

# Ocean surgeonfish *Acanthurus bahianus*. II. Fishing effects on longevity, size and abundance?

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**ABSTRACT:** The ocean surgeonfish *Acanthurus bahianus*, an abundant small herbivore on reefs throughout the tropical west and central Atlantic, is a significant component of Caribbean trap-fishery catches. To assess effects of fishing on this species we compared its longevity, survivorship, size and abundance at localities throughout its range that have differing intensities and targets of fishing. Temperature explains nearly all of the geographic variation in maximum longevity of *A. bahianus*, and most of the variation in adult survivorship, with no indications of consistent fishing effects on either. Variation in maximum and median length (1.6-fold) and in abundance (16-fold) also are not consistently related to fishing. *A. bahianus* has similar demographic characteristics at 2 neighbouring (50 km apart) offshore Venezuelan reefs, one a well protected reserve, the other with intense fishing for predators. At Panamá, the abundance of adult *A. bahianus* showed no trend of change from 1979 to 1997, as the local density of subsistence fishers increased by ~70%. The lack of consistent fishing-effects on this species found in this and some other studies may reflect a combination of (1) resilience to fishing mortality arising from rapid growth to asymptotic size, early maturity, small size and abundance, and (2) strong, natural, large- and small-scale spatial variation in demography and abundance obscuring any such effects. Effects of non-catastrophic fishing on sedentary reef-fishes with similar demographic characteristics probably will be revealed only through comparisons of subpopulations in adjacent fished and no-take areas involving careful consideration of small-scale habitat effects.

**KEY WORDS:** Surgeonfish · *Acanthurus bahianus* · Tropical west Atlantic · Demography · Density · Fishing effects

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## INTRODUCTION

The ocean surgeonfish *Acanthurus bahianus* is widely distributed in the west Atlantic. It ranges from Bermuda to central Brazil, and is common at the central Atlantic islands of Ascension and St. Helena (Randall 2002, Rocha et al. 2002). Besides being one of the most widespread tropical west Atlantic shore fishes, *A. bahianus* is one of the commonest small (it reaches ~600 g), herbivorous reef-fishes throughout its range. In parts of the Caribbean where there are intensive trap-fisheries for reef-fishes, *A. bahianus* is a major component of trap-catches (Munro 1983, 2000,

Reeson 1983, Koslow et al. 1989, 1994, Recksiek et al. 1991, Beets 1997, Sary et al. 1997, Garrison et al. 1998, Robichaud et al. 2000), is important in subsistence fisheries (Randall 2002), and is of minor commercial significance (Froese & Pauly 2004). Trapping is the primary method by which this species is fished.

Information on geographic and habitat variation in the body size structures and densities of fish populations, and in individual longevity, survivorship and growth rates provides the necessary context for determining effects of fishing. Here we present the results of the second part of a study that had 2 main aims. Our first aim (Robertson et al. 2005, this volume) was to pro-

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vide a basic description of range-wide variation in the demography of a common and widely distributed tropical reef-fish, and assess the extent and natural causes of variation in its longevity, survivorship, growth and size, both across a large latitudinal gradient and among habitats within locations. The second aim, which is discussed here, was to assess effects of fishing on a common, small, reef-fish that experiences great variation in fishing pressure throughout its range.

There is no question that fishing strongly influences the demography and abundance of some reef-fishes in some parts of the tropical NW Atlantic, most notably at locations (e.g. Jamaica) where human densities are high and there are intensive and uncontrolled subsistence and commercial trap-fisheries (e.g. see Munro 1983, Roberts 1995, Chiappone et al. 2000, Jackson et al. 2001, Rogers & Beets 2001). However, there is considerable variation in the intensity, methods and targets of reef-fish fisheries across the large range of the ocean surgeonfish. This presents an opportunity to determine if effects of fishing readily can be disentangled from those of natural influences on the demography and abundance of a species that does not represent a universal, high-value fishing target. To do so we compared the longevity, adult survivorship, size and density of the ocean surgeonfish across a set of geographically widely dispersed reefs exposed to varying patterns of fishing, a method frequently employed in analyses of fishing effects (Jennings & Polunin 1996, Choat et al. 2003, Hawkins & Roberts 2003, Dulvy et al. 2004, Williamson et al. 2004).

