Effects of fishing on sex-changing Caribbean parrotfishes

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Abstract

We studied parrotfish (Scaridae) assemblages on coral reefs in relation to fishing pressure around six Caribbean islands. Fishing intensity ranged from virtually none in Bonaire, and increased through Saba, Puerto Rico, St Lucia and Dominica to extremely high levels in Jamaica. In St Lucia we also compared parrotfish assemblages between fishing grounds and fully protected marine reserves, from 1995, 6 months prior to establishment, to 2001. Within each country we performed replicate counts of the number and size of all parrotfish species within, or passing through our counting area. From these data we calculated biomass for seven species. Biomass of the two largest species, *Sparisoma viride* and *Scarus vetula,* was greatest in islands with low fishing pressure ($P < 0.001$). By contrast, smaller species constituted an increasing proportion of the total parrotfish assemblage as fishing pressure increased ($P < 0.001$ in all cases). Parrotfish are protogynous hermaphrodites with two distinct colour phases. The initial phase is predominantly female, and the terminal phase exclusive to sexually mature males. The average size of all species except *Sc. vetula* tended to decrease with increasing fishing pressure. Furthermore, percentages of fish that were terminal phase males showed order of magnitude declines with increasing fishing pressure for *Sp. viride* and *Sc. vetula*. Terminal males of these species were absent from counts in Jamaica and virtually absent from Dominica suggesting that persistence of these populations may depend on recruitment from distant sources. Following reserve implementation in St Lucia, all species, except uncommon *Sp. chrysopterum*, increased in mean biomass ($P < 0.001$ in all cases). In 6 years the total biomass for all species combined increased to become nearly four times as high in reserves and almost twice as high in fishing grounds [$P < 0.001$ (year effect); $P < 0.001$ (protection effect); $P < 0.001$ (year×protection)], and mean size of five species increased significantly in both reserves and fishing grounds.
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1. Introduction

Exploited fisheries provide insights into how human, biological and physical perturbations can affect life history, rates of population increase, population persistence and community composition of affected species (Hutchings, 2000). For example, fishing has been held partly responsible for decreasing the age of sexual maturity in North Sea plaice (*Pleuronectes platessa*; Rijnsdorp, 1989), Northeast Arctic cod (Jørgensen, 1990) and Norwegian herring (Toresen, 1986). It has also been implicated in causing a decline in body weight of Pacific pink salmon (*Oncorhynchus gorbuscha*). Ricker (1981) explains the latter by suggesting that size selective fishing gear favours a greater survival of smaller individuals, while

for Northeast Arctic cod, fishing may have had indirect effects on the cod's food source (Law, 2000). By reducing stock biomass fishing could result in more food for survivors allowing them to grow faster and mature earlier (Godø and Moksness, 1987). By contrast Buxton (1993) found that in South Africa, growth rates of the sparid fish *Chrysoblephus cristiceps* were slower in fishing grounds than in a nearby marine reserve, while those of *Chrysoblephus laticeps* were the same in both.

Fishing can act at the evolutionary level through selection on genetic variation in phenotypic traits (Law, 2000), or invoke phenotypic plasticity alone (Reznick, 1993). If ecological or evolutionary changes do occur the results may prove difficult to reverse (Law, 2000; Trexler and Travis, 2000). For example, at the population level fishing may eliminate behavioral traits transferred through generations by larger, older fish which are most susceptible to being caught. This has been demonstrated in Norwegian herring, where migration

patterns were disrupted then never re-established after stocks collapsed in the late 1960s (Dragesund et al., 1980).

Recent laboratory work on Atlantic silverside (*Menidia menidia*) by Conover and Munch (2002) has shown that fishing can have swift effects at the evolutionary level. By experimentally removing 90% of the largest individuals, 90% of the smallest, or taking a random selection of fish, they showed that in only four generations the average biomass of those left to spawn was six times lower when big fish had been removed compared to small. Hence it appears that by targeting large individuals fishing could exert evolutionary pressure for fish to be smaller and grow slower. In the spiny lobster (*Panulirus argus*), orange roughy (*Hoplostethus atlanticus*) and North sea plaice, genetic responses to fishing pressure have increased individual fecundity, although not compensated for reduced reproductive output at the population level caused by over-fishing (Rijnsdorp et al., 1991; Jennings et al., 2001). Where fishing reduces the average size of individuals this will lower population reproductive output since bigger fish produce many times more eggs than smaller ones (Bohnsack, 1990).

Fishing may also lower recruitment by preventing fish from living long enough to survive through periods when conditions are poor for offspring survival. Recruitment rates are highly variable (Jones, 1991) but in populations with an extended age structure there are always likely to be some sexually mature fish spawning when conditions are good for recruitment. However, if fishing reduces the number of mature age classes, individuals may not survive long enough to ever encounter favorable conditions. This could be particularly problematic for long lived, late maturing species. For example, fishing has seriously depleted rockfish (Scorpaenidae) populations along the west coast of North America (Sadovy, 2001). Some of these species can live over a hundred years (Andrews et al., 2001) and not reproduce until their late teens (Kelly et al., 1999).

Birkeland and Friedlander (2001) warn that fishing can be particularly problematic for species such as moi (*Polydactylus sexfilis*), where the sexes are sized differently. In Hawaii, overfishing has so reduced numbers of the larger females that most moi are now male or immature juveniles and their average size is 5 cm less than it was in the 1960s. Such changes greatly reduce reproductive potential.

Species which change sex are likely to be very sensitive to over-fishing, since in order to do this, individuals must first attain some minimum size (Francis, 1992). If fishing prevents individuals from growing large enough to undergo sex change, it could result in populations becoming non-reproductive, unless species can compensate by changing sex earlier. If fish are inflexible in the size at which they change sex, or are limited by some minimum size, species could disappear from heavily fished areas unless recruitment continues from elsewhere. Studies of how fishing affects sex ratios in sequential hermaphrodites have revealed declines in the proportion of males (Buxton, 1993; Coleman et al., 1996; McGovern et al., 1998).

In this study we examine how fishing affects seven species of Caribbean parrotfish (Scaridae) from two different sub-families (Scarinae and Sparisomatinae). All are sequential hermaphrodites in which females can change into males. Depending on the species they can do this before or after maturity (Robertson and Warner, 1978). Females from the genus *Scarus* (Scarinae) will always turn into males if they live long enough, but they cannot change sex before they are sexually mature (Robertson and Warner, 1978). In the genus *Sparisoma* (Sparisomatinae), some females do not appear to change sex no matter how big they grow but a small proportion turn into males before reaching sexual maturity (Robertson and Warner, 1978). Amongst Caribbean parrotfish, all Sparisomatinae are born female whereas some Scarinae are born male, although this pattern does not hold outside the Caribbean (Choat and Robertson, 1995). Fish born male are known as primary males, whilst fish that have changed sex are called secondary males. There is no evidence that any species of parrotfish can undergo a sex change reversal.

Most species of parrotfish exhibit at least two distinct color phases, known as initial and terminal colouration and some also have a characteristic juvenile pattern. Both primary and secondary males must pass through initial phase colouration before attaining the terminal phase (Robertson and Warner, 1978). In the Sparisomatinae, terminal phase colouration is exclusive to sexually mature males, but fish showing initial phase colouration can be female or male and either immature or mature. Van Rooij et al. (1996a) report that more than 90% of initial phase *Sparisoma viride* in Bonaire are female, and there is a broad size range over which these fish can change into terminal males. Initial phase males rarely spawn, and terminal males will chase them from their territories (van Rooij et al., 1996a). No mature male Scarinae have initial colouration (Robertson and Warner, 1978).

