bohnsack and Bannerot (1986) stationary point technique. Of these, 96 counts were at a depth of 5 m and 101 at 15 m.

On each fish count we laid a 10 m tape measure on the reef and used it to denote the diameter of a cylinder extending 5 m above the reef. For 15 min, we recorded the number and estimated the size in centimetres of all non-cryptic species present within or passing through this cylinder. Whilst laying out the tape we would record any large, wary species within the counting area that our presence might scare away. During counts we also recorded the presence of any cryptic species to give an indication of total species numbers. Within each counting area we estimated total percentage hard coral cover and fleshy algal cover. We made semi-quantitative estimates of reef structural complexity on a scale of 0–5 where 0 corresponds to somewhere totally flat and featureless and 5 represents maximum imaginable reef complexity. Prior to the start of data collection, divers trained to achieve consistency with

each other in their estimates of cover and structural complexity. Comparing results against more laborious methods of estimating cover revealed that our levels of accuracy were within approximately 5%.

3. Sediment monitoring

Rates of sedimentation were measured between 1997 and 2001 at 11 locations throughout the SMMA (Fig. 1). Sediment traps were collected every two weeks over seven time periods of 2–6 months during both wet and dry seasons. Sediment traps consisted of 4 cm diameter PVC pipes, 15 cm deep in which the sediment accumulated. At each location there were two traps fixed at 25 cm above the reef. After traps were brought out of the water their contents were suction filtered on Whatman No. 1 filter paper (0.45 μm), then sun dried for at least 24 h before being weighed. From these samples sedimentation rates in $\text{mg cm}^{-2} \text{day}^{-1}$ were calculated.

Eleven of the 16 sites where we performed fish counts contained sediment traps. For those that did not, we derived an estimate of sedimentation rates by interpolating values from the closest traps on either side.

4. Data analyses

We used a before-after-control-impact pairs (BACIP) analytical design (see Russ, 2002 for a detailed discussion of study designs for detecting effects of marine reserves) to compare changes in fish biomass between marine reserves and fishing grounds from 1995 to 2002. We made one pre-protection census in 1995 and six post-protection censuses thereafter. The BACIP approach is acknowledged to be the most powerful method for distinguishing the effects of reserves from those of background environmental variability (Underwood, 1994; Russ, 2002). Each of the four reserves was paired with an

adjacent fishing area that lay within 150–500 m of the reserve border. Pairs were matched on the basis of proximity and similarity of reef physical and biological characteristics, meaning that reserve and control sites are not all evenly spaced throughout the study area (Fig. 1). To approximately balance replication among treatments and within pairs, 24 fish counts from two sites within marine reserves were excluded from the analysis.

We analysed data from the BACIP experiment using a three-way ANOVA with protection (reserve vs. fishing grounds) and time (year) as fixed factors, and location (four reserve-fishing ground pairs) as a random factor. In all analyses data were pooled across depths, since 4-way ANOVAs with depth as an additional factor showed depth to be non-significant. Removal of this term reduced the number of interactions in the ANOVA, simplifying interpretation of the results. The term of greatest interest in this analysis is the protection \times time interaction. Where there is no difference at the start and there is a significant interaction this implies divergence over time. If reserves are allowing fish stocks to increase then higher levels of biomass will be attained in reserves. The effects of location are also of much interest because if reserves perform differently, then effects may develop strongly in some, but little, or not at all in others.

In summary, the design we used is imperfect because we only have one pre-protection census where three are generally recommended, (Russ, 2002). However, it improves on most studies of marine reserves (Willis et al., 2003; Sale et al., 2005) because (1) it involves several reserves as opposed to just one, (2) it compares changes between reserves and fishing grounds over time rather than in a single snapshot, and (3) it benefits from both pre- and post-protection data. To facilitate interpretation of ANOVA results, we graphed change in biomass over time for reserve and fishing grounds for each of the four reserve-control locations.

We used stepwise multiple regression to determine which of six parameters most affected the change in fish biomass that occurred between 1995 and 2002. These parameters were: protection from fishing, mean level of sedimentation, mean percentage cover of hard coral, mean level of structural complexity, change in mean hard coral cover between 1995 and 2002, and change in mean structural complexity over the same period. Average coral cover and change in average coral cover were not significantly associated (Spearman's $\rho = 0.46$, NS, $n = 18$), nor were average structural complexity and change in average structural complexity ($\rho = 0.11$, NS, $n = 18$). Having established the independence of these measures, all were entered into the multiple regression.

5. Results

Changes over seven years within St. Lucia's Soufrière Marine Management Area for total fish biomass, coral and algal cover, reef structural complexity and species richness are shown in Fig. 2. In the pre-protection census of 1995, there was virtually no difference between marine reserves and fishing grounds in the total biomass of fish (Fig. 2(a)). By the final census in 2002, total biomass had more than quadrupled in

reserves and tripled in fishing grounds. Following storm waves from Hurricane Lenny in 1999 biomass build-up dipped slightly then rapidly recovered.

As fish stocks were increasing, reef habitat was suffering from the effects of storms, sedimentation (Sladek Nowlis et al., 1997) and coral diseases (Nugues, 2002). At the outset of protection coral cover was 1.8 times greater in reserves than fishing grounds. During the study, percentage coral cover fell by 46% in reserves and by 35% in fishing grounds (Fig. 2(c)), reserves being more severely impacted by hurricane waves. Levels of structural complexity were also higher in reserves than in fishing grounds prior to protection (Fig. 2(d)). This pattern remained consistent over time despite reserves decreasing in structural complexity after Hurricane Lenny. In fishing grounds structural complexity did not appear to have been much affected by the hurricane.

Percentage algal cover was initially highest in fishing grounds where it rose by 57% during the study (Fig. 2(b)). In reserves algae did not increase until 2000 when levels rose rapidly after Hurricane Lenny. However, three years after the storm algal cover was declining in reserves but not in fishing grounds, though trends can be difficult to discern over only a three year period. Trends in species richness increased initially with build-up of biomass, but levelled off after three years of protection (Fig. 2(e)). The rise reflects the fact that as species become more abundant they are more likely to be encountered in fish counts.

Results of the BACIP analysis on fish biomass and species richness are given in Table 1 and presented visually for each family in Figs. 3–7, and for all families combined in Fig. 8. In terms of main effects, protection alone was not significant for any family because biomass usually started out at similar levels in fishing grounds and reserves before diverging (Figs. 3–7). In all families, biomass changed significantly over time (Table 1) and almost always increased (Figs. 3–7). Location alone was not significant in any case (Table 1).