To assess the influence of fishing on *Acanthurus bahianus* we considered common expectations about effects of fishing on tropical reef-fishes (see Polunin & Roberts 1995, Roberts 1995, Chapman & Kramer 1999, Rogers & Beets 2001, Russ 2002, Graham et al. 2003, Hawkins & Roberts 2003, Willis et al. 2003a,b, Dulvy et al. 2004): among locations, density, longevity, survivorship and size should decrease with increasing levels of trap-fishing, which directly targets *A. bahianus*. In addition, we examined whether survivorship and longevity of the ocean surgeonfish increase with increasing selective fishing pressure that targets piscivorous reef-fishes (groupers and snappers), but not the ocean surgeonfish itself. To do so we compared populations at locations ranging from a large, well protected reserve to areas with dense human populations and intensive trap-fisheries or selective fisheries. These study areas included 2 adjacent reef systems off the coast of Venezuela that have very similar habitats and environmental regimes, but very different fishing regimes. We use data we collected at many of the study areas, plus information on *A. bahianus* from 7 published studies of fishing effects in different parts of the Caribbean.

## MATERIALS AND METHODS

**Sampling locations.** We collected data at 14 locations, and used published information on sizes of *Acanthurus bahianus* from 3 others (Fig. 1). Those locations vary greatly in latitude and habitat characteristics, and range from highly isolated oceanic islands, to nearshore islands and reefs, to continental shoreline reefs.

**Fishing patterns and sampling activity at study areas.** The areas of coral reef given for some of the following have been taken from Spalding et al. (2001).

Ascension and St. Helena (data collection March to July 1992) are small islands with small human populations (~1600 people on 90 km<sup>2</sup> land and ~6000 people on 122 km<sup>2</sup> land; respectively) and shelf areas of ~50 and ~110 km<sup>2</sup>, respectively. General fishing pressure (no trapping) on reef-fishes is low at both islands, although there is a small export fishery at St. Helena for a shallow water grouper (Edwards 1990). *Acanthurus bahianus* is common at both islands (D. R. Robertson pers. obs.).

We conducted fieldwork at Barbados in July 2000. This island, with a dense human population (274 000 people on 430 km<sup>2</sup> land) and <100 km<sup>2</sup> shallow reef, has an extensive trap-fishery for reef-fishes (Robichaud et al. 2000).

The human population density of Belize (data collection September 2002) is fairly low (250 000 on 23 000 km<sup>2</sup> land). Moderately intense selective fishing (directed at predatory reef-fishes and large scarids, and based largely on methods other than traps (Koslow et al. 1994) occurs throughout much of its large area of reef (1330 km<sup>2</sup>). Fishing is uncontrolled in our study area around Carrie Bow Cay. Abundances of predatory fishes and large parrotfishes were low there (J. H. Choat & D. R. Robertson unpubl. data), although we saw no active traps during our work. As our study area is ~20 km from the nearest town or village, there is little unselective commercial and subsistence fishing such as that which targets surgeonfishes elsewhere in Belize (Polunin & Roberts 1993).

Bermuda (data collection October 2001 and July 2002) has a dense human population (65 000 people on 53 km<sup>2</sup> land) and only 370 km<sup>2</sup> reef. A high-intensity trap-fishery was terminated by law in 1990, and this ban has been well enforced since then. Current levels of line fishing for carnivorous reef-fishes are inadequate to supply the local market and a considerable amount of fish is imported (B. Luckhurst pers. comm. 2002). Herbivorous fishes such as parrotfishes and surgeonfishes have not been fished since the trap-fishery ended.

The entire reef system around the island of Bonaire (15 000 people, 285 km<sup>2</sup> land, 26 km<sup>2</sup> reef; data col-

