Species-specific impacts of a small marine reserve on reef fish production and fishing productivity in the Turks and Caicos Islands

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Date submitted: 7 November 2001 Date accepted: 3 July 2002

SUMMARY

Marine reserves are widely considered to potentially benefit reef fisheries through emigration, yet the empirical basis for predicting the extent of this for small reserves is weak. The effects of fishing pressure and habitat on biomass and catch per unit effort (CPUE) of three species of exploited reef fish were studied at South Caicos, Turks and Caicos Islands. Distribution and abundance of hogfish (*Lachnolaimus maximus*) and white margate (*Haemulon album*) were inversely correlated with cover of fleshy macroalgae. Nassau grouper (*Epinephelus striatus*) were positively associated with vertical relief, but were unaffected by algal cover. Mean size, density, and biomass of hogfish were higher in a small (4 km²) marine reserve than on fished reefs, as was biomass of white margate. CPUE of hogfish was inversely related to distance from the centre of the reserve, suggesting that spillover of this species from the reserve to adjacent reefs may enhance local yields, possibly providing economic incentives for fishers to comply with reserve regulations. Fishing pressure, however, had no apparent effect on Nassau grouper. Larger fishes and those that migrate to spawn, such as economically valuable Nassau grouper, may move over too large a range to be effectively protected by small marine reserves. Small reserves may not protect all fish, but they can increase the biomass of smaller or more sedentary reef fishes and may be a useful tool for the conservation or management of species such as hogfish. Other policy options, such as seasonal spawning closures or total allowable catches, need to be considered for larger, more mobile fishes in the Turks and Caicos Islands.

Keywords: marine protected areas, catch per unit effort (CPUE), fishing pressure, Nassau grouper, spillover

INTRODUCTION

In recent years, the establishment of marine reserves closed to fishing has been promoted as a cost-effective means to protect exploited species from overfishing (Bohnsack 1993; Russ & Alcala 1996; Murray *et al.* 1999; Roberts *et al.* 2001). The potential ecological advantages of marine reserves are thought to be the maintenance of a critical spawning-stock biomass to ensure recruitment supply to fished areas, and the possible enhancement of yields in areas adjacent to the reserve via emigration of adult fish (Johnson *et al.* 1999; Roberts *et al.* 2001). Marine reserve proponents have argued that they are simple and inexpensive to monitor and enforce, thereby having cost advantages over more traditional effort- or catch-oriented fisheries management alternatives (Bohnsack 1993; Polunin & Roberts 1993).

Whether or not marine reserves achieve their ecological and economic potential depends partly on the behaviour of local fishers. If compliance is poor, reserve benefits may prove difficult to achieve because of unsustainable fishing pressure and/or escalating enforcement costs (Mascia 2000). The probability of compliance will increase in common pool resource systems when local users, who bear most of the costs of an area closure, derive direct benefits from that closure (Ostrom 1990). For many areas with limited opportunities for economic diversification, it will be critical that fishers benefit from improved fishing opportunities arising from the emigration of commercially important fishes from marine reserves if they are to be viable. Numerous studies have shown that marine reserves contain a higher abundance and/or mean size of fish than adjacent fished reefs (see Koslow *et al.* 1988; Russ & Alcala 1989, 1996; Polunin & Roberts 1993; Rakitin & Kramer 1996; Wantiez *et al.* 1997; Johnson *et al.* 1999; Tupper & Juanes 1999; Roberts *et al.* 2001), and several studies have shown an increase in catch per unit effort (CPUE) in fishing grounds adjacent to marine reserves (Alcala & Russ 1990; Bennett & Attwood 1991; McClanahan & Kaunda-Arara 1996; McClanahan & Mangi 2000; Roberts *et al.* 2001; Kelly *et al.* 2002). However, to date there is little evidence that marine reserves can increase total catches, such that the loss of fishing grounds is mitigated by increased catches outside the reserve (McClanahan & Mangi 2000).

The degree of emigration or 'spillover' from marine reserves, which should increase fishery landings and/or CPUE in adjacent fishing grounds, depends on the rate of fish migration across reserve boundaries (DeMartini 1993).

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Reef fishes are generally considered sedentary, although the scale of movement varies among species (Chapman & Kramer 1999, 2000; Meyer *et al.* 2000). Some studies have shown that many species of fish migrate considerable distances to forage (Hobson 1973; Bryant *et al.* 1989; Helfman 1993; Burke 1995) or reproduce (Shapiro 1987; Bolden 2000). In contrast, however, other research has found no emigration from reserves (Buxton & Allen 1989) or that the difference in density between fished and protected reefs was not related to species mobility (Chapman & Kramer 1999). Whether a marine reserve is a preferred policy tool will, thus, depend on species- and site-specific factors. Implementing reserves for species, or in areas, where size and/or abundance increased within the reserve but where spillover was insignificant would amplify incentives for fishers to disregard reserve regulations. At best this would be inefficient, because of the need for costly monitoring and enforcement and, at worst, ineffective for either fisheries or conservation purposes. In these situations, it is likely that other policy tools provide higher fisheries benefits than marine reserves and, thus, gain the support from fishers necessary for successful implementation.