As noted in Section 2, the interaction between protection and time is of great interest in BACIP since it indicates divergence in the dependent variable between treatment and controls. A significant protection \times year interaction was found in parrotfish (Fig. 6) and surgeonfish (Fig. 7), showing that these families responded strongly to protection. In surgeonfish the divergence of biomass occurred towards the end of the study after reserves had been protected for six or seven years, except in Location 2 where patterns were unclear. In parrotfish, biomass increased more rapidly in reserves than in fishing grounds in three of the four locations. This does not mean that effects of protection were absent in other families. If reserve effects were strong in some locations, but weak or absent in others, there would not be a significant protection \times year interaction, but location would interact significantly with these factors.

There were significant interactions among location and one or both of protection and time, for all families except surgeonfish, indicating that trajectories of change in biomass differed among the four reserve-fishing ground pairs. Strong effects of protection developed in Location 1 for groupers, snappers and parrotfish which all increased in reserves

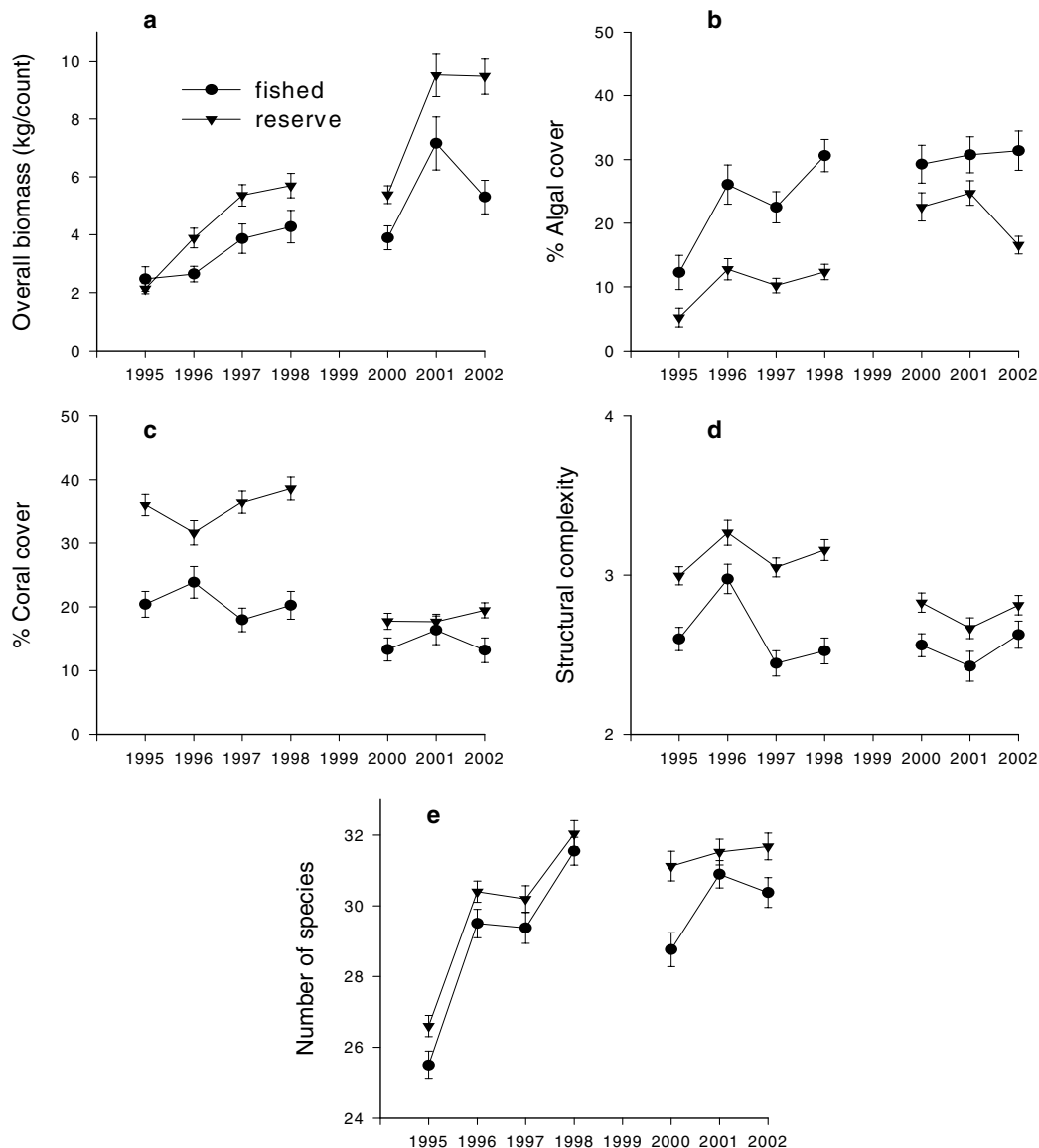


Fig. 2 – Changes over time within the SMMA for mean values per count (\pm SE) of: (a) biomass of groupers (*Serranidae*), snappers (*Lutjanidae*), grunts (*Haemulidae*), parrotfish (*Scaridae*) and surgeonfish (*Acanthuridae*) combined; (b) percentage algal cover; (c) percentage coral cover; (d) structural complexity; (e) number of species. Note there are no data for 1999.

(Figs. 3–7). By contrast, except for groupers, the effect of protection was weak or absent in Location 2 (Figs. 3–7). Protection effects in Locations 3 and 4 were less consistent, developing strongly for some families, and weakly or not at all for others (see Figs. 3–7).

Fig. 9 illustrates differences in habitat between marine reserves and fishing grounds in each of the four Locations. The percentage coral cover and structural complexity was greater in reserves than fishing grounds for Locations 1, 3 and 4 but not for Location 2, while algal cover showed the opposite pattern.

Results of the stepwise regression show that only two of the six habitat factors tested had any significant influence on reserve performance. Forty four percent of the variance

in build-up of total fish biomass was explained by protection from fishing and an additional 28% by levels of sedimentation ($F_{2,15} = 18.8$, $p \leq 0.001$ for the combined model). Neither average measures of coral cover and structural complexity nor their rates of change over time had any significant effect on the rate of build-up of fish biomass. These results are shown graphically in Fig. 10 together with bivariate regression results computed separately for sites in reserves and fishing grounds. Comparison of regression lines in Fig. 10(a) and (b) reveals that rates of biomass build-up were twice as high in reserves as in fishing grounds regardless of levels of coral cover or structural complexity prevailing at study sites. Fig. 10(c) shows how rates of biomass build-up declined with increasing sedimentation rate.