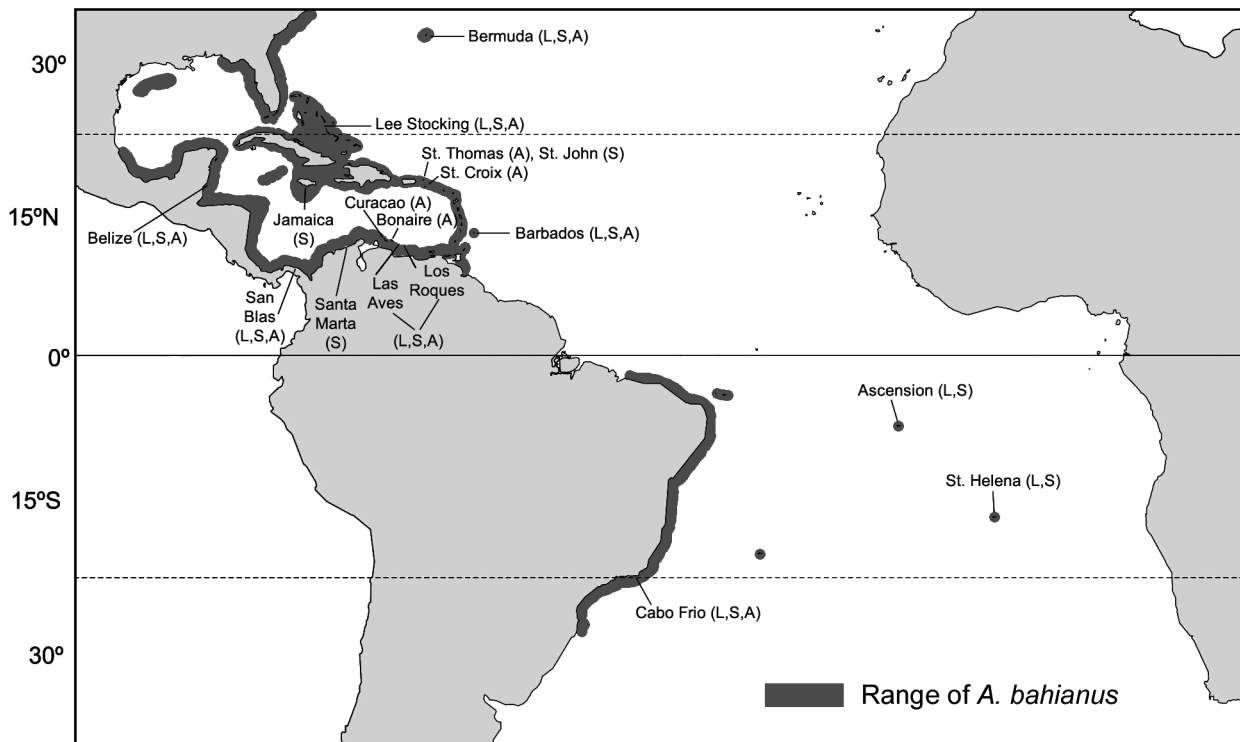


Fig. 1. Locations for which data on *Acanthurus bahianus* are presented. L: longevity and survivorship data; S: size data; A: abundance data

lection August 1992) is a reserve, with no organised reef fishery and fishing (by hook-and-line only) mainly for pelagic species (Choat et al. 2003, Hawkins & Roberts 2003). At nearby Curaçao (205 000 people, ~450 km<sup>2</sup> of land, ~50 km<sup>2</sup> of reef; data collection August 1992) predatory reef fishes are uncommon, due to a long history of overfishing. However, there has been virtually no trap-fishing there for at least the past 2 decades (P. Hoetjes pers. comm. 2005)

In contrast there is a substantial human population, few protected areas and intensive generalised fisheries that include trapping at St. Croix and St. Thomas (data collection at both July 1992), and St. John (published data on size; Randall 1963, Garrison et al. 1998) (110 000 people, 135 km<sup>2</sup> land, ~200 km<sup>2</sup> reef for these 3 islands together).

The coast around Cabo Frio, in Brazil (data collection October 1997) is densely populated (~150 000 people, ~10 km<sup>2</sup> reef; population and reef area from C. Ferreira pers. comm. 2003). Fishing using a variety of methods is uncontrolled and intensive (although *Acanthurus bahianus* is not fished), and large amounts of fishes are shipped to the nearby large city of Rio de Janeiro (C. Ferreira pers. comm. 2003).

Jamaica (published data on body size; Reeson 1983, Sary et al. 1997) has a dense human population (2.6 million, 4400 km<sup>2</sup> land, 1240 km<sup>2</sup> reef), and one of the most

intensive trap-fisheries in the Caribbean (Munro 1983, Koslow et al. 1989, 1994, Sary et al. 1997). The human population density in the Bahamas is fairly low (295 000 people on 10 000 km<sup>2</sup> land, 3150 km<sup>2</sup> reef), especially in the general vicinity of Lee Stocking Island (data collection November 1998, 1999), which is well away from population centers. We saw no evidence of trap-fishing, and predatory reef-fishes were not uncommon there during our work there (Choat et al. 2003).