In this research, we examine evidence for emigration of three commonly targeted fish, Nassau grouper (*Epinephelus striatus*), hogfish (*Lachnolaimus maximus*), and white margate (*Haemulon album*), from a small marine reserve near South Caicos, Turks and Caicos Islands (TCI). Nassau grouper are the preferred target for local consumption (Rudd & Tupper 2002) and fetch the highest price at dockside (up to US$ 3.50 per kg). White margate are the most commonly landed fish due to their higher relative abundance. Landing prices are typically around US$ 2.20 per kg for the smaller margate and hogfish. The rapid development of tourism on the nearby island of Providenciales has recently increased demand for reef fish and fishers may sell Nassau grouper directly to restaurants at up to US$ 15.00 per kg (Rudd & Tupper 2002). Some South Caicos fishers have begun to target grouper, as the value of the catch is often worth the expense of travelling 60 km to land the catch in Providenciales when their catch exceeds about 90 kg.

The objective of this study was to investigate the role of fishing pressure on density, size and biomass of reef fishes in and adjacent to a small marine reserve (the Admiral Cockburn Land and Sea National Park) in the TCI. In addition, we monitored CPUE of reef fish from waters adjacent to the reserve and from occasional confiscated catches within the reserve, as a function of distance from the reserve centre. The study addressed the following specific questions: (1) are spatial variations in fish density, size and biomass attributable to habitat structure or to level of protection? (2) Assuming that the efficiency of spear fishing decreases with depth, do the effects of protection differ among reefs at different depths? (3) Does CPUE of fish differ among zones of different fishing pressure? (4) Does CPUE of reef fish decrease with increasing distance from a protected area? We suggest that species-specific differences in the conservation and fisheries benefits that small marine reserves provide have important consequences for the viability of marine reserves as a conservation policy option for the TCI.

METHODS

Study sites and species

The study area was located at South Caicos, on the eastern end of the Caicos Bank, Turks and Caicos Islands (Fig. 1). The Caicos Bank is a shallow, oolitic limestone platform that rises abruptly from depths of 2000–4000 m. The platform is bordered by extensive coral reefs that are distinguished by their steep, abrupt drop-off. These shelf edge reefs typically occur at 15–20 m depth and drop almost vertically to a depth of several hundred metres. The Caicos Bank also supports extensive shallow sand flats, mangroves, seagrass beds, and shallow patch reefs.

The study area was broadly divided into three zones: (1) the Admiral Cockburn Land and Sea National Park (ACLSNP) from the south-eastern tip of South Caicos (High Point) to the south-western tip of Long Cay (SWLC). This 4 km² zone was closed in 1992 to all fishing except recreational hook and line fishing from shore, although some poaching occurs (M. Tupper, personal observation 1999). An adjacent marine reserve, the East Harbor Lobster and Conch Reserve, has an area of approximately 12 km², consisting mainly of shallow sand and algal plains. (2) The area north of the ACLSNP from High Point to Plandon Cay. This zone is only lightly fished due to rough sea conditions and the prevalence of sharks. (3) The area south of the ACLSNP from SWLC past the Fish Cays (Fig. 1), to the Ambergris Cays. Moderate fishing pressure is concentrated in this area, which is shallower and less turbulent than the windward zone north of the ACLSNP.