Table 1 – Three-way ANOVAs for fish biomass in reserves and fishing grounds at four locations within the SMMA

Family/factor	df	F-value	Significance
<i>Groupers</i>			
Protection	1, 3	3.2	NS
Time	6, 18.1	2.9	0.036
Location	3, 2.9	0.9	NS
Protection × time	6, 18	1.7	NS
Protection × location	3, 18	14.1	P < 0.001
Time × location	18, 18	0.7	NS
Protection × year × location	18, 1239	3.6	P < 0.001
<i>Snappers</i>			
Protection	1, 3	1.8	NS
Time	6, 18.1	13.9	P < 0.001
Location	3, 2.6	0.6	NS
Protection × time	6, 18	0.8	NS
Protection × location	3, 18	7.3	0.002
Time × location	18, 18	0.5	NS
Protection × year × location	18, 1239	3.5	P < 0.001
<i>Grunts</i>			
Protection	1, 3	0.6	NS
Time	6, 18.2	4.4	0.007
Location	3, 2.7	0.8	NS
Protection × time	6, 18.1	0.2	NS
Protection × location	3, 18	6.4	0.004
Time × location	18, 18	0.6	NS
Protection × year × location	18, 1239	1.0	NS
<i>Parrotfish</i>			
Protection	1, 3	6.0	NS
Time	6, 18.1	30.0	P < 0.001
Location	3, 2.9	0.7	NS
Protection × time	6, 18.1	4.6	0.005
Protection × location	3, 18	18.4	P < 0.001
Time × location	18, 18	0.6	NS
Protection × year × location	18, 1239	2.1	0.004
<i>Surgeonfish^a</i>			
Protection	1, 3.1	4.6	NS
Time	6, 18.2	4.3	0.007
Location	3, 0.1	30.0	NS
Protection × time	6, 18.1	2.3	0.03
Protection × location	3, 18	0.2	NS
Time × location	18, 18	0.9	NS
<i>Total fish biomass</i>			
Protection	1, 3	2.5	NS
Time	6, 18.1	35.7	P < 0.001
Location	3, 2.6	0.6	NS
Protection × time	6, 18	1.4	NS
Protection × location	3, 18	9.5	0.001
Time × location	18, 18	0.3	NS
Protection × year × location	18, 1239	3.2	P < 0.001

a The non-significant 3-way interaction was removed to allow SPSS to calculate Satterthwaite's mean square on the F ratio for location. Some degrees of freedom are not integers because of Satterthwaite's effect.

ferent locations. Some reserves performed consistently better than others and some families showed a stronger response to protection than others. Biomass increases were particularly strong amongst herbivorous fish. Parrotfish biomass increased more rapidly in reserves than fishing grounds in three of the four locations. In the one location where this divergence did not occur, the biomass built up steadily in both. For surgeonfish build-up of biomass occurred slowly until there was a rapid gain in reserves in the last year of the study. Amongst predators, protection resulted in a large biomass increase in reserves for groupers and a smaller increase for snappers. In grunts, a family that feeds on invertebrates, biomass increases were similar between reserves and fishing grounds, except at one location where fishing grounds showed a more rapid increase.

Fish biomass increased during this study despite falling coral cover. In reserves coral cover almost halved, and in fishing grounds it fell by a third. However, multiple regression results showed that the rate of loss of coral cover and structural complexity had no significant effect on the rate of build-up of fish biomass. Nor did average levels of coral cover or structural complexity present at a location throughout the study correlate significantly with change in biomass. Protection from fishing was the single most important factor responsible for improving fish stocks. By contrast, sedimentation had a significant negative impact on rate of fish biomass increase. However, whether this is a causal relationship remains unclear. Other work has shown that sedimentation causes coral death (Sladek Nowlis et al., 1997), so it is strange that rate of build-up of fish biomass was unrelated to rate of change in coral cover if sedimentation is causing corals to decline in these sites. Perhaps the impact of coral disease and hurricane damage, which have also caused coral mortality in the marine park (Nugues, 2002) can help explain this result. On the other hand, some coral communities are known to be resilient to sedimentation (Brown et al., 2002) and further work is needed to resolve the question.

This study supports growing evidence that marine reserves benefit fisheries by fostering increase in fish spawning stocks (Gell and Roberts, 2003; Halpern, 2003). Its BACIP design is among the most powerful yet used to test for the effects of reserves (Russ, 2002; Willis et al., 2003; Sale et al., 2005), benefiting from multiple reserve-control pairs and from pre-protection data. Even so it is not perfect. Ideally in a BACIP analysis, several episodes of sampling should precede the treatment and several follow it. Hence, a shortcoming of this study was the single pre-protection census. Such difficulty in obtaining multiple pre-treatment samples commonly afflicts studies with a BACIP design (Russ, 2002; Gell and Roberts, 2003). This problem is usually caused by lack of opportunity, time or money. For example, once the need for a marine reserve has been agreed, and a suitable location decided, people are very keen to initiate protection without further delay. This reason prevented further pre-treatment sampling in our study.

A second limitation of our study is that fishing grounds are not true controls for reserves. If fishing grounds were completely unaffected by protection, then biomass might be expected to remain approximately constant over time in controls (or decrease as displaced fishers intensify effort)

6. Discussion

Commercially exploited fish stocks built up rapidly over time in the Soufrière Marine Management Area both in reserves and adjacent fishing grounds. However, there were variable patterns of change among five families of fish across four dif-

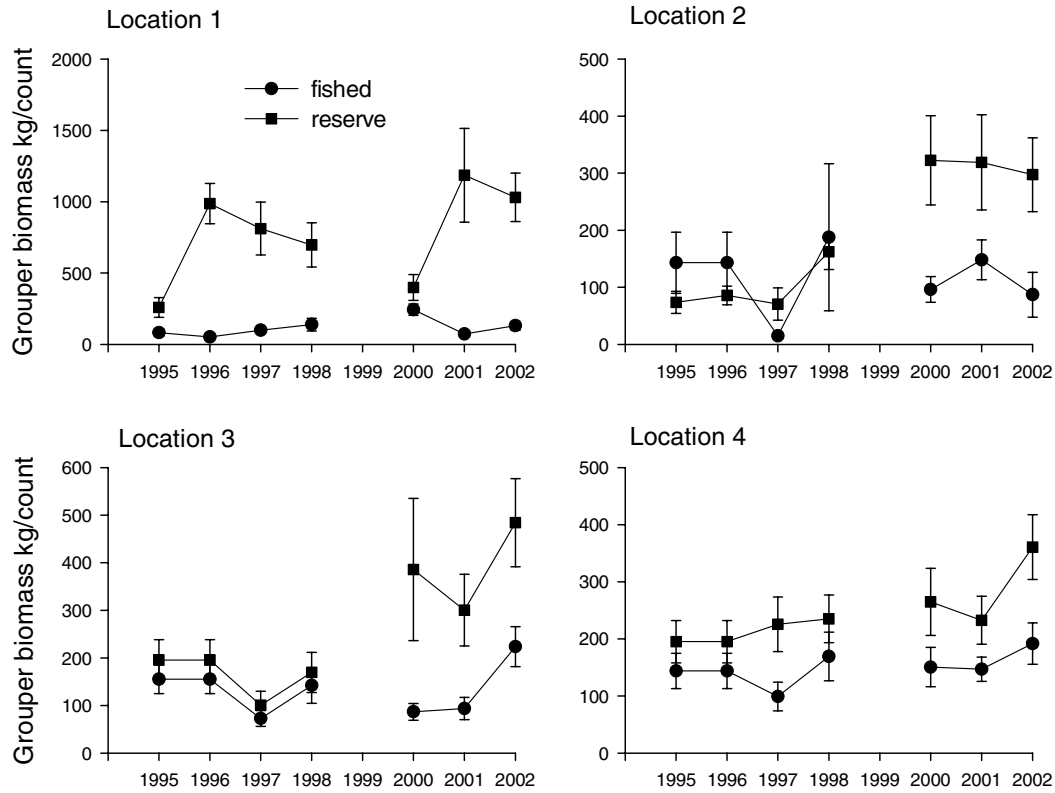


Fig. 3 – Mean biomass per fish count (\pm SE) of groupers in marine reserves (■) and fishing grounds (●) at four locations within the SMMA. Note there are no data for 1999.