Parrotfishes have complex social behaviours. Three Caribbean species, *Sp. viride* (van Rooij et al., 1996a), *Scarus iserti* (Ogden and Buckman, 1973) and *Sparisoma aurofrenatum* (Clavijo, 1982) are known to hold territories in which a single terminal male co-exists with several females. Such territories appear to benefit both feeding and reproduction (van Rooij et al., 1996b). Fertilization occurs externally in parrotfishes and there is no parental care. In *Sp. viride*, resident males within single-male territories usually make daily spawnings with resident females (van Rooij et al., 1996a). Since territories of bigger males contained more females, male size appears important to reproductive success.

Sp. viride and *Sc. iserti* also hold territories in multi-male groups and for *Sp. viride* in Bonaire these may contain up to 14 terminal phase males and about twice as many females (van Rooij et al., 1996a). In both types of territory females assisted with defence (van Rooij et al., 1996a). *Sp. viride* from multi-male groups do not mate inside their territory. Instead, the largest males from multi-male groups fiercely defend temporary spawning sites at depths below 30 m (van Rooij et al., 1996a). Such behaviour has also been reported in *Sparisoma rubripinne* which do not hold feeding territories (Robertson and Warner, 1978). In *Sp. viride*, males defending deep water spawning sites have the highest mating rates.

Mating strategies appear to be spatially variable in parrotfish. For example, in the Virgin Islands and Puerto Rico, *Sc. iserti* don't hold territories, and usually mate in pairs at deep water spawning sites (Randall and Randall, 1963; Barlow, 1975). In Jamaica this species exhibited similar foraging strategies to those shown in the Virgin Islands and Puerto Rico but mating occurred in groups (Colin, 1978). *Sp. rubripinne* exhibits group spawning at predictable sites in the Virgin Islands (Colin, 1978), but not in Panama (Robertson and Warner, 1978). Such complexity suggests that parrotfish are highly adaptable and can change their social strategies in response to factors such as population density and resource availability (Thresher, 1984).

In this study we examine five predictions about how fishing pressure could affect parrotfish assemblages and test them using two approaches. The first compares coral reefs among six Caribbean islands subjected to very different levels of fishing pressure, while the second compares fished areas within marine reserves in the island of St Lucia. Usually studies compare protected areas with nearby fishing grounds (Roberts and Hawkins, 2000) providing valuable information on how species respond once fishing stops, but failing to exclude historical impacts which may obscure fishing effects. For example, if heavy fishing pressure has extirpated a suite of species, the nature of fish stocks recovering in marine reserves will be constrained by past history. An advantage of our approach was that it allowed us to examine communities that were more in equilibrium with fishing intensities in their area than reserve and non-reserve comparisons could provide. By also examining changes over time in fishing grounds and marine reserves we could assess responses of parrotfish to protection, following years of exploitation.

We test predictions that fishing will: (1) decrease population densities; (2) have a greater impact on larger species compared to small; (3) reduce the average size of parrotfish; (4) limit the availability of terminal phase males, and (5) cause species to change sex at smaller sizes.

2. Methods

We censussed parrotfishes on reefs around the Caribbean islands of Bonaire, Saba, Puerto Rico, St Lucia, Dominica and Jamaica between 1994 and 2001 (Fig. 1). St Lucia was sampled at yearly or biennial intervals, while other islands were each sampled once. In Bonaire 36 counts were performed at 5 m and 36 at 10 m; in Saba, 40 at 5 m, 33 at 15 m; in Puerto Rico, 56 at 5 m and 42 at 15 m; in Dominica, 32 at 5 m and 32 at 15 m and in Jamaica, 64 at 5 m and 48 at 15 m. In St Lucia
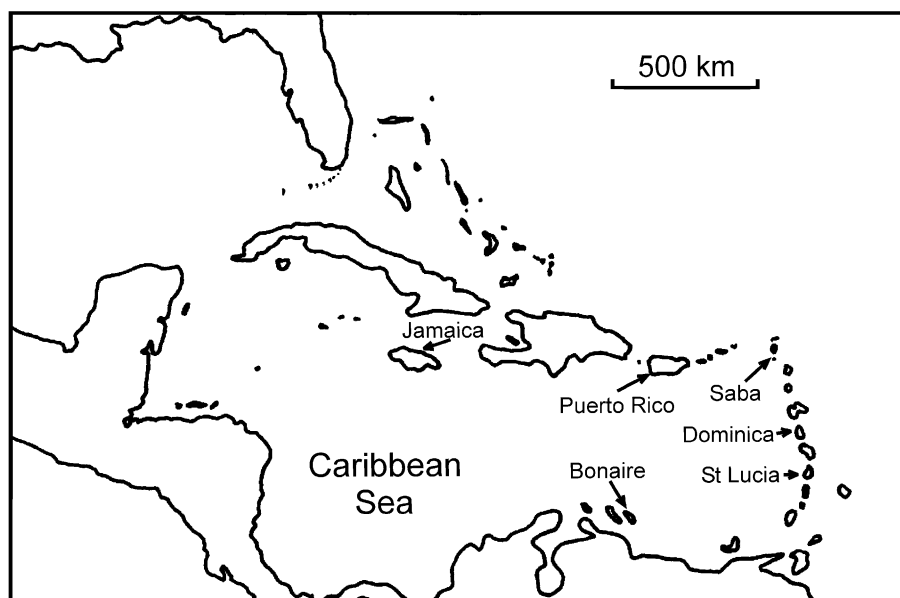

Fig. 1. Map of the study area including the location of study sites.

we always made, 138 counts at 5 m and 137 at 15 m. In all analyses, data were pooled across depth.

We used an adaption of the stationary point visual census technique (Bohnsack and Bannerot, 1986). A 10-m tape was used to mark the diameter of a cylinder that extends 5 m above the reef. During each 15-min count we estimated size (total length to nearest cm) and number, of all parrotfish species present within, or passing through the cylinder. We also noted whether individuals had initial or terminal phase colouration. The location of our first count was our entry point into the water and subsequent counts were made along the same depth contour. Counts were always separated by distances of at least 10 m.

Data are presented for eight of the 13 species of Caribbean parrotfish: *Sparisoma viride*, *Scarus vetula*, *Sparisoma chrysopterum*, *Sparisoma rubripinne*, *Scarus taeniopterus*, *Sparisoma aurofrenatum*, *Scarus iserti* and *Sparisoma atomarium* (listed in decreasing size order). The first four are large (maximum total length 45–60 cm), the next three medium sized (maximum total length 25–33 cm) and *Sp. atomarium* is a small parrotfish (maximum total length 11 cm). This species is relatively cryptic and difficult to count accurately, so was only included in one analysis. In some analyses data for *Sc. taeniopterus* and *Sc. iserti* were pooled because we could not distinguish between these two species in their initial colour phase. Where data are only presented on terminal phase males, the two species are considered

independently. The three largest Caribbean parrotfish, *Scarus coeruleus*, *Scarus coelestinus* and *Scarus guacamaia*, were excluded from analyses because they were extremely rare or absent from our study sites. The other two species, *Cryptotomus roseus* and *Sparisoma radians* occur primarily in sea grass beds.

3. Cross Caribbean comparisons across a gradient of fishing pressure

Fishing intensities differed considerably among islands. However, we could not compare absolute levels of fishing pressure because available information was not standardized. Hence we have ranked islands for their fishing pressure using published studies, personal observations, plus information gained from fisheries departments and marine park personnel (Table 1). To summarise, reefs in Bonaire were virtually unfished and in Saba were very lightly fished. Fishing pressure in Puerto Rico was moderately high, it was higher still in St Lucia and very high in Dominica. Reefs in Jamaica were extremely heavily exploited. We also derived a more quantitative measure of relative fishing pressure by dividing the length of reef available in local fishing grounds by the number of active fishers (Table 1).