Within these three zones, 12 sites representing two depth strata were surveyed. The depth strata included shallow reefs 3–4 m in depth and deep reefs at approximately 15 m depth. Within each depth stratum, similar habitats were surveyed. Shallow reefs consisted of fringing reefs dominated by *Montastrea annularis* and *Acropora palmata*. Deep reefs were situated along the shelf edge and were dominated by high relief spur and groove formations, primarily consisting of *M. annularis*. At each site, per cent cover of benthic substrata was quantified along four line-intercept transects, each 10 m in length. Substrata were characterized as macroalgae (fleshy, filamentous turf, calcareous green, branching coralline or encrusting coralline), live coral, octocoral, sponge, hard substrate (dead coral, rubble, limestone pavement), and sand. In addition, maximum vertical relief and substrate rugosity were measured on each transect. Substrate complexity was estimated by fitting a fine-link brass chain to the bottom contours along the transect line. The total distance covered
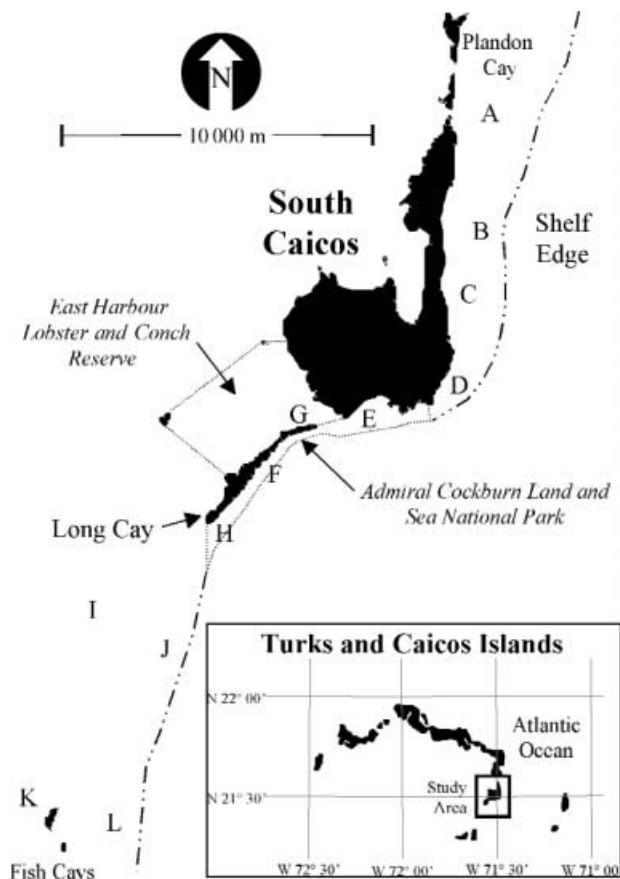
Figure 1 Admiral Cockburn Land and Sea National Park, South Caicos, Turks and Caicos Islands. Study sites include: A = Coast Guard (low fishing pressure, shallow depth); B = Catacombs (low pressure, deep); C = Horseshoe Reef (low pressure, shallow); D = Highland House (low pressure, deep); E = East Bay Spur (marine reserve, deep); F = Troy's Dream (marine reserve, deep); G = Admiral's Aquarium (marine reserve, shallow); H = South End Long Cay (marine reserve, shallow); I = Trophy Hall (high fishing pressure, shallow); J = South Slope (high pressure, deep); K = Fish Cay (high pressure, shallow); L = Fish Cay Wall (high pressure, deep).

by the chain was then divided by 10 m (the horizontal distance covered by the transect line), producing an index of substrate rugosity (Tupper & Boutilier 1997).

Census technique

In order to compare our results to those of previous studies in other regions, we replicated the survey methods used by Sluka *et al.* (1996*a*) and Chiappone *et al.* (2000). At each site, abundance and total length (to the nearest cm) of target fish species were visually estimated along ten haphazardly placed transects measuring 20 m × 5 m. Observers were trained in transect width estimation prior to conducting surveys; transect width estimation was conducted according to Sluka *et al.* (1996*a*). Observers were also trained to estimate total length of fishes by visually estimating the size of fish models to the

nearest centimetre (see Sluka *et al.* 1996*a*). Observers were not permitted on research dives until their size estimations of models were within 5% of the actual value. For each transect, biomass of individual species was estimated from numbers and lengths of fish using published length-weight relationships (Froese & Pauly 2001). The biomass for each species was then summed to arrive at an estimate of total fish biomass for the transect.

Dockside monitoring

All fishers interviewed in this study used similar gear, namely a Hawaiian sling. Fishers were interviewed upon their return to processing plants to unload their catch. Each fisher was asked where they had fished that day and how many hours they had spent fishing as opposed to travelling between sites. Where multiple fishers occupied one boat, hours spent fishing was recorded for each individual. Sites visited were categorized as being either north or south of the reserve as described above. Since fishers must make the decision to travel north or south early in the morning, depending on weather and sea conditions, each boat fished only one zone per day.

After interviewing all persons aboard the boat, the interviewer examined the catch. All fish were identified to species level, measured to the nearest cm fork length (FL) and weighed to the nearest g using an electronic scale. Fish larger than 10 kg were weighed to the nearest 0.5 kg using a hand-held spring scale. Since fishing pressure was expected to influence both size and abundance of exploited fishes, CPUE was calculated as both the number of fish caught per fisher per hour and the weight of fish per fisher per hour. Both measures of CPUE were calculated for hogfish, Nassau grouper and white margate individually.

Statistical analysis

Data were tested for normality of distribution using the Wilke-Shapiro test (Sokal & Rohlf 1995) and homogeneity of variance using Levene's test (Zar 1999). For each species and for combined species data, density, fork length, and biomass were non-normally distributed and variances were heterogeneous. Following log (x + 1) transformation, data were retested and found to meet the assumptions of parametric analysis of variance (ANOVA). Density, fork length, and biomass were then analysed using a two-way ANOVA. The fixed factors were level of protection (lightly-fished northern zone, ACLSNP, and fished southern zone) and depth (shallow fringing reefs versus deep shelf-edge reefs). Tukey's HSD (honestly significant difference) was used as a post-hoc multiple comparison test. For each of the three study species, least squares regressions of biomass against the measured habitat variables were conducted to determine the effects of habitat characteristics on fish distribution.