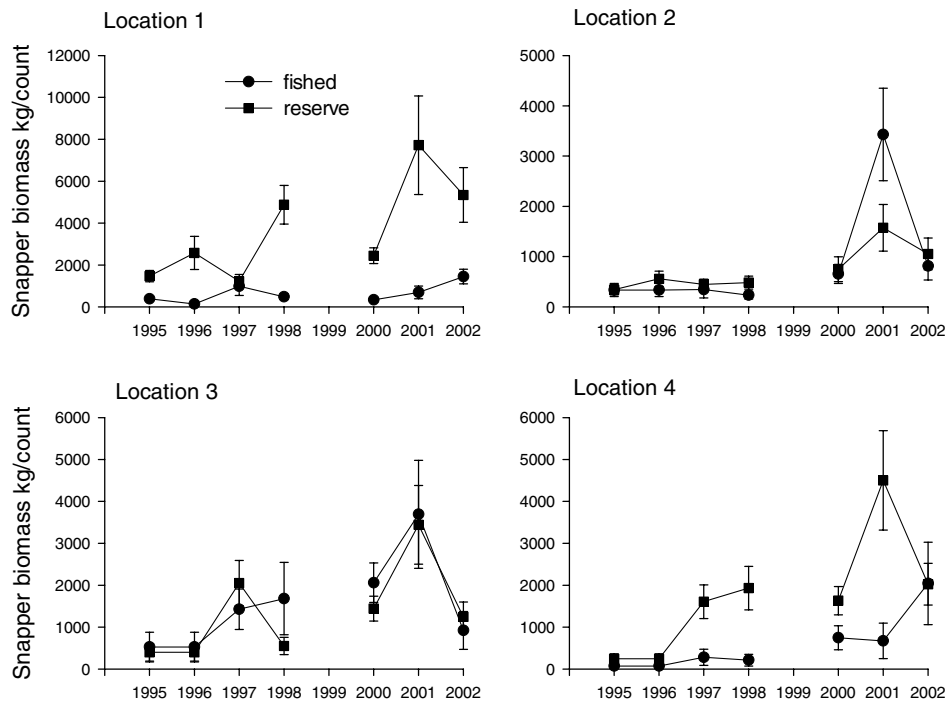


Fig. 4 – Mean biomass per fish count (\pm SE) of snappers in marine reserves (■) and fishing grounds (●) at four locations within the SMMA. Note there are no data for 1999.

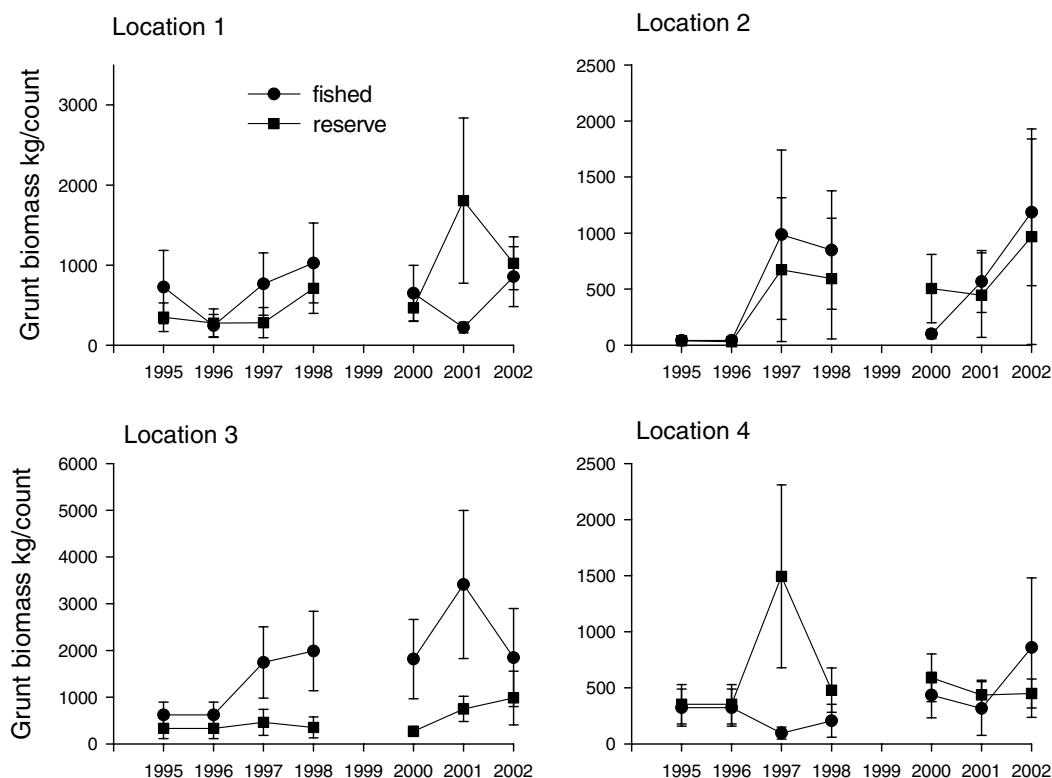


Fig. 5 – Mean biomass per fish count (\pm SE) of grunts in marine reserves (■) and fishing grounds (●) at four locations within the SMMA. Note there are no data for 1999.