The entire Los Roques Archipelago (data collection July 2000 and August 2002) is a well protected reserve, with restricted fishing and a small human population (1500 people, 350 km<sup>2</sup> reef). Our study area was in a part of the reserve where no fishing for reef-fishes is allowed (see Choat et al. 2003). At nearby (50 km to the west) Las Aves Archipelago (data collection August 2002) there are no controls on fishing. Although Las Aves (~100 km<sup>2</sup> reef) is uninhabited except for a small (<10 people) military base, there is intensive fishing for piscivorous reef-fishes (among others) by fishers using hook-and-line, traps, nets and spearguns. Fishers work on small boats based at large cities (e.g. La Guira) on the nearby mainland coast of Venezuela. Densities and sizes of target species were notably lower than at Los Roques (J. H. Choat, D. R. Robertson & J. M. Posada unpubl. data).

The autonomous Kuna Yala region of Panamá that includes our Punta de San Blas study area (censuses August 1979 to 1997, collections in 1995 to 1997) has a moderate human population density (~40 000 people, 5500 km<sup>2</sup> land, ~680 km<sup>2</sup> reef) with little development of tourist facilities or export of finfishes. Subsistence fishing for reef- and pelagic fishes is done mainly by hook-and-line and nets, although there is some spear-fishing for snappers and groupers. Only a few small traps were in use between 1979 and 1997 in the study area (D. R. Robertson monthly observations throughout that period).

Santa Marta (Colombia) (published data on size; Duarte & Acero 1992) currently has a population of ~415 000 people. There are few reef areas in the immediate vicinity of this city: When data were collected there on *Acanthurus bahianus* in the early 1980s (Duarte & Acero 1992), there was intensive selective fishing for carnivorous fishes, while *A. bahianus* was not fished. Today there is an intensive generalized trap-fishery (A. Acero pers. comm. 2004).

**Field sampling methods.** The methods we used to take population samples of *Acanthurus bahianus* to obtain data on size, growth, survivorship and longevity at 10 localities spanning 56° of latitude are described in Robertson et al. (2005). To ensure that we obtained a representative sample at each location, we made collections at at least 5 sites separated by distances of kilometres, and across a range of habitats used by the ocean surgeonfish at the different sites. To estimate the abundance of adult *A. bahianus*, counts were made of fish other than small juveniles in 30 × 10 m belt transects (see Choat et al. 2003) by J. H. Choat at 11 locations in the NW Atlantic. Such transects are suitable for estimating densities of this species because it is relatively small, common and sedentary. At each location counts were made in a minimum of 2 well separated habitats, with at least 5 replicate transects separated by distances of at least 100 m in each habitat. In addition, at Bermuda, J. Pitt made counts of adults over periods of 30 min in 7 m diameter circles at a variety of sites in different habitats. For Cabo Frio we relied on data on counts of adults in 20 × 2 m transects made by C. Ferreira (pers. comm. 2002) in the general area where our collections were made. Both sets of counts were converted to numbers of individuals 300 m<sup>-2</sup>.

**Assessing effects of fishing.** Robertson et al. (2005) analysed otolith growth increments to age individual *Acanthurus bahianus* taken in population samples at 10 locations, and obtain data on maximum and asymptotic size, age–size relationships, growth rates and lifetime growth trajectories, maximum age and average annual survivorship of adults.

Information on fishing patterns at the different locations is not sufficiently precise to allow ranking or

quantification of relative differences in fishing pressure among all locations. However, our study areas can be divided into 2 groups for the purposes of most of our comparisons: (1) high-trapping sites, at which general fishing pressure is intense and *Acanthurus bahianus* is a target, and (2) low-trapping sites, where the ocean surgeonfish is essentially untargeted, although fishing pressure on piscivorous reef-fishes may vary considerably.

**Effects on longevity and survivorship:** Robertson et al. (2005) found inverse linear relationships between mean sea temperature and both maximum longevity and annual survivorship across 10 locations. They suggested that this pattern is related to a decline in mortality costs of reproduction with increasing latitude. We predicted that, if fishing affects mortality rates of *Acanthurus bahianus*, then its longevity and survivorship should be (1) lower than that expected due to temperature at sites with intensive trap-fisheries (which should increase mortality of *A. bahianus*), and (2) higher than that expected from temperature at locations with heavy fishing on piscivores, but not on the ocean surgeonfish itself (which should reduce mortality of *A. bahianus*). To assess these predictions we examined whether longevity and survivorship at the 6 most heavily fished locations (Barbados, Bermuda, Belize, Cabo Frio, Las Aves and Panamá) were greater or less than that expected from a linear relationship between temperature and longevity (or survivorship) at the 4 low-fishing locations (Ascension, Lee Stocking, Los Roques and St. Helena).