For all species, CPUE was square root transformed after adding a constant of 0.5 to account for zero catch data

(Johnson *et al.* 1999). Transformed CPUE data met the assumptions of parametric analysis and were compared among zones using one-way analysis of variance (ANOVA). Data on the distance from reserve centre was non-normal despite monotonic transformations. Spearman rank correlations were therefore used to determine the relationship between CPUE and distance from the reserve centre. Correlations were conducted for pooled data and separately for distance north and south of the reserve centre.

RESULTS

Effects of habitat, depth and fishing pressure

The two-way ANOVAs comparing habitat characteristics between different depths and zones of fishing pressure indicate there were differences among zones of fishing pressure and/or depths for all substrates except sponge, crustose coralline algae and sand (Table 1). Post-hoc comparisons revealed that fleshy algal cover (primarily brown algae of the genera *Sargassum*, *Dictyota*, *Turbinaria* and *Lobophora*) was significantly higher in the fished southern zone than elsewhere (Tukey's HSD, $p < 0.05$) and was also higher on shallow reefs than on deep reefs (Tukey's HSD, $p < 0.05$). Cover of filamentous algal turf was higher in the ACLSNP than outside (Tukey's HSD, $p < 0.05$). Cover of calcareous green algae was lower in the fished zone than in the ACLSNP or the lightly-fished zone (Tukey's HSD, $p < 0.05$). Branching coralline algae were more common in the lightly-fished zone than elsewhere (Tukey's HSD, $p < 0.05$). Both stony coral and octocoral cover were higher within the ACLSNP than outside (Tukey's HSD, $p < 0.05$). The coverage of hard substrate was lower within the ACLSNP than in either fished area (Tukey's HSD, $p < 0.05$). Topographic complexity and vertical relief were both higher on the northern windward reefs than in the ACLSNP or the southern zone (Tukey's HSD, $p < 0.05$), and vertical relief of deep reefs was higher than that of shallow reefs in all zones (Table 1).

Fishing pressure and depth had a marked influence on fish length, density and biomass of hogfish and white margate, while Nassau grouper were unaffected by fishing pressure (Table 2). Length, density, and biomass of hogfish were all significantly higher on deeper reefs. Density of Nassau grouper was higher on deeper reefs, although their length did not differ between depths (Table 2). Density of white margate was higher on shallow reefs, but their mean length was greater on deeper reefs. Length, density and biomass of hogfish were all significantly lower in the fished zone, but did not differ between the reserve and the lightly-fished zone (Tukey's HSD, $p > 0.05$ for all comparisons). The significant interaction effects shown in Table 2 result from lower mean length and biomass on deep reefs in the fished zone than on shallow reefs in the lightly-fished and protected zones (Tukey's HSD, $p < 0.05$). Length of white margate did not vary with fishing pressure. Density of white margate was greater in the reserve than in the fished zone (Tukey's HSD, $p < 0.05$). Biomass of white margate was significantly lower in the fished zone than the lightly-fished or protected zones (Tukey's HSD, $p < 0.05$) but did not differ with depth (Table 2).

Least squares regression indicated that fleshy algal cover had a weak but significant negative effect on the biomass of hogfish on both shallow ($r^2 = 0.24$, $p < 0.05$) and deep ($r^2 = 0.22$, $p < 0.05$) reefs. Similarly, biomass of white margate was inversely related to the cover of fleshy algae on both shallow ($r^2 = 0.29$, $p < 0.01$) and deep ($r^2 = 0.32$, $p < 0.001$) reefs. Nassau grouper was unaffected by fleshy algal cover, but showed a weak positive association with vertical relief on both shallow ($r^2 = 0.30$, $p < 0.001$) and deep ($r^2 = 0.34$, $p < 0.001$) reefs.

Dockside monitoring

Over the course of this study, local government fishery officers caught three poachers and confiscated their catch. This represented approximately five hours of effort (Table 3). Although the sample size of catches from the reserve is low, the opportunity to sample illegal catches from protected areas is rare and so the data have been included in this analysis. For hogfish, Nassau grouper and the total catch, CPUE was much lower (half or less) in the fished zone than in the lightly-fished or protected zones but did not differ between the latter two zones (Tukey's HSD, $p < 0.05$ for all comparisons). Only white margate had a lower CPUE within the ACLSNP than outside, but it also supported a higher CPUE in the lightly-fished than the fished zone. It should be noted that, when questioned, two of three poachers indicated that they were specifically targeting hogfish and Nassau grouper. Thus the CPUE of margate within the ACLSNP may not reflect its actual distribution.