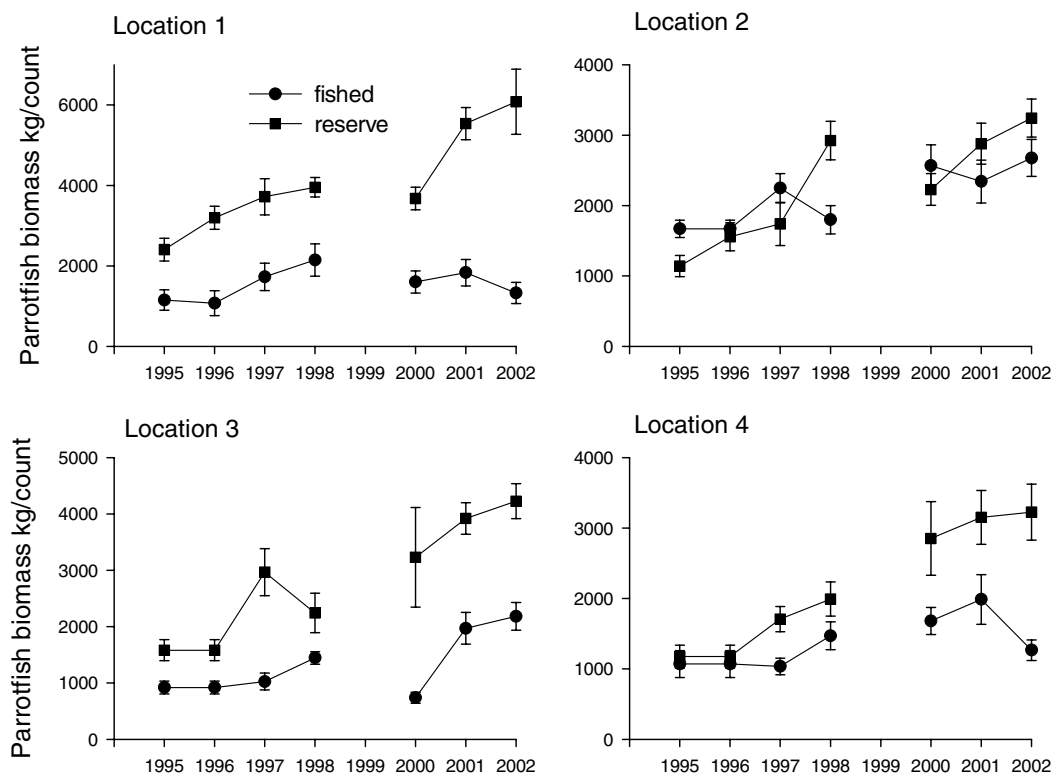


Fig. 6 – Mean biomass per fish count (\pm SE) of parrotfish in marine reserves (■) and fishing grounds (●) at four locations within the SMMA. Note there are no data for 1999.

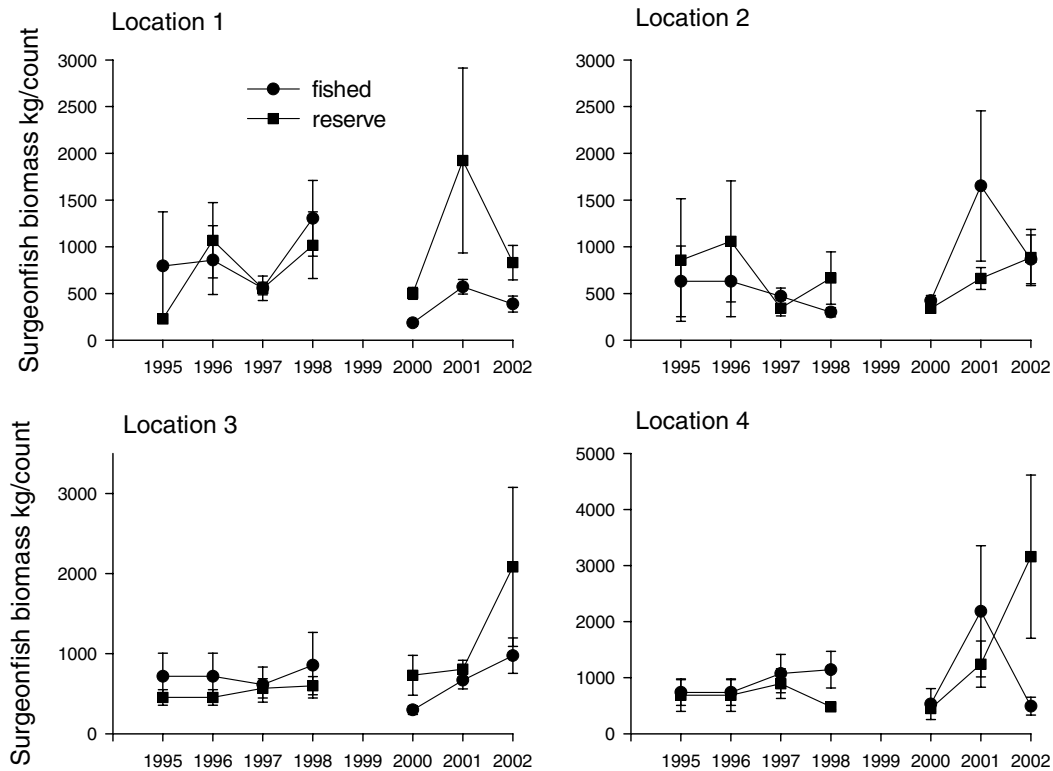


Fig. 7 – Mean biomass per fish count (\pm SE) of surgeonfish in marine reserves (■) and fishing grounds (●) at four locations within the SMMA. Note there are no data for 1999.

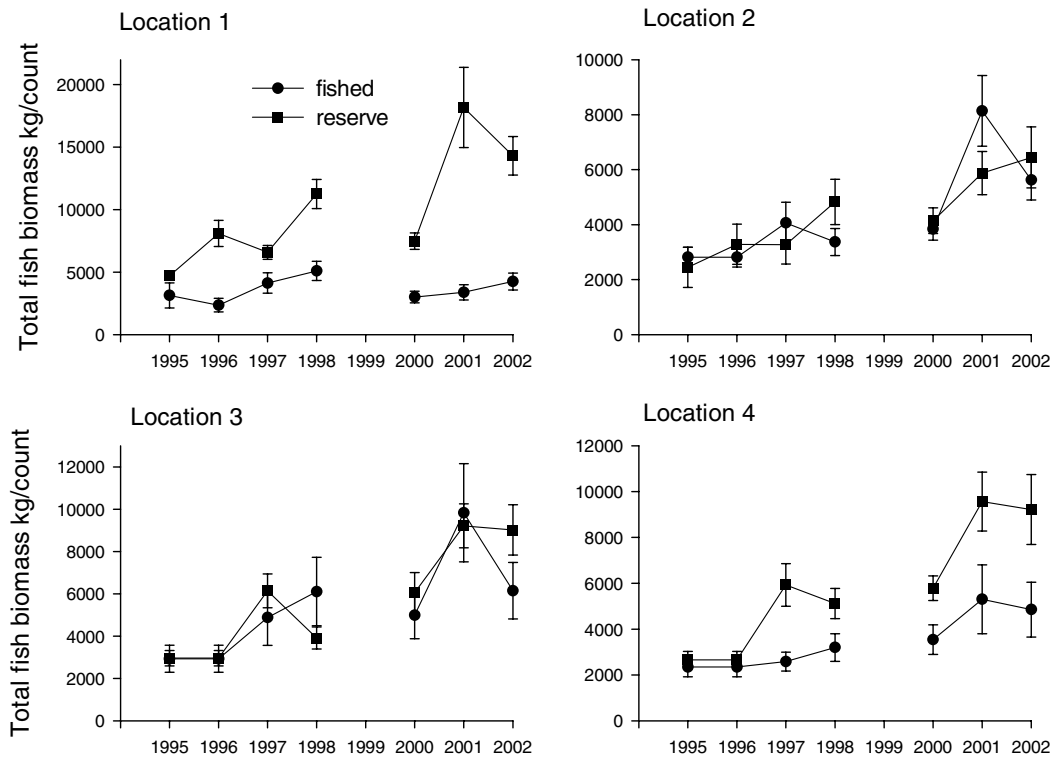


Fig. 8 – Mean biomass per count (\pm SE) of groupers, snappers, grunts, parrotfish and surgeonfish combined, in marine reserves (■) and fishing grounds (●) at four locations within the SMMA. Note there are no data for 1999.