The presence of this fishing pressure gradient allowed us to study how fishing affects parrotfish abundance, biomass, size structure, and the size of transition from

Table 1
Fishery characteristics in each of the study sites

Location	No. active fishers	Length of reef fished (km)	Gears used	Species targeted	Fishing intensity (km of reef per fisher)	Reference
Bonaire	4 full-time	61.8 km	Hook and line	Near reef pelagics (e.g. jacks, rainbow runners)	15.45	Bonaire Marine Park pers. comm., and pers. obs.
Saba	10 part-time = 0.83 f.t.e.[a]	6.9 km	Spear	Mainly predatory fish such as large snappers and groupers	8.31	Saba Marine Park pers. comm., and pers. obs.
Puerto Rico	64 full-time, 2 part-time = 65 f.t.e.[a]	78.3 km	Lines, trap, nets, spear	Predominantly snappers, but grunts and near reef pelagics important. A wide variety of reef associated species also targetted	1.20	Matos-Caraballo (1997), Morelock et al (1994)
St. Lucia	25 full-time, 4 part-time = 27 f.t.e.[a]	8.4 km	Traps, hook and line, limited spearing, few gill nets	Wide range of species including many small-bodied planktivores, invertivores, omnivores and herbivores. Predators are highly desirable but only limited numbers caught. Inedible species are used for bait	0.31[b]	Gell et al (2001), Goodridge (1996)
Dominica	32 full-time, 47 part-time = 56 f.t.e.[a]	18.5 km	Traps, hook & line, extensive spear and nets	Wide range of species including many small-bodied planktivores, invertivores, omnivores and herbivores. Predators are highly desirable but only limited numbers caught. Inedible species are used for bait	0.33[b]	Guiste, H. Chief Fisheries Officer, Dominica. pers. comm., Roberts and Hawkins (1996)
Jamaica	58 full-time, 24 part-time = 70 f.t.e.[a]	9.9 km	Traps, hook and line, extensive spear and nets	Virtually everything larger than 10 cm is targeted. Majority of catch is small-bodied. Large predators desirable but extremely uncommon	0.14	Sary (1995), Sandeman and Woodley (1994), Allison (1992)

[a] f.t.e. = Full-time equivalents. In Saba we assumed that each fisher fished for one day in every two weeks (assuming a six day working week) since all fishing on this island is recreational. Hence, each fisher is considered 1/12th a full time equivalent. In all other countries where fishing is done on a commercial or subsistence basis we assumed that part-time fishers fished for half of their time.

[b] The amount of reef available to fishers in St Lucia and Dominica is virtually identical. However, since the range of gears used in St Lucia was more limited, i.e. less spear and net fishing, we considered this island to be slightly less heavily fished than Dominica.

initial phase to terminal phase. We calculated parrotfish biomass from estimates of fish size and numbers using length-weight relationships (Bohnsack and Harper, 1988). We used intervals of 3 cm to graph size structures of the larger species (*Sp. viride*, *Sc. vetula*, *Sp. chrysopterum* and *Sp. rubripinne*). The percentages of fish with terminal phase colouration are also presented. As noted earlier, all fish in the terminal phase are male, while most, but not all with initial phase colouration are female. In these cross Caribbean comparisons, data for St Lucia were taken from the 1995 pre-marine reserve census when fishing pressure was at its highest.

4. A network of marine reserves in St Lucia

In 1995 four fully protected marine reserves were established in St Lucia. They were interspersed between fishing grounds along 11 km of coastline in the Soufrière Marine Management Area (SMMA) and incorporated approximately 35% of the coral reef habitat (Roberts et al., 2001).

We began the parrotfish census in St Lucia before protection was instigated in designated areas and using two-way ANOVA, with level of protection and time as factors, have examined how the biomass of parrotfish communities has responded to protection from fishing. We also present data on changes over time in the biomass, mean size and size frequency distribution for seven different species. Where appropriate we analysed these trends using one-way ANOVA and post hoc LSD tests.

5. Results

5.1. Cross Caribbean comparisons across a gradient of fishing pressure

5.1.1. Measures of abundance and biomass

Fig. 2 shows the mean number of individuals and mean biomass per count for each species in each country. Table 2 reports results from one-way ANOVAs and

post hoc LSD tests for these measures. Biomass of the largest species, *Sp. viride*, was significantly higher in the lightly fished islands of Bonaire and Saba than in the other more heavily fished islands (one-way ANOVA: $F_{5,693} = 57.0$, $P < 0.001$). The other large parrotfishes *Sc. vetula*, *Sp. chrysopterum* and *Sp. rubripinne*, were generally more common in Bonaire and/or Saba than the more heavily fished islands and, apart from *Sp. chrysopterum*, their biomass tended to decrease with increasing fishing pressure (Table 2).

The smaller parrotfish, *Sc. taeniopterus* and *Sc. iserti* combined, and *Sp. aurofrenatum* were abundant in all islands, and their abundance tended to increase with increasing fishing pressure (Table 2). The smallest parrotfish *Sp. atomarium*, was much more abundant in Jamaica than anywhere else (post hoc LSD test, $P < 0.001$). Fig. 3 shows species composition, based on biomass, over the gradient of increasing fishing pressure. Smaller species, particularly *Sc. taeniopterus* and *Sc. iserti* featured much more prominently in countries with greater fishing pressure, while larger species made up declining fractions of the assemblage.

6. Size frequencies and color phase ratios

For each species of parrotfish, Fig. 4 shows the percentage frequency of different size classes in each country. Generally, there were marked declines in abundance of large fish as fishing pressure increased.

Fig. 5 shows the average size of both terminal and initial phase fish among all islands for all species except terminal male *Sp. chrysopterum*, which were not analysed due to insufficient data. The size of all species in both colour phases was significantly different among islands and tended to decrease with increasing fishing pressure [one-way ANOVAs: $F_{4,283} = 169.1$, $P < 0.001$ (terminal), $F_{5,1735} = 78.5$, $P < 0.001$ (initial), *Sp. viride*; $F_{4,222} = 686.1$, $P < 0.001$ (terminal), $F_{4,453} = 5.2$, $P < 0.001$ (initial), *Sc. vetula*; $F_{5,48} = 5.0$, $P < 0.01$ (initial), *Sp. chrysopterum*; $F_{4,45} = 37.2$, $P < 0.001$ (terminal), $F_{4,59} = 19.8$, $P < 0.001$ (initial), *Sp. rubripinne*; $F_{5,218} = 127.5$, $P < 0.001$ (terminal), *Sc. taeniopterus*;

Table 2
One-way ANOVAs for abundance and biomass of parrotfish across the Caribbean wide gradient of fishing pressure