CPUE of hogfish decreased with increasing distance from the reserve and with increasing distance across both the southern and northern boundaries (Table 4). No relationships were found between CPUE of Nassau grouper or CPUE of the total catch and distance from the reserve centre. CPUE of white margate was not related to distance in general or distance across the southern boundary, but increased with distance across the northern boundary (Table 4).

DISCUSSION

Influence of habitat

The most noticeable difference in habitat among the three zones of fishing intensity was the much greater coverage of fleshy macroalgae in the fished zone. The higher coverage of fleshy macroalgae on the reefs in the southern zone was partially a result of past storm damage (M. Tupper, unpublished data 2000), but to some extent it may also have stemmed from coral death due to destructive fishing methods, particularly the widespread, intensive use of

Table 1 Two–way ANOVAs comparing benthic habitat variables between deep and shallow reefs at varying levels of protection from fishing. NS = not statistically significant at Bonferroni adjusted α (0.01).

| Benthic substratum (% cover) | Means (± 1 standard deviation) | | | | | | Two-way ANOVA | | | | | |
| | ACLSNP | | Lightly fished | | Fished | | Protection | | Depth | | Interaction | |
	Deep	Shallow	Deep	Shallow	Deep	Shallow	F	p	F	p	F	p
Fleshy algae	10.9 ± 6.2	12.2 ± 5.9	12.4 ± 7.3	14.1 ± 9.2	27.4 ± 16.3	39.6 ± 12.9	33.1	<0.001	18.2	<0.01	2.4	NS
Filamentous (turf) algae	7.2 ± 2.2	7.4 ± 4.4	6.3 ± 4.3	6.5 ± 5.4	6.7 ± 4.6	6.0 ± 2.1	12.4	<0.01	3.3	NS	5.1	NS
Calcareous green algae	3.6 ± 2.1	2.8 ± 1.6	2.4 ± 1.8	3.2 ± 1.9	1.6 ± 1.2	1.4 ± 1.1	9.1	<0.01	2.1	NS	2.0	NS
Branching coralline algae	1.3 ± 0.9	1.1 ± 1.7	1.1 ± 1.3	1.5 ± 1.6	0.4 ± 0.3	0.6 ± 0.5	12.7	<0.01	3.1	NS	2.3	NS
Crustose coralline algae	5.2 ± 3.3	5.1 ± 3.7	4.6 ± 2.8	4.3 ± 4.9	4.8 ± 3.6	4.1 ± 2.5	3.4	NS	2.8	NS	1.8	NS
Stony coral (live)	35.1 ± 12.2	38.7 ± 12.0	24.3 ± 10.0	25.4 ± 9.8	22.4 ± 8.3	24.4 ± 12.9	39.3	<0.001	2.7	NS	1.3	NS
Octocoral	5.8 ± 1.4	6.4 ± 2.1	6.7 ± 2.7	2.3 ± 1.3	3.7 ± 1.8	2.0 ± 1.7	16.0	<0.001	15.3	<0.001	9.5	<0.01
Sponge	2.4 ± 1.1	1.2 ± 0.8	2.0 ± 1.5	0.9 ± 1.0	1.5 ± 0.7	0.7 ± 0.7	2.5	NS	16.2	<0.001	1.2	NS
Hard bottom	58.7 ± 8.6	51.7 ± 7.7	68.9 ± 9.0	64.0 ± 8.9	56.8 ± 9.9	63.8 ± 8.7	8.8	<0.01	1.3	NS	1.1	NS
Sand	8.2 ± 5.7	7.6 ± 7.7	8.7 ± 7.6	6.4 ± 5.5	7.2 ± 6.6	7.7 ± 6.2	2.0	NS	1.8	NS	1.9	NS
Topographic complexity	2.5 ± 0.9	2.6 ± 0.8	3.2 ± 0.7	3.1 ± 0.8	3.1 ± 1.0	2.6 ± 0.8	7.1	<0.01	2.6	NS	2.7	NS
Vertical relief (cm)	106.4 ± 23.3	66.8 ± 6.7	154.8 ± 47.9	124.9 ± 36.7	114.5 ± 33.6	81.9 ± 31.0	14.3	<0.001	15.9	<0.001	1.1	NS

Table 2 Two–way ANOVA comparing the influence of depth and level of protection on total length (cm), density (individuals per 100 m^2), and biomass (g wet wt per 100 m^2) of commonly-exploited reef fishes in the Turks and Caicos Islands. NS = not statistically significant at Bonferroni adjusted α (0.01).