**Effects on body size:** We assessed the relationship between body size and fishing by comparing both maximum and median standard length at different locations. Maximum size, which is a good proxy for asymptotic size, is directly related to mean sea temperature at the 10 locations where we made population samples (Robertson et al. 2005). We expected that, if fishing affects size in *Acanthurus bahianus*, then maximum size at locations with heavy trap-fishing would be less than the size predicted from the size–temperature relationship at locations where there is little or no such fishing.

Faunce et al. (2002) found that median absolute size of a commonly fished snapper was greater inside than outside no-take reserves at Florida, which they attributed to absence of fishing in the reserves. Inspection of their data also shows that maximum size did not differ among those locations, indicating that, while fishing may have reduced the abundance of large fish, it had not prevented some reaching the local maximum size. To test for an adverse effect of fishing on median size in *Acanthurus bahianus*, while controlling for geographic variation in maximum size due to other effects (e.g. temperature), we assessed whether relative

median size (median size as a % of maximum size at the same location) was consistently lower at heavily trapped locations than at untrapped locations. Note that inclusion of localities with heavy selective fishing for piscivores among the untrapped locations should tend to enhance any contrasts in size (and abundance—see next subsection) arising from differences in fishing-mortality rates of *A. bahianus*.

**Effects on abundance:** We compared densities of adult *Acanthurus bahianus* at locations with high and low levels of trap-fishing, expecting them to be lower in heavy-trapping locations if there is a fishing effect. In addition, we also examined change in adult abundance over time as fishing pressure changed at Panamá. Between 1980 and 2000 the population of subsistence fishers in that study area increased by ~70% (Anonymous 1982, 2002). D. R. Robertson made annual censuses (from 1979 to 1997) of adult *A. bahianus* on 18 patch reefs scattered throughout the 15 km<sup>2</sup> San Blas study site, and monthly censuses (between 1978 and 1998) of newly recruited juveniles in 14 permanent plots distributed over that study area (see Robertson 1992, Robertson & Kaufmann 1998). Using these data, we assessed whether there was a trend of change in adult abundance during that period, and how any pattern of change in adult abundance related to fluctuations in recruitment strength over that period. Methods used to derive standardized estimates of the abundance of adults and annual recruitment from the census data follow those of Robertson et al. (1999).

## RESULTS

### Variation in longevity and survivorship relative to fishing

The inverse relationship between maximum longevity of *Acanthurus bahianus* and temperature across all 10 locations was very strong:  $r^2 = 0.94$  (Fig. 2A). Thus very little of the variation in longevity was not explained by temperature alone. Maximum longevity differed by 2 yr or more from the temperature-predicted, low-fishing level at 4 of 6 high-fishing locations (Fig. 2A), exceeding that level (11 yr) by 4 yr at Barbados (intensive trap-fisheries, reduced longevity expected), and by 2 yr at Bermuda (predicted 30 yr) and Belize (predicted 8 yr) (selective fishing on predators, increased longevity expected at both locations), and was 4 yr less than the predicted level (25 yr) at Cabo Frio (heavy selective fishing on predators, increased longevity expected). There was no difference between longevity (12 yr) at Los Roques and Las Aves, despite the large difference in fishing regimes at these locations.