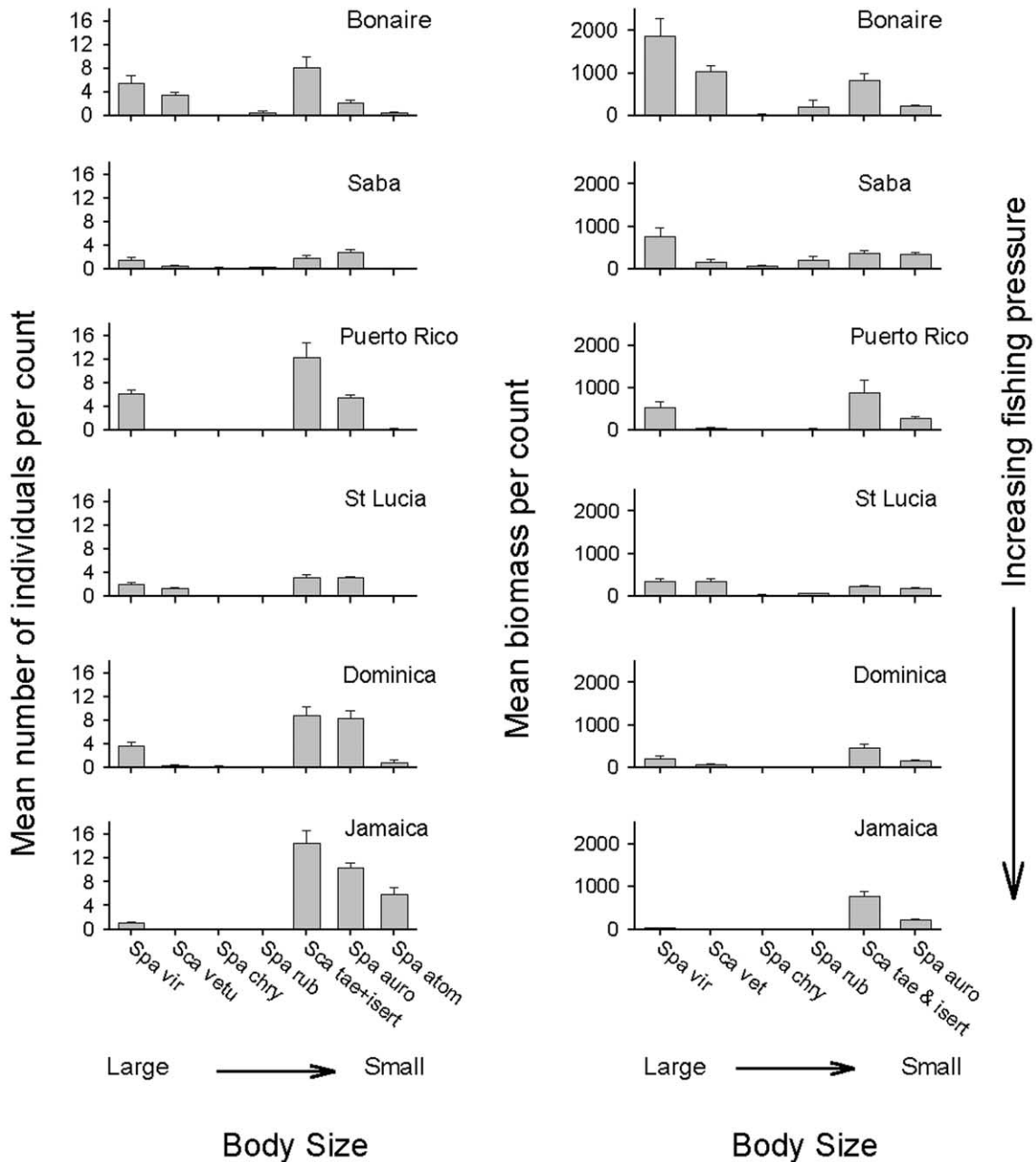| Species	Abundance		Biomass	
	ANOVA	Direction of change	ANOVA	Direction of change
Sp. viride	$F_{5,693} = 62.87$, $P < 0.001$	↓ with ↑ fishing	$F_{5,693} = 57.05$, $P < 0.001$	↓ with ↑ fishing
Sc. vetula	$F_{5,693} = 108.75$, $P < 0.001$	↓ with ↑ fishing	$F_{5,693} = 84.78$, $P < 0.001$	↓ with ↑ fishing
Sp. chrysopterum	NS		$F_{5,693} = 4.35$, $P < 0.01$	Unclear
Sp. rubripinne	$F_{5,693} = 5.89$, $P < 0.001$	↓ with ↑ fishing	$F_{5,693} = 10.02$, $P < 0.001$	↓ with ↑ fishing
Sc. taeniopterus + iserti	$F_{5,693} = 51.74$, $P < 0.001$	Unclear	$F_{5,693} = 22.39$, $P < 0.001$	Unclear
Sp. aurofrenatum	$F_{5,693} = 113.93$, $P < 0.001$	↑ with ↑ fishing	$F_{5,693} = 15.41$, $P < 0.001$	Unclear
Sp. atomarium	$F_{5,693} = 100.83$, $P < 0.001$	↑ with ↑ fishing	Not available	

Fig. 2. Mean abundance and biomass per count (±95% C.I.) for parrotfish (Scaridae), where species are arranged along the *x*-axis in order of decreasing size. Spa vir = *Sparisoma viride,* Sca vet = *Scarus vetula,* Spa chry = *Sp. chrysopterum,* Spa rub = *Sp. rubripinne,* Sca tae + isert = *Sc. taeniopterus* and *Sc. iserti,* Spa auro = *Sp. aurofrenatum,* Spa atom = *Sp. atomarium.* Abundance of *Sc. taeniopterus* and *Sc. iserti* was combined because in the field it was impossible to distinguish the young fish of these species. Biomass data for *Sp. atomarium* are not available. Graphs are stacked in order of decreasing fishing pressure (top least, bottom most fished).

$F_{4,413} = 48.3$, $P < 0.001$ (terminal), *Sc. iserti*; $F_{5,510} = 171.4$, $P < 0.001$ (terminal), $F_{5,2770} = 97.0$, $P < 0.001$ (initial), *Sp. aurofrenatum*].

The fraction of terminal phase fish and the size at first sex change of each species in each country are shown in Table 3 (see also Fig. 4). In the two largest species, *Sp. viride* and *Sc. vetula,* the fraction of terminal phase fish showed order of magnitude decreases with increasing fishing pressure. For *Sp. aurofrenatum,* the fraction of

terminal phase declined by two thirds. Other species showed no clear trends in relation to fishing pressure. In heavily fished islands, initial phase *Sp. viride* generally transformed into terminal males at smaller sizes than in lightly fished islands (Fig. 4). As a specific example the smallest terminal male recorded in Saba was 29 cm whereas in Dominica it was 17 cm (Table 3). In Saba, fish still retained initial phase colouration at sizes where fish were always terminal males in heavily fished coun-
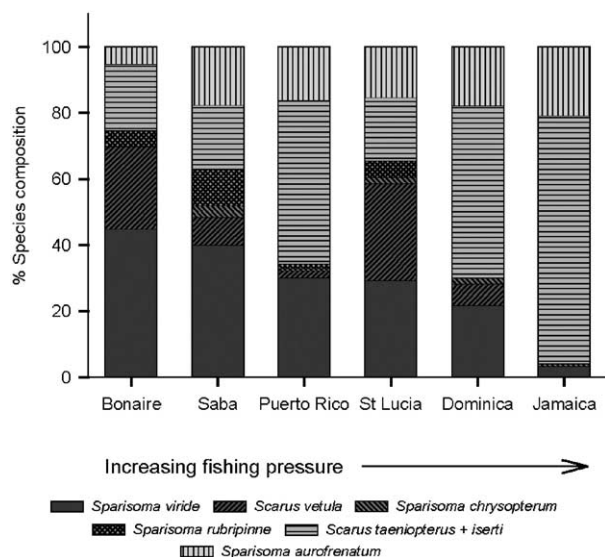
Fig. 3. Species composition based on biomass of parrotfish over a gradient of increasing fishing pressure.

Fig. 4. Size frequency distribution of each parrotfish species over a gradient of increasing fishing pressure. Light bars = initial phase; dark bars = terminal phase.

tries (Fig. 4). In Jamaica no terminal male *Sp. viride* were recorded (Table 3) and the biggest fish seen was 18 cm. Outside the counts only one 15 cm transitional male was observed in Jamaica in twelve days of diving.

There is some indication that *Sc. vetula* (Fig. 4) are also flexible in the size at which they can change into terminal males but data are less compelling than for *Sp. viride*. For example, in lightly fished Bonaire and Saba, the smallest terminal males were 23 and 28 cm respectively (Table 3) and most fish did not become terminal males until they were bigger than 30 cm (Fig. 4). In more heavily fished St Lucia, the smallest terminal male was 16 cm (Table 3) and there were eight terminal males of 16–23 cm. The total number of fish per count decreased by more than threefold for this species as fishing pressure increased and none were seen in Jamaica (Fig. 2).