| | Means (± 1 standard deviation) | | | | | | Two-way ANOVA | | | | | |
| | Reserve | | Lightly fished | | Fished | | Protection | | Depth | | Interaction | |
	Deep	Shallow	Deep	Shallow	Deep	Shallow	F	p	F	p	F	p
Nassau grouper												
Length	62 ± 9.5	61 ± 12.8	57 ± 13.8	59 ± 5.7	61 ± 6.5	58 ± 14.5	1.2	NS	1.4	NS	1.4	NS
Density	0.61 ± 0.3	0.55 ± 0.5	0.90 ± 0.4	0.65 ± 0.5	0.65 ± 0.4	0.45 ± 0.4	1.9	NS	9.8	<0.01	1.5	NS
Biomass	3660 ± 1619	3300 ± 1217	4895 ± 764	3535 ± 570	3900 ± 1261	2448 ± 1243	1.3	NS	11.7	<0.01	1.0	NS
Hogfish												
Length	31 ± 7.2	24 ± 8.3	32 ± 7.8	25 ± 8.8	24 ± 8.6	21 ± 7.6	148.1	<0.001	35.2	<0.001	5.7	<0.01
Density	1.9 ± 1.2	1.1 ± 0.2	1.1 ± 0.9	0.7 ± 0.4	0.3 ± 0.2	0.2 ± 0.1	44.0	<0.001	31.5	<0.001	1.5	NS
Biomass	728 ± 478	177 ± 61	421 ± 279	121 ± 79	48.4 ± 19	32 ± 15	30.0	<0.001	74.9	<0.001	8.3	<0.01
White margate												
Length	28 ± 5.5	26 ± 6.2	30 ± 5.2	24 ± 4.4	30 ± 6.1	26 ± 6.2	0.6	NS	12.8	<0.001	1.2	NS
Density	9.3 ± 2.0	20.3 ± 4.7	10.0 ± 1.4	10.7 ± 2.5	2.6 ± 0.6	4.6 ± 2.2	10.3	<0.01	5.8	<0.01	1.7	NS
Biomass	2922 ± 1369	6378 ± 1992	3142 ± 1676	1726 ± 450	817 ± 337	742 ± 189	22.2	<0.001	1.2	NS	1.5	NS

Table 3 One-way ANOVAs of catch per unit effort (CPUE) for commonly exploited reef fishes of the Turks & Caicos Islands. NS = not statistically significant.

Level of protection	Fishers interviewed	Hours fished	CPUE (kg hr⁻¹ person⁻¹)			
			Nassau grouper	Hogfish	White margate	Total catch
Reserve	3	5	0.5 ± 0.6	9.1 ± 2.4	0.2 ± 0.4	17.9 ± 6.2
Lightly fished	28	98	0.4 ± 0.6	8.2 ± 3.1	3.2 ± 2.0	17.8 ± 6.8
Fished	113	456	0.7 ± 0.9	0.8 ± 0.8	0.7 ± 0.4	3.2 ± 2.1
One-way ANOVA			$F = 1.3$ NS	$F = 50.0$ $p < 0.001$	$F = 16.3$ $p < 0.001$	$F = 29.5$ $p < 0.001$

chlorine and detergents to drive spiny lobster from their shelter sites (W. Clerveaux, Turks and Caicos Department of Environment and Coastal Resources, personal communication 1999). In addition to having the highest coverage of algae, the shallow southern reefs suffered the highest fishing pressure and supported the lowest density and biomass of hogfish and white margate. It is difficult to separate the effects of fleshy algal cover and fishing pressure on the biomass of hogfish and white margate. McClanahan *et al.* (2000, 2001) determined that benthic habitat structure had a greater effect than management (i.e. control of fishing pressure) on abundance of herbivorous reef fish in Belize. They reported increases in abundance of six fish species, including four herbivorous species and two species that fed primarily on invertebrates, following experimental reductions of fleshy macroalgal cover on patch reefs. In our study, however, the large differences in density and biomass of hogfish and white margate between the fished zone and reserve, coupled with strong, bidirectional spillover of hogfish from the marine reserve, suggest that fishing pressure was an important factor in determining the distribution and abundance of these two species. Furthermore, neither species exhibited an affiliation for substrates such as live coral or turf algae, the coverage of which might be reduced by fleshy algal growth (Hughes 1994). Since both species feed primarily on infaunal invertebrates in sandy bottoms, rather than foraging on the reef (Humann 1994), it seems likely that fleshy algal cover would have a lesser effect on their distribution in comparison to herbivorous species or species that feed on reef-associated invertebrates.

The highest per cent cover of live stony coral and octocoral occurred within the ACLSNP, but this is probably not a function of protective management. Rather, the site of the ACLSNP was chosen based on the health of its reefs (which are visited regularly by live-aboard dive boat operations), queen conch spawning habitat and adjacent inshore conch and lobster nursery grounds. Regardless, the higher coral cover within the reserve had no effect on the density or biomass of the three study species, none of which were associated with live coral cover.