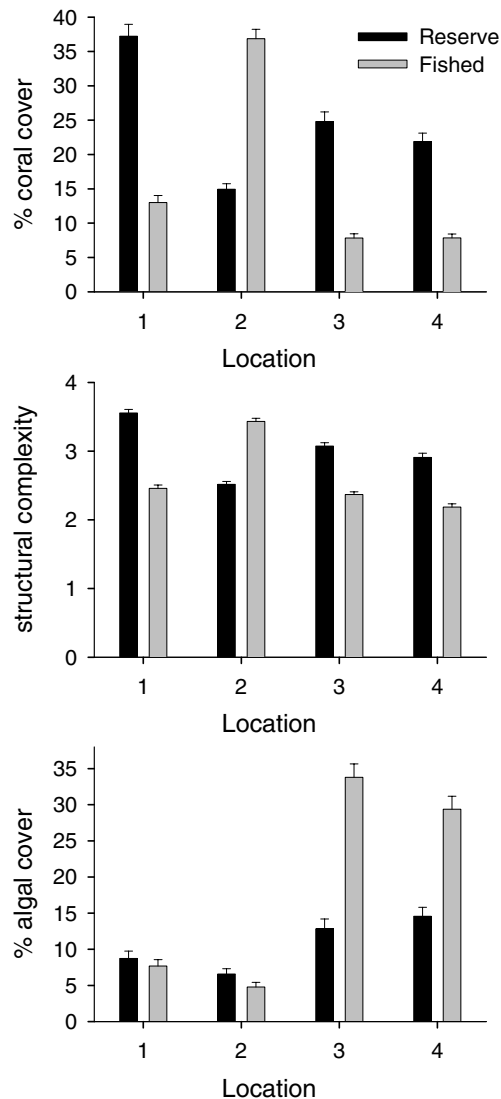


Fig. 9 – Mean values per count (\pm SE) of hard coral cover, algal cover and structural complexity between marine reserves and fishing grounds at four locations within the SMMA.

and increase in reserves. However, if, as expected, fish and their offspring “spillover” from reserves (Bohnsack, 1998) then biomass in adjacent fishing grounds will also increase, albeit more slowly than in reserves. Hence, although time may strongly affect biomass, the divergence in biomass between reserves and fishing grounds may develop slowly and it could take a while before the interaction between protection and time becomes significant. One way to counteract this problem would be to use control sites that were more distant from treatments. However, this is also problematic because the effects of reserves may extend over large distances (tens of kilometres) due to export of eggs and larvae (Shanks et al., 2003). In this study, well-developed reefs are restricted to the southern part of a small island that is only 44 km long. It was therefore not possible to find unaffected control sites in St. Lucia. Logistic constraints prevented controls being used on the adjacent island of St. Vincent; but even there, problems of potential ecological differences between sites and varia-

tions in fishing pressure and methods used would still remain (Gell and Roberts, 2003).

Despite some drawbacks, this study provides strong support that protection from fishing increases fish biomass and that there is spatial variation in the extent of this effect across different reserves. A previous study within the SMMA (Roberts et al., 2001) showed that after five years of protection average catches in fishing grounds rose by up to 90%.

All the families we studied are prime targets for the reef fishery, but some responded more strongly to protection than others. One reason that parrotfish and surgeonfish might have done well is that during this study there was a proliferation of their algal food which could have added to stock improvements brought about by protection. During the first years of the study, algal cover was higher in fished areas than reserves, and it also increased there faster. However, following damage to coral from Hurricane Lenny in 1999, algal cover rose sharply in reserves until it almost approached levels in fishing grounds. Hence, over the course of this study herbivores in both reserves and fishing grounds benefited from a large improvement in food resources.

Three years after the storm algal cover in fishing grounds remained high, whereas in reserves it had fallen. Since the biomass of herbivorous fish was higher in reserves than in fishing grounds the grazing pressure in reserves would be greater. It appears that within the SMMA, protection from fishing resulting in larger populations of herbivorous fish may have helped in the mitigation of reef degradation by algal over-growth.

It is logical that increased algal abundance could benefit herbivorous species. However, it is surprising that overall fish biomass build-up did not appear related to levels of hard coral cover and structural complexity, or their decline over time. We do not know how these characteristics influence the fitness of any particular fish species or family, but it seems reasonable to expect that there will be different responses to habitat characteristics in the suite of species that we studied. As our four study locations all contained at least one family that increased vigorously over time it is possible that in summing across families we have obscured habitat effects at the level of species and families. Taken at face value, the results indicate that fish communities and fisheries can benefit from protective management even if coral cover and structural complexity are low or declining. If this remains a long-term effect, it is a reassuring finding since coral reefs throughout the world are currently being rapidly degraded (Wilkinson, 2002) and the trend seems likely to continue (Hughes et al., 2003). However, in a similar study of Papua New Guinea reserves, Jones et al. (2004) found that declining coral cover had a major negative impact on fish populations both inside and outside marine reserves. Coral cover fell from an average of ~66% to a low of ~7% over the eight year course of their study. At the same time, over 75% of fish species decreased in abundance with over half falling by 50% or more. The difference in outcome of coral decline between Jones et al.’s site and ours might be due to the fact that very few Caribbean fish species have an obligate dependency on corals at any stage in their lives. By contrast, many Indo-Pacific species have strong associations with living coral and 11% of Jones et al.’s species had an obligate relationship (Jones et al., 2004).