At the depths censused, *Sp. chrysopterum* and *Sp. rubripinne* were uncommon everywhere (Fig. 4), and there is only a hint of flexibility in the size at which they
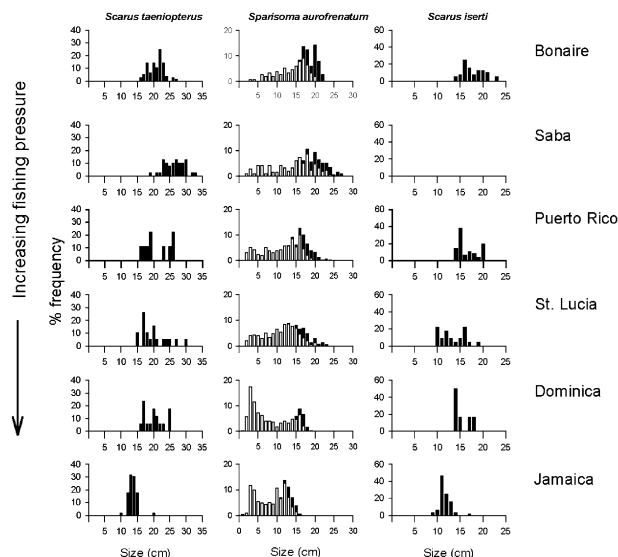
can change sex. For *Sp. chrysopterum*, lightly fished Bonaire had no terminal males (probably because they were in shallow water) but initial phase fish were large, whereas in heavily fished Dominica and Jamaica there were neither large initial phase fish nor any terminal males. However, the data are not completely consistent as the smallest terminal males in lightly fished Saba were 6 cm smaller than the smallest in much more heavily fished St Lucia (19 cm in Saba versus 25 cm in St Lucia) (Table 3). For *Sp. rubripinne*, terminal males were the most common colour phase in all countries except Bonaire (Fig. 4). In lightly fished Saba but not Bonaire the smallest terminal males were a lot bigger than those in heavily fished islands (Fig. 4).

From Fig. 5 it is clear that for *Sc. taeniopterus* and *Sp. aurofrenatum*, size of terminal males decreased as fishing pressure increased. These species clearly transformed into terminal males at smaller sizes in Jamaica than anywhere else (Fig. 4). *Sc. iserti* was absent from Saba,

Table 3
The fraction of terminal phase fish and the size at first sex change (cm) of each species in each country[a]

	Sp. viride		*Sc. vetula*		*Sp. chrysopterum*		*Sp. rubripinne*		*Sc. taeniopterus*		*Sp. aurofrenatum*		*Sc. iserti*	
	% terminal	Min. size	% terminal	Min. size	% terminal	Min. size	% terminal	Min. size	% terminal	Min. size	% terminal	Min. size	% term.	Min size
Bonaire	27	24	44.1	23	0	–	35.5	24	–	16	35.9	16	–	14
Saba	22.3	29	36.1	28	61.5	19	56.5	33	–	19	25.2	17	–	–
Puerto Rico	12.5	15	30.7	25	16.7	18	55.6	17	–	16	21.8	13	–	14
St Lucia	11.7	19	26.8	16	16.7	25	45.2	25	–	15	14.4	13	–	11
Dominica	5.6	17	5.6	35	0	–	100	16	–	16	9.4	15	–	14
Jamaica	0	–	0	–	0	–	0	–	–	10	11.5	11	–	10

[a] No figures are given for the fraction of terminal phase *Sc. taeniopterus* and *Sc. iserti* because initial phase fish of these species were indistinguishable.
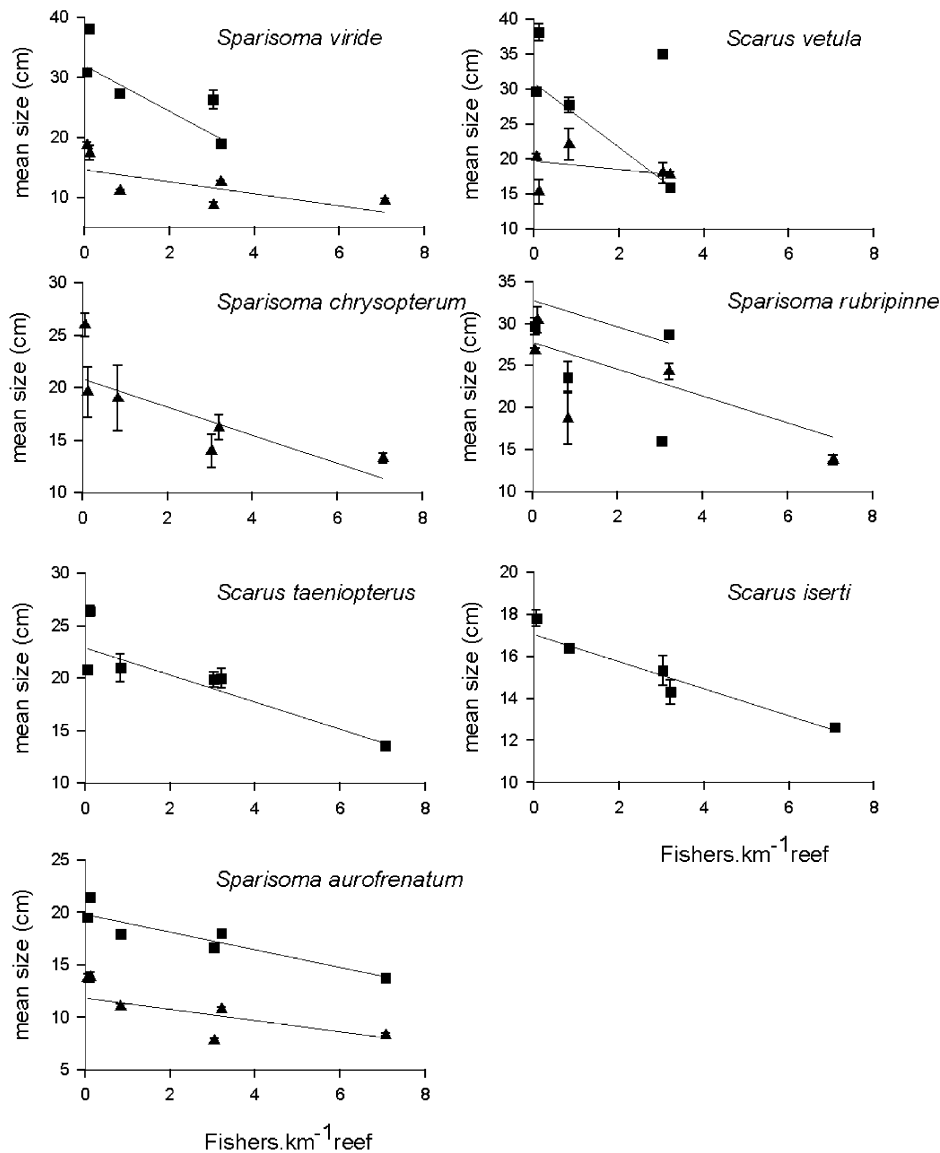
Fig. 5. Mean size (±S.E.) of parrotfish over a gradient of increasing fishing pressure where (▲) are initial phase and (■) are terminal phase. Graphs show first order linear regression results.

otherwise it showed similar patterns, although differences between Jamaica and the other islands were not so pronounced (Figs. 4 and 5).