A previous study at South Caicos (Tupper 2002) found no differences in Nassau grouper abundance in a variety of habitat types (channel reefs, fringing reefs, patch reefs and shelf edge reefs). Similarly, Sluka *et al.* (1996*b*, 1997) found no habitat associations for Nassau grouper in the Exuma

Table 4 Spearman rank correlations of the catch per unit effort (CPUE, kg fisher⁻¹ hr⁻¹) versus distance from the centre of the Admiral Cockburn Land and Sea National Park (ACLSNP). Data are presented for overall distance, distance north from the ACLSNP centre (towards the lightly-fished zone) and distance south from the ACLSNP centre (towards the fished zone). NS = not statistically significant at Bonferroni adjusted α (0.005).

Direction	Species	Spearman R	p
North and south	Nassau grouper	0.13	NS
	Hogfish	−0.41	<0.001
	White margate	0.07	NS
	Total catch	0.06	NS
North only	Nassau grouper	0.09	NS
	Hogfish	−0.39	<0.001
	White margate	0.62	<0.001
	Total catch	0.06	NS
South only	Nassau grouper	0.19	NS
	Hogfish	−0.47	<0.001
	White margate	−0.20	NS
	Total catch	−0.22	NS

Cays. The results of this study support previous studies on Nassau grouper that suggest it may be more important to protect reefs in general than to attempt to protect 'optimal' grouper habitat from fishing (Sluka *et al.* 1996*a*, *b*; Tupper 2002).

Influence of depth and fishing pressure

In general, fish were larger and more abundant on deeper (15–20 m) reefs than shallow (3–4 m) reefs. However, the lack of significant interactions between depth and fishing pressure suggest that response to fishing pressure does not vary with depth over the range of depths. While depth may afford some protection from spear fishing in the form of reduced harvesting efficiency, it is perhaps more likely that these species move to deeper water as they grow (Appeldoorn *et al.* 1997). In the case of Nassau grouper, no differences in size, abundance or biomass were found between zones of different fishing intensity (see below), so fishing intensity would not explain the greater abundance and biomass on deeper reefs.

For two of the three species in this study, fishing pressure appeared to have a significant influence on fish populations. Hogfish were smaller and less abundant where fishing was

most intense, and biomass of white margate was higher inside the ACLSNP than outside. Moreover, CPUE of hogfish declined with increasing distance from the marine protected area (MPA) centre. This suggests that spillover from the ACLSNP can enhance local fishery yields outside its boundaries.

The presence of the South Caicos marine reserve, however, appeared to have no impact on the distribution and abundance of Nassau grouper in this study. In contrast, Sluka *et al.* (1996*a*) found higher density of Nassau grouper in the protected Exuma Cays Land and Sea National Park than on fished reefs outside the Park. Why would the MPA have an impact on white margate and hogfish, but not Nassau grouper? It is possible that the size of the reserve relative to home range of the fishes plays an important role in the results.

Despite a recent increase in research effort (Holland *et al.* 1993, 1996; Samoilys 1997; Zeller 1997; Chapman & Kramer 1999, 2000; Meyer *et al.* 2000), little is known of the specific movements or home range size of exploited coral reef fishes (Kramer & Chapman 1999). In general, it is understood that the longer the time spent outside the reserve, the more vulnerable fish become to fishing mortality (Kramer & Chapman 1999) and that the extent of home range is most strongly influenced by body size. Large and schooling species have larger home range sizes (Samoilys 1997; Zeller 1997) and tend to move further than small or solitary species. Larger fishes such as grouper are therefore more likely to cross reserve boundaries, while smaller species may spend all their time within MPA boundaries (Holland *et al.* 1993, 1996; Meyer *et al.* 2000).

The home range of Nassau grouper has been studied by Bolden (2002) in the Exuma Cays. She found that a 60 cm FL grouper (a typical adult size at South Caicos) had a home range area of approximately 18 000 m^2. In contrast, the area covered by the ACLSNP is only 4 km^2 (slightly larger when considering suitable habitat within the adjoining East Harbour Lobster and Conch Reserve). Home range sizes of hogfish and white margate are currently unknown, but Kramer & Chapman (1999) analysed the relationship between body size and home range size for 29 species of reef fish, including members of the families Labridae and Haemulidae. By pooling data for these species they determined that home range area in m^2 increased with the 3.53 power of body length in mm. Assuming an average fork length of about 250 mm for both hogfish and white margate, these regressions result in home range areas of 600 m^2 for the two smaller species. These are obviously rough estimates, taken from a conglomerate picture of other species. However, it is apparent that the home range of adult Nassau grouper is markedly larger than the ACLSNP, while hogfish and white margate probably have home ranges smaller than the protected area. Nassau grouper density was higher in the Exuma Cays Land and Sea Park (ECLSP) than in surrounding fished areas (Sluka *et al.* 1996*a*), but the area covered by the ECLSP is 442 km^2. Thus, the differences in

response to protection may relate to the home-range size of reef fish relative to the size of the marine reserve.