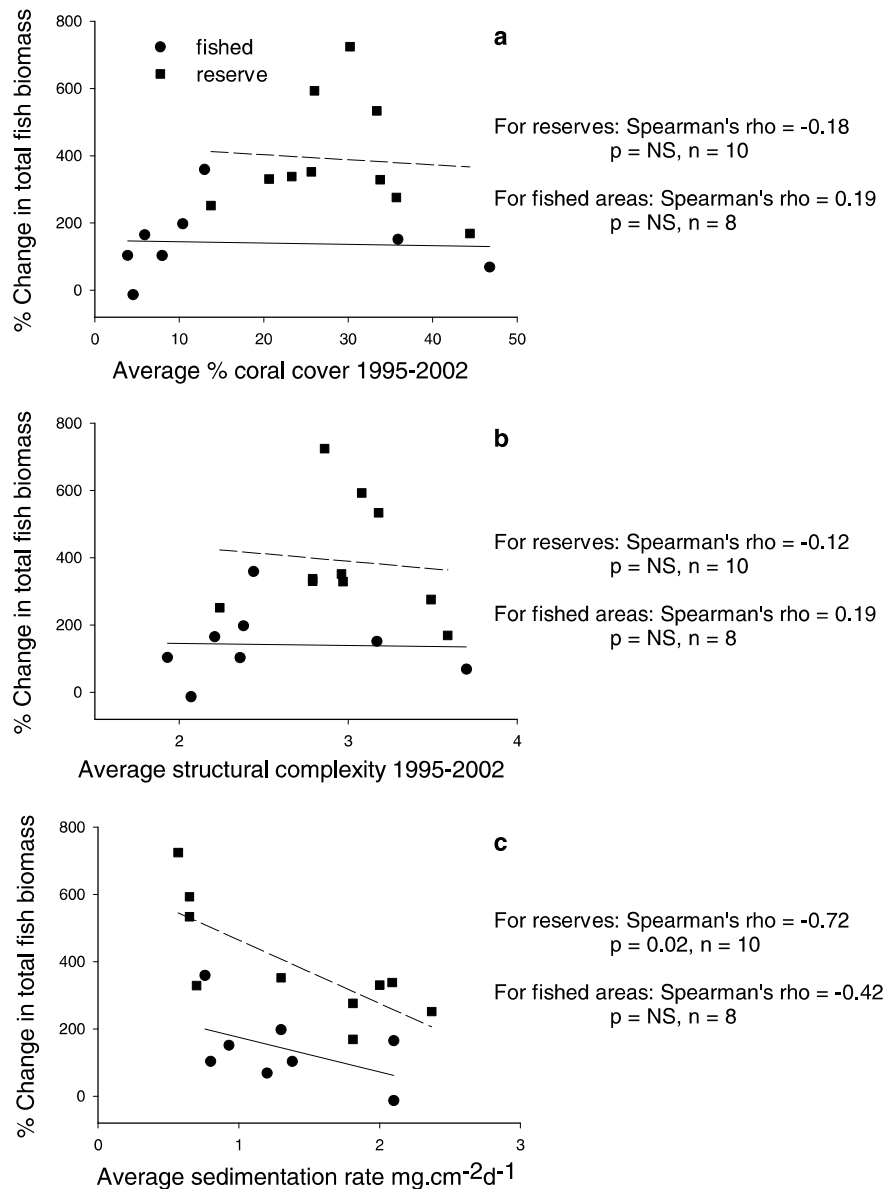


Fig. 10 – Regressions of percentage change in mean fish biomass for groupers, snappers, grunts, parrotfish and surgeonfish combined, between 1995 and 2002 vs. mean (a) hard coral cover, (b) structural complexity and (c) sedimentation rate over the same time period. Dashed lines represent regression lines for data from reserves and solid lines are regression lines for data from fished areas. Regression coefficients are shown separately for reserves and fishing grounds in each case. Note that regressions indicate rates of biomass build-up were approximately twice as great in reserves as in fishing grounds, regardless of the values for measures of habitat characteristics or pollution input.

The strength of the effect of protection from fishing we found and the weakness of habitat influences on reserve performance suggests that setting up reserves in areas with poorer quality habitats may be beneficial where protection cannot be secured for the best sites. Having said this, one problem with placing reserves in poorer habitats, such as in areas with low coral cover, is that they may be unable to support species that could recover if conditions were better. This could lessen over time if reserves improve habitat characteristics such as invertebrate cover and biomass (e.g. Carreiro-Silva and McClanahan, 2001). In reality this study, like the one by Jones et al. (2004), highlights the limitations of reserves

in holding back reef degradation. Where it differs, is by showing that despite reef degradation, reserves can still help recover a high biomass of fish.

In summary, this study shows that reserves are effective tools for increasing stocks of commercially important species. At this Caribbean site, reserve performance was not obviously related to habitat characteristics of high coral cover and complexity that are commonly used as guides in siting coral reef protected areas. However, it did appear to be adversely affected by high sedimentation rates. While reserves placed in damaged or degraded habitats can produce benefits, networks should include reserves in

areas of high quality habitat to protect a wider range of communities.

Acknowledgements

We thank the UK Natural Environmental Research Council, UK Darwin Initiative, UK Department for International Development, University of Puerto Rico Seagrant and USAID for funding this work. Thanks to Scuba St. Lucia and the Soufrière Marine Management Area for generous use of their facilities during field trips. Also special thanks to St. Lucia's Department of Fisheries, Michael and Karyn Allard, Kai Wulf and Ronnie Nicholas for supporting our work in St. Lucia.