7. Population changes in relation to marine reserve protection

Fig. 6 shows changes in parrotfish biomass over time in St Lucia. Since marine reserves were established (6 months after the 1995 census) the biomass of all species except *Sp. chrysopterum*, has increased in both fishing grounds and reserves [two-way Anova: $F_{5,1170} = 10.5$, $P < 0.001$ (year effect); $F_{1,1170} = 74.0$, $P < 0.001$ (protection effect); $F_{5,1170} = 3.2$, $P < 0.01$ (year×protection), *Sp. viride*; $F_{5,1170} = 5.3$, $P < 0.001$ (year effect); $F_{1,1170} = 48.3$, $P < 0.001$ (protection effect); N.S. (year×protection), *Sc. vetula*; $F_{5,1170} = 5.8$, $P < 0.001$ (year effect); $F_{1,1170} = 8.4$, $P < 0.01$ (protection effect); N.S. (year×protection), *Sp. rubripinne*; $F_{5,1170} = 16.6$, $P < 0.001$ (year effect); $F_{1,1170} = 8.3$, $P < 0.01$ (protection effect); N.S. (year× protection), *Sp. taeniopterus + iserti*; $F_{5,1170} = 33.1$, $P < 0.001$ (year effect); $F_{1,1170} = 52.5$, $P < 0.001$ (protection effect); N.S. (year×protection), *Sp. aurofrenatum*]. There was no effect of protection on *Sp. chrysopterum* but biomass did fluctuate significantly between years [$F_{5,1170} = 4.4$, $P < 0.01$ (year effect); N.S. (protection effect); $F_{5,1170} = 2.7$, $P < 0.05$ (year*protection), *Sp. chrysopterum*]. Total parrotfish biomass increased significantly over time and was significantly higher in protected areas than in fishing grounds [two-way ANOVA: $F_{5,1170} = 32.8$, $P < 0.001$ (year effect); $F_{1,1170} = 124.5$,
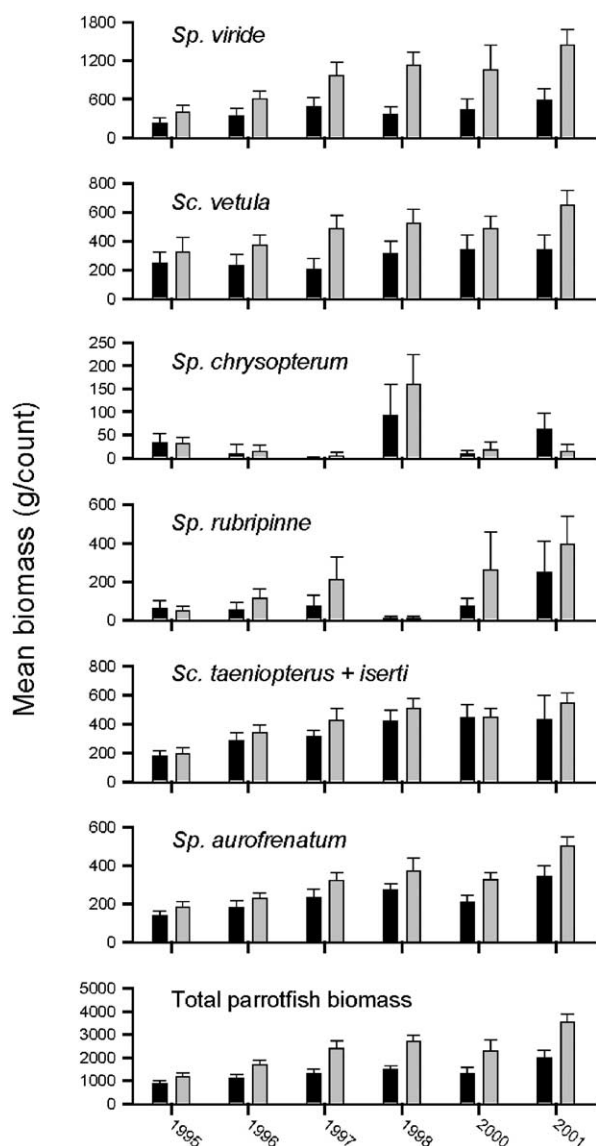
Fig. 6. Mean biomass (±95% C.I.) per count for parrotfish, over time in St Lucia. Dark bars = fished areas, light bars = marine reserves. Note there are no data for 1999. Graphs are stacked in order of decreasing parrotfish size.

$P < 0.001$ (protection effect); $F_{5,1170} = 4.7$, $P < 0.001$ (year×protection; Fig. 6)].

The average size of most species increased over time [one-way ANOVAs: $F_{5,474} = 22.7$, $P < 0.001$ (terminal); $F_{5,4917} = 19.5$, $P < 0.001$ (initial), Sp. viride; $F_{5,707} = 552.3$, $P < 0.001$ (terminal), $F_{5,1777} = 13.1$, $P < 0.001$ (initial), Sc. vetula; $F_{5,213} = 13.7$, $P < 0.001$ (terminal), N.S. (initial), Sp. rubripinne; $F_{5,479} = 20.1$, $P < 0.001$ (terminal), Sc. taeniopterus; $F_{5,1161} = 60.5$, $P < 0.001$ (terminal); Sp. aurofrenatum)], except for Sp. chrysopterum, Sc. iserti and initial phase Sp. aurofrenatum which fluctuated [one-way ANOVAs: $F_{5,20} = 2.9$, $P < 0.05$ (terminal), N.S. (initial), Sp. chrysopterum; $F_{5,7119} = 51.4$, $P < 0.001$ (initial), Sp. aurofrenatum; $F_{5,244} = 4.8$, $P < 0.001$ (terminal), Sc. iserti)].

Fig. 7 compares trends in the average size of terminal males between St Lucia's reserves and fishing grounds for all species except Sp. chrysopterum for which there were inadequate data. Sp. viride, Sc. vetula, Sc. taeniopterus and Sp. aurofrenatum all changed significantly over time, increasing in both reserves and fishing grounds, and differed with respect to protection from fishing, with terminal males in reserves being larger than in fishing grounds [two-way ANOVA: $F_{5,498} = 13.3$, $P < 0.001$ (year effect), $F_{1,498} = 22.8$, $P < 0.001$ (protection effect) $F_{1,498} = 2.4$, $P < 0.05$ (year×protection), Sp. viride; $F_{5,442} = 14.3$, $P < 0.001$ (year effect), $F_{1,442} = 7.3$, $P < 0.01$ (protection effect), N.S. (year×protection), Sc. vetula; $F_{5,312} = 5.5$, $P < 0.001$ (year effect), $F_{1,312} = 21.1$, $P < 0.001$ (protection effect), $F_{1,312} = 3.2$, $P < 0.01$ (year×protection), Sc. taeniopterus; $F_{5,787} = 30.0$, $P < 0.001$ (year effect), $F_{1,787} = 33.0$, $P < 0.001$ (protection effect), $F_{1,787} = 5.2$, $P < 0.001$ (year×protection), Sp. aurofrenatum)]. In Sp. rubripinne fish increased significantly in size, but there was no significant difference between reserves and fishing grounds ($F_{5,134} = 11.9$, $P < 0.001$ (year effect), N.S. (protection effect), N.S. (year×protection). Sc. iserti did not increase significantly over time, nor did protection affect this species.

Fig. 8 compares size frequency data before reserves were established, with that 6 years later, between fishing grounds and marine reserves for terminal males of each species. In Sp. viride, fish appeared to be changing sex at larger sizes in reserves but not in fishing grounds. For Sc. vetula, Sp. rubripinne, Sc. taeniopterus and Sp. aurofrenatum there were increasing sizes at sex change in both reserves and fishing grounds. Sc. iserti showed no tendency to change sex at larger sizes over time.