The lack of a measurable protective effect on Nassau grouper may also stem from its long-distance spawning migration. Nassau grouper may travel tens to hundreds of km to participate in spawning aggregations (Bolden 2000). Nassau grouper from South Caicos travel approximately 40 km to a large spawning aggregation at Phillips Reef, off the island of East Caicos around the full moon in January (T. Morris, personal communication 1999; M. Tupper, personal observations 2000). However, the aggregation is rarely fished due its remote location and rough seas, making it unlikely that fishing mortality outside the reserve during the spawning migration is a factor.

Finally, the failure of the ACLSNP to enhance grouper biomass within its boundaries may have been exacerbated by poaching. Poaching appeared to be a relatively rare occurrence over the course of this study (1999–2000). However, poachers may have operated at night and on Sundays and holidays, when enforcement officers were inactive.

Management implications

The ACLSNP may not be large enough to protect effectively large reef fishes such as the Nassau grouper, which have large home ranges and/or undergo seasonal spawning migrations. However, even at fairly low levels of fishing pressure, smaller, more sedentary species, such as hogfish and white margate can apparently benefit from small marine reserves (see Kramer & Chapman 1999; Meyer *et al.* 2000). The effectiveness of the small reserve in increasing fish size, biomass and emigration suggests that local fishers derive some economic benefits from the ACLSNP. It is not clear, however, if the economic benefits from spillover exceed the opportunity cost of closing the area.

The lack of protection provided to Nassau grouper by small marine reserves is disturbing. Small marine reserves are functionally the only control on fishing pressure for inherently vulnerable Nassau groupers throughout much of their range (see Chiappone *et al.* 2000; Tupper 2002). If the reserves are ineffective, the fishery operates under *de facto* open access: there are no annual fisheries landing limits, individual trip limits, size regulations, or gear limitations outside of these reserves. In addition, Nassau grouper has nonextractive economic value for the dive tourism industry (Rudd & Tupper 2002). Depletion of stocks could impose economic costs on the dive industry because divers' willingness to pay for dive charters (or MPA entry fees) decreases as grouper size and abundance decrease.

If the ACLSNP is ineffective for Nassau grouper conservation purposes because of its small size, what policy options exist that might protect Nassau grouper stocks around South Caicos? An obvious option would be to increase the size of the ACLSNP, to encompass an area that provides adequate protection for small and large reef fish. The likelihood of fishers and government adopting this option is low, however,

because a larger no-take reserve close to South Caicos would impose high opportunity costs on lobster fishers. A larger reserve would close important lobster fishing grounds adjacent to South Caicos and south to Fish Cays, and could become very difficult to monitor and enforce.

Another option would be implementation of a seasonal closure on spawning grounds where Nassau grouper are known to aggregate. Closures of grouper (predominantly red hind, *Epinephelus guttatus*) spawning aggregation sites have been successfully implemented in the US Virgin Islands (Beets & Friedlander 1999). However, recent research indicates that Nassau grouper spawning aggregations may exhibit plasticity in timing and location, such that an aggregation which occurs at a certain time or place in one year may be shifted by several hundred metres to a few kilometres another year, or may occur one or two months earlier or later (M. Tupper, unpublished data 2000). If a closure is implemented at a given spawning site or for a particular period, there is a chance that in subsequent years, the spawning aggregation may occur outside the spatial or temporal boundaries of the closure. Thus, seasonal spawning closures might have to be several months in length (for example, November through March) in order to be effective.

The use of catch controls, especially setting an appropriate total allowable catch (TAC), possibly in conjunction with seasonal closures during the spawning season, seems to hold more promise. A conservative TAC could have pragmatic advantages over other options: local fishers would maintain access to fishing grounds for lobster and reef fishes other than Nassau grouper and enforcement efforts might focus on shore-based restaurant buyers, reducing more expensive field enforcement costs. A further analysis would be required to fully understand the incentives of various stakeholders and the likelihood of various policy measures successfully protecting Nassau grouper stocks in the TCI.

In conclusion, the small marine reserve near South Caicos appears to provide effective protection for the small reef fishes, white margate and hogfish. Our results are confounded somewhat by the overgrowth of fleshy macroalgae in the fished zone, which negatively affected the abundance of these species. An inverse relationship between distance from the centre of the reserve and CPUE for hogfish also strongly suggests spillover of commercial fish from the reserve. The lack of difference in size and abundance of Nassau grouper inside and outside the reserve, however, illustrates the need to consider site- and species-specific factors in policy design. Given the ecological, cultural and institutional context in which South Caicos fishers operate, marine reserves are unlikely to provide sufficient protection for Nassau grouper as fishing pressure continues to increase. Conservation of this species may require stronger state regulation and traditional fisheries management tools such as seasonal spawning closures and conservative TACs.

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