REFERENCES

- Anderson, T.W., Sabado, B.D., 1995. Correspondence between food availability and growth of a planktivorous temperate reef fish. *Journal of Experimental Marine Biology and Ecology* 189, 65–76.
- Berkeley, S.A., Chapman, C., Sogard, S.M., 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* 85, 1258–1264.
- Bohnsack, J.A., 1998. Application of marine reserves to reef fisheries management. *Australian Journal of Ecology* 23, 298–304.
- Bohnsack, J.A., 1990. The Potential of Marine Fishery Reserves for Reef Fish Management in the US Southern Atlantic. NOAA Tech. Memo NMFS-SEFC-261. National Oceanic and Atmospheric Administration, Miami.
- Bohnsack, J.A., Bannerot, S.P., 1986. A Stationary Visual Census Technique for Quantitatively Assessing Community Structures of Coral Reef Fishes. Technical report NMFS-41. National Oceanic and Atmospheric Administration, Miami, FL.
- Bradshaw, C., Veal, L.O., Hill, A.S., Brand, A.R., 2001. The effect of scallop dredging on Irish Sea benthos: experiments using a closed area. *Hydrobiologia* 465, 129–138.
- Brown, B.E., Clarke, K.R., Warwick, R.M., 2002. Serial patterns of biodiversity change in corals across shallow reef flats in Ko Phuket, Thailand, due to the effects of local (sedimentation) and regional (climatic) perturbations. *Marine Biology* 141, 21–29.
- Carreiro-Silva, M., McClanahan, T.R., 2001. Echinoid bioerosion and herbivory on Kenyan coral reefs: the role of protection from fishing. *Journal of Experimental Marine Biology and Ecology* 262, 133–153.
- Cocklin, C., Craw, M., McAuley, I., 1998. Marine reserves in New Zealand: use rights, public attitudes and social impacts. *Coastal Management* 26, 213–231.
- Connell, S.D., 1998. Effects of predators on growth, mortality and abundance of a juvenile reef-fish: evidence from manipulations of predator and prey abundance. *Marine Ecology Progress Series* 169, 251–261.
- Côté, I.M., Mosqueira, I., Reynolds, J.D., 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *Journal of Fish Biology* 59, 178–189.
- Davidson, R.J., 2001. Changes in population parameters and behaviour of blue cod, (*Parapercis colias*: Pinguipedidae) in Long Island – Lokomohua Marine Reserve, Marlborough Sounds, New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems* 11, 417–435.
- Delaney, J.M., 2003. Community capacity building in the designation of the tortugas ecological reserve. *Gulf and Caribbean Research* 14, 163–169.
- Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology and Evolution* 18, 448–455.
- Halpern, B.S., 2003. The impact of marine reserves: do reserves work and does reserve size matter. *Ecological Applications* 13, S117–S137.
- Heslinga, G.A., Orak, O., Nigramengior, M., 1984. Coral reef sanctuaries for *Trochus* shells. *Marine Fisheries Review* 46, 73–80.
- Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nystrom, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B., Roughgarden, J., 2003. Climate change, human impacts and the resilience of coral reefs. *Science* 301, 929–933.
- 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.
- Jones, G.P., 1991. Post-recruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: Sale, P.F. (Ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, pp. 294–328.
- Jones, G.P., McCormick, M.I., Srinivasan, M., Eagle, J.V., 2004. Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Science* 101, 8251–8253.
- Kaiser, M.J., Spence, F.E., Hart, P.J.B., 2000. Fishing gear restrictions and conservation of benthic habitat complexity. *Conservation Biology* 14, 1512–1525.
- Kawasaki, H., Sano, M., Shibuno, T., 2003. The relationship between physical complexity and recruitment of the coral reef damselfish *Pomacentrus amboinensis*: an experimental study using small-scale artificial reefs. *Ichthyological Research* 50, 73–77.
- Kelly, S., 2001. Temporal variation in the movement of spiny lobster *Jasus edwardsii*. *Marine and Freshwater Research* 52, 323–331.
- Lloret, J., Planes, S., 2003. Condition, feeding and reproductive potential of white seabream *Diplodus sargus* as indicators of habitat quality and the effect of reserve protection in the northwestern Mediterranean. *Marine Ecology Progress Series* 248, 197–208.
- Lock, K., Newman, P., 2001. Skomer Marine Nature Reserve Scallop Survey 2000. Countryside Council for Wales Science Report, UK.
- McClanahan, T.R., Mangi, S., 2000. Spill-over of exploitable fishes from a marine park and its effect in the adjacent fishery. *Ecological Applications* 10, 1792–1805.
- Murawski, S.A., Brown, R., Lai, H.-L., Rago, P.J., Hendrickson, L., 2000. Large-scale closed areas as a fisheries management tool in temperate marine ecosystems: the George's Bank experience. *Bulletin of Marine Science* 66, 775–798.
- NRC (National Research Council), 2002. *Effects of Trawling and Dredging on Seafloor Habitat*. National Academy Press, Washington DC.
- Nugues, M., 2002. Impact of a coral disease outbreak on coral communities in St. Lucia: what and how much has been lost. *Marine Ecology Progress Series* 229, 61–71.
- Ratz, H.J., Lloret, J., 2003. Variation in fish condition between Atlantic cod (*Gadus morhua*) stocks, the effect on their productivity and management implications. *Fisheries Research* 60, 369–380.
- Roa, R., Bahamonde, R., 1993. Growth and expansion of an exploited population of squat lobster (*Pleuroncodes monodon*) after 3 years without harvesting. *Fisheries Research* 18, 305–319.

- Roberts, C.M., 2000. Selecting marine reserve locations: optimality versus opportunism. *Bulletin of Marine Science* 66, 581–592.
- Roberts, C.M., Ormond, R.F.G., 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Marine Ecology Progress Series* 41, 1–8.
- Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P., Goodridge, R., 2001. Effects of marine reserves on adjacent fisheries. *Science* 294, 1920–1923.
- Rodwell, L.D., Barbier, E.B., Roberts, C.M., McClanahan, T.R., 2003. The importance of habitat quality for marine reserve – fishery linkages. *Canadian Journal of Fisheries and Aquatic Science* 60, 171–181.
- Rowe, S., 2001. Movement and harvesting mortality of American lobsters (*Homarus americanus*) tagged inside and outside no-take reserves in Bonavista Bay, Newfoundland. *Canadian Journal of Fisheries and Aquatic Science* 58, 1336–1346.
- Russ, G.R., 2002. Yet another review of marine reserves as reef fishery management tools. In: Sale, P.F. (Ed.), *Coral Reef Fishes*. Academic Press, San Diego, pp. 421–443.
- Russ, G.R., Alcala, A.C., 1996. Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecological Applications* 6, 947–961.
- Sale, P.F., Cowen, R.K., Danilowicz, B.S., Jones, G.P., Kritzer, J.P., Lindeman, K.C., Planes, S., Polunin, N.V.C., Russ, G.R., Sadovy, Y.J., Steneck, R.S., 2005. Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology and Evolution* 20, 74–80.
- Shanks, A.L., Grantham, B.A., Carr, M.H., 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* 13, S159–S169.
- Shears, N.T., Babcock, R.C., 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* 132, 131–142.
- Sladek Nowlis, J., Roberts, C.M., Smith, A.H., Siirila, E., 1997. Human-enhanced impacts of a tropical storm on nearshore coral reefs. *Ambio* 26, 515–521.
- Tawake, A., Parks, J.E., Radikedike, P., Aalbersberg, B., Vuki, V., Salafsky, N., 2001. Harvesting clams and data. Involving local communities in monitoring: A case in Fiji. *Conservation Biology in Practice* 2, 32–35.
- Underwood, A.J., 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecological Applications* 4, 3–15.
- Wantiez, L., Thollot, P., Kulbicki, M., 1997. Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. *Coral Reefs* 16, 215–224.
- Wilkinson, C., 2002. Status of coral reefs of the world. Australian Institute of Marine Science, Townsville.
- Willis, T.J., Parsons, D.M., Babcock, R.C., 2001. Evidence for long-term site fidelity of snapper (*Pagrus auratus*) within a marine reserve. *New Zealand Journal of Marine and Freshwater Research* 35, 581–590.
- Willis, T.J., Millar, R.B., Babcock, R.C., Tolimieri, N., 2003. Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse. *Environmental Conservation* 30, 97–103.
- Yamasaki, A., Kuwahara, A., 1990. Preserved area to effect recovery of overfished Zuwai crabs stocks off Kyoto Prefecture. In: *Proceedings of the International Symposium on King and Tanner Crabs*, November 1989, Anchorage, Alaska, pp. 575–585.