8. Discussion

Fishing has had predictable effects on parrotfish communities in the Caribbean. Biomass of larger species declined as fishing intensified and smaller species came to constitute a greater proportion of the total assemblage. In the most heavily fished islands, adults of two of the largest species, Sp. viride and Sc. vetula were virtually absent. In all species, fishing pressure also appears to have reduced the size of fish and it has decreased the proportion of terminal males in four out of five species. In St Lucia, marine reserves helped rebuild stocks of all parrotfish except uncommon Sp. chrysopterum. In 5 years, total parrotfish biomass almost quadrupled within the marine reserves and nearly doubled within fishing areas. Most species increased in size throughout the study area and there was evidence that, as populations built up, some species were changing into terminal males at larger sizes.
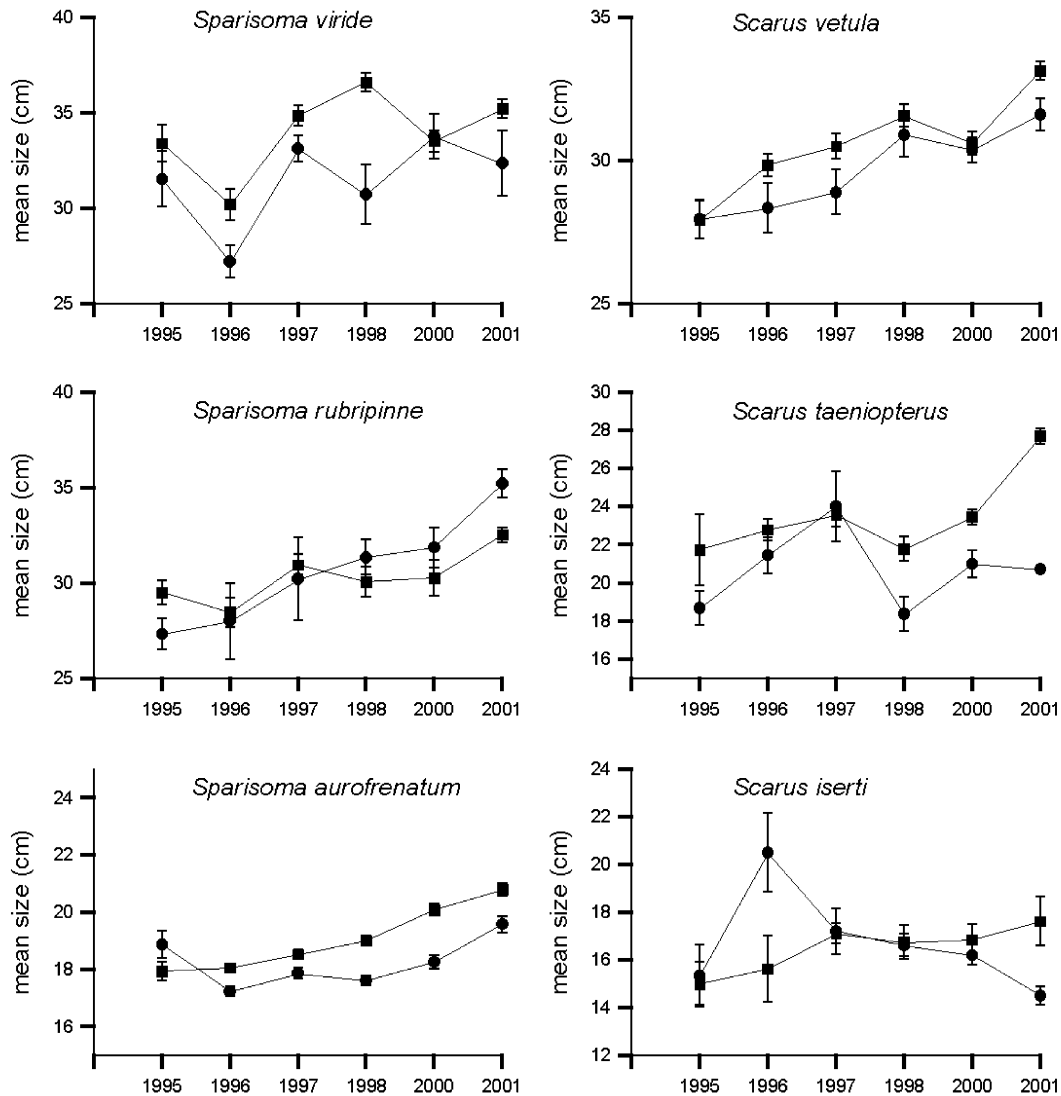
Fig. 7. Mean size (±S.E.) of terminal phase parrotfish in marine reserves (■) and fishing grounds (●) in St Lucia. Note there are no data for 1999.

Fishing could impose strong selective pressure on fish to change sex at smaller sizes by favouring individuals that change sex earlier, until such genotypes come to dominate populations (Palumbi, 2001). Alternatively, if the size at which fish change sex is under social and/or hormonal control, fishing could still decrease it by reducing densities of larger terminal phase males and triggering initial phase fish to change sex at smaller sizes. This would lower the average size of both terminal males and initial phase females. In the small, haremic serranid, *Anthias squamipinnis*, removing males triggers larger females to change sex (Shapiro, 1981). In Caribbean hogfish (*Lachnolaimnus maximus*) it has been suggested that sex change at small sizes may be due to genetic factors causing differential growth, whereas in larger fish behavioral factors are probably more important (Claro et al., 2001).

Compensating for fishing pressure by changing sex at a smaller size will only succeed if individuals still live long enough to get large enough to change sex. As fractions of terminal males fall, females may have difficulties in finding a terminal male to spawn with even if some remain. Our data suggest this could be happening in the most heavily fished islands. At our study sites in Jamaica and Dominica, *Sp. viride* and *Sc. vetula*, may be failing to reproduce, although in *Sp. viride*, females could potentially mate with initial phase males. The fact that juveniles of *Sp. viride* were common in both islands suggests that this species may be replenished by eggs and larvae from elsewhere (Roberts, 1997). Such dependence on external sources of recruitment could become increasingly necessary as fishing pressure rises.

Coleman et al. (1996) found that over 20 years, the percentage of male gag grouper (*Mycteroperca microlepis*) in the Gulf of Mexico fell from 17 to 1% and from 36 to 18% for *Mycteroperca phenax*. Both these groupers reproduce at mass spawning aggregations where they are particularly vulnerable to over-fishing. Gilmore

and Jones (1992) suggest that the largest males are the easiest to catch because they are the most aggressive. In Coleman et al.'s study the sex ratio of a third grouper, *Epinephelus morio*, which did not aggregate to spawn remained constant over time. Along the Atlantic coast of the southeastern USA, McGovern et al. (1998) found similar declines in proportions of male gag, with figures falling from 20 to 6% over 19 years. Their study also revealed that female gag were maturing at smaller sizes. In Nassau groupers (*Epinephelus striatus*), another species of protogynous hermaphrodite that reproduce at spawning aggregations, Claro et al. (2001) found a high
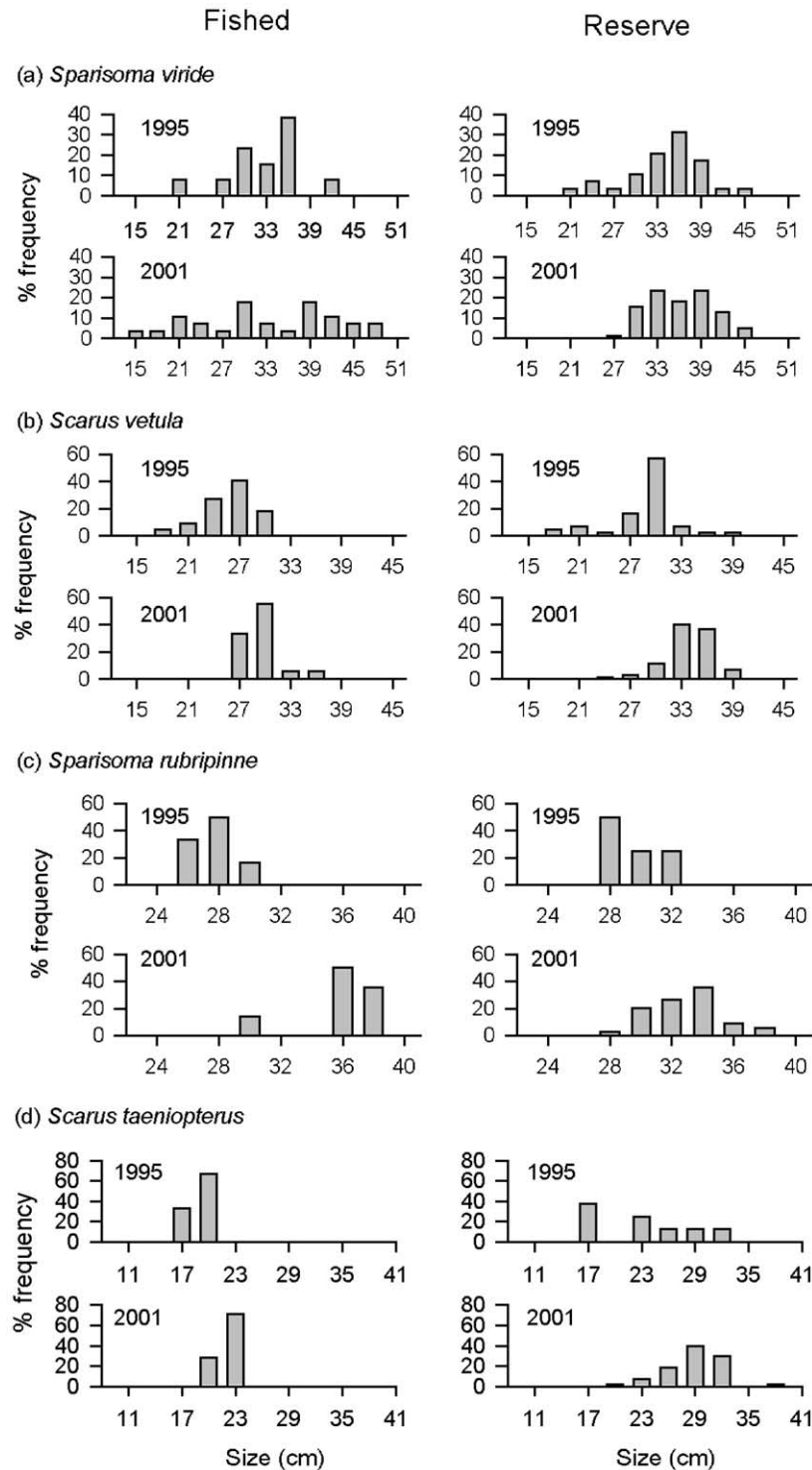

Fig. 8. Size frequency distribution of terminal phase parrotfish in St Lucia in marine reserves (right column) and fishing grounds (left column) between 1995 (6 months before protection was instigated) and 2001.
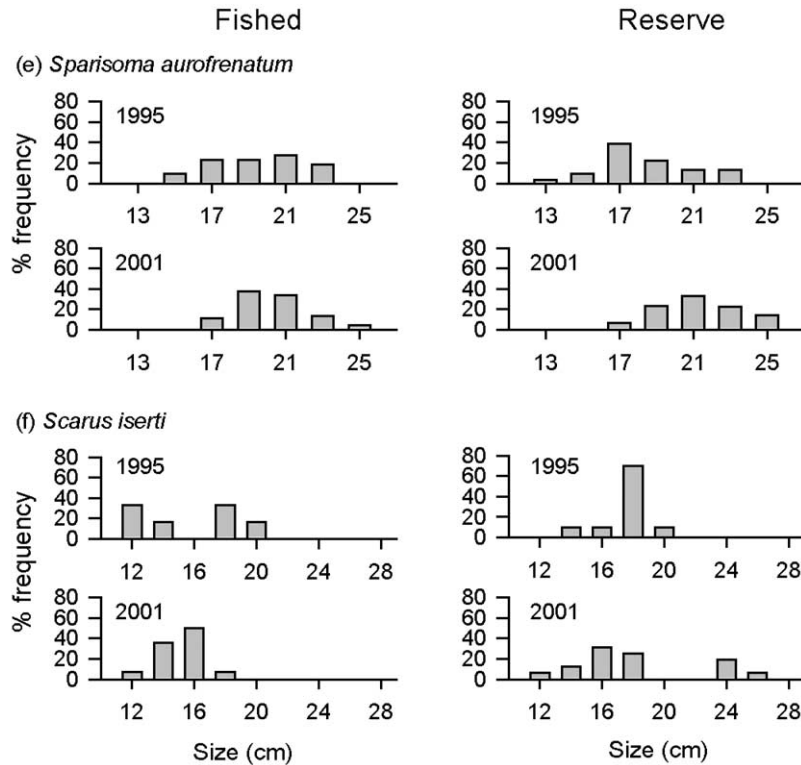
Fig. 8 (*continued*).

proportion of individuals (36%) in transition between female and male in Cuba. They attribute this to loss of males from overfishing at spawning aggregations.

A study in South Africa by Buxton (1992) revealed that sex ratios of the protogynous hermaphroditic sparids *Chrysoblephus laticeps* and *Chrysoblephus cristiceps*, showed greater skew towards females in exploited Port Elizabeth, compared to the nearby Tsitsikamma marine reserve which had been closed to fishing for 25 years. Buxton suggests that this was due to larger males being selectively removed by the recreational line fishery. When Buxton modelled his results it appeared that even low fishing intensities would still skew sex ratios towards females. In a previous study of these species, Buxton (1990) showed that *C. cristiceps* changed sex at smaller sizes and matured earlier in Port Elizabeth than in the Tsitsikamma marine reserve, but that *C. laticeps* did not, possibly because smaller sized *C. laticeps* could not be caught by the sampling methods he used. Buxton (1993) also reported that on the east coast of South Africa, recreational fisheries did not appear to be reducing the age at which *C. laticeps* and *C. cristiceps* first changed sex, despite the fact that immature *C. cristiceps* were being targeted. He suggested that recruitment from other areas was probably sustaining stocks. Garratt (1985), also used this reasoning to explain why catches of another sparid, *Chrysoblephus puniceus* had not declined in Natal despite high fishing effort and a decline in the proportion of males.

Changes in population composition over time in St Lucia suggest that sex change may be more under social control than genetic in the species we studied. All showed an increase in the size of terminal males after marine reserves were established. If fishing had selected out genotypes for delayed sex change it is unlikely that the population could have reversed back to changing sex at bigger sizes over such a short period.

If the average size within a population falls, so does its reproductive output, because in fish there is an exponential relationship between body length and egg production (Bohnsack, 1990). Because bigger fish produce many more eggs than smaller fish, large females play a disproportionately important role in replenishing populations. Since fishing pressure appears to influence the size of initial phase fish, it will also affect egg production by a greater fraction than simple differences in biomass imply.

Parrotfish have complex social structures and reproductive strategies, as described in the introduction. The dramatic differences that we found amongst islands in population density and sexual structure implies that fishing will affect parrotfish social behaviour and reproductive success. Perhaps some of the Caribbean wide, intraspecific differences in social behaviour that we noted earlier, could have been brought about by fishing.

One species which did well in Jamaica and Dominica was *Sp. atomarium*, which is normally too small to get caught in fish traps. This parrotfish obviously thrives in algae, which was most abundant amongst our study

sites in these islands (Hawkins and Roberts, in press). Environmental differences between islands will certainly have some influence on our results. Indeed our findings only indicate that species differ among islands, not that fishing pressure causes the relationships. However, our results uphold all of the predicted effects of fishing described in the introduction, suggesting that fishing effects dominate other inter-island differences.

9. Recommendations for managing protogynous hermaphrodites

This study provides further evidence that protogynous hermaphrodites are particularly susceptible to over-fishing and that marine reserves are very important in helping populations recover and restocking fisheries that target such fish (Roberts et al., 2001). It supports other research that marine reserves increase species biomass (Roberts and Polunin, 1994; Russ and Alcala, 1996a, b; Babcock, 1999), abundance (Palsson and Pacunski, 1995; Watson et al., 1996), and allow fish to grow larger (Bell, 1983; Castilla and Duran, 1985; Buxton and Smale, 1989; Chapman and Kramer, 1999; Edgar and Barrett, 1999), although the average size of a species may not increase if growth is offset by high rates of recruitment (Wantiez et al., 1997). By giving protected individuals the opportunity for unconstrained growth, reserves also sustain genetic variability within populations (Trexler and Travis, 2000). By allowing development of more natural population structures, reserves protect diversity of behavioural and reproductive strategies. This range of benefits makes marine reserves an important tool for managing intensive, multi-species, artisanal fisheries which target protogynous hermaphrodites.

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