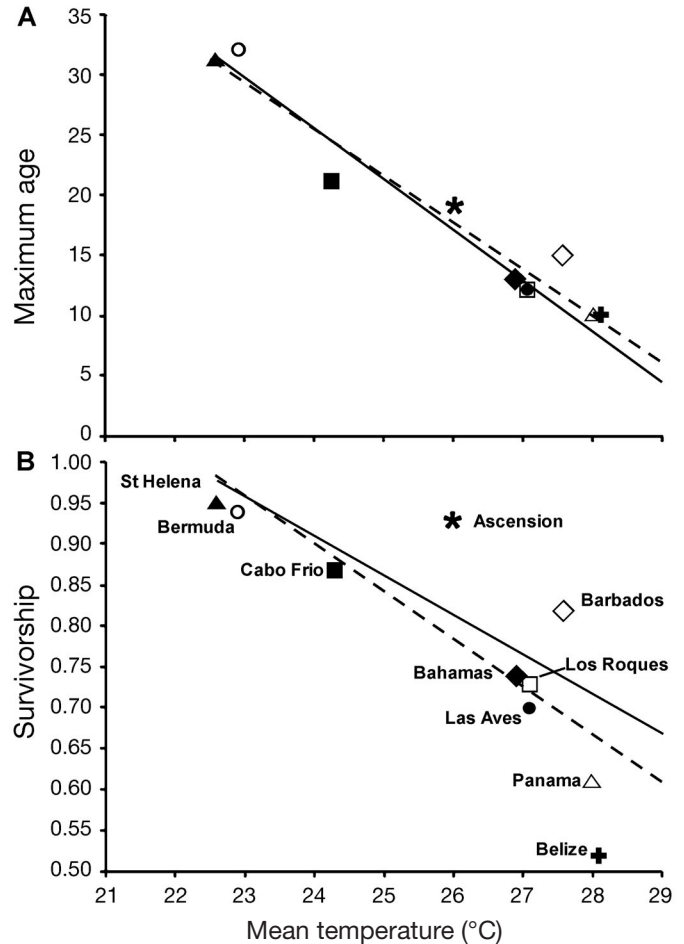


Fig. 2. *Acanthurus bahianus*. Relationships of (A) maximum longevity (age, yr) and (B) mean annual survivorship to mean sea temperature. Dashed lines: linear relationship for all 10 sites (from Robertson et al. 2005); continuous lines: relationship for 4 low-fishing sites (Ascension, Los Roques, Lee Stocking, St. Helena)

The inverse linear relationship between average adult survivorship and temperature across the 10 locations was weaker ( $r^2 = 0.67$ ; Fig. 2B) than that between maximum longevity and temperature. Survivorship deviated by more than 5% from the temperature-predicted, low-fishing level at 4 of 6 high-fishing locations (Fig. 2): exceeding this level by 8% at Barbados (the reverse of an expected fishing effect), and being lower than this level at Belize (by 20%), Las Aves (by 6%) and Panamá (by 12%) (the reverse of the expected fishing effect in each case). Survivorship was 3% greater at Los Roques than at Las Aves, the reverse of an expected fishing effect.

Thus, among the high-fishing locations, deviations from the temperature-predicted patterns were consistent with fishing effects in 2 of 6 cases for maximum longevity, but in none of 6 cases for survivorship.

Table 1. *Acanthurus bahianus*. Size at 16 locations (arranged in descending order of mean sea surface temperature, SST) with varying levels of fishing. Predicted max. SL: relationship between maximum standard length (SL) and temperature ( $y = -8.24x + 413.7$ ,  $r^2 = 0.65$ ) at all sites except those with moderate to heavy fishing; Median SL: of fish >8.5 cm SL, size of recruitment to trap-fishery at Jamaica (see Reeson 1983); Colombia data: for Punta Betin, Santa Marta, where there is a seasonal upwelling. Because this upwelling area is small, its temperature signal did not appear in the coarse-scale satellite data; hence we used onsite temperature records collected at this location during 1984 and 1985 (A. Acero pers. comm., who provided raw data from Duarte & Acero 1992). 1: present study; 2: Reeson (1983); 3: Sary et al. (1997) and Z. Sary (pers. comm. 2003); 4: Randall (1963), and J. E. Randall (pers. comm. 2003); 5: Garrison et al. (1998); 6: Chapman (1997); 7: Duarte & Acero (1992). Data in boldface relate to sites with high to moderate levels of fishing on the ocean surgeonfish

Location	Mean SST (°C)	Relative fishing pressure on <i>A. bahianus</i>	Year period	Max. SL (mm) Actual (predicted)	Median SL (mm) (% of max.)	Source
Belize	28.1	Low	2002	191 (181)	143 (75)	1
Jamaica						
Port Royal	28.0	<b>High</b>	<b>1970s</b>	<b>169 (183)</b>	<b>~115 (73)</b>	2
Pedro Cays	28.0	<b>Moderate</b>	<b>1970s</b>	<b>190 (183)</b>	<b>~132 (69)</b>	2
Pedro Bank	28.0	Low	1970s	190 (183)	~142 (74)	2
Serrania Bank	27.9	<b>Moderate</b>	<b>1970s</b>	<b>185 (184)</b>	<b>~152 (82)</b>	2
Discovery Bay	28.1	<b>High</b>	<b>1990s</b>	<b>209 (181)</b>	<b>~121 (58)</b>	3
Panamá	28.0	Low	1990s	198 (183)	134 (68)	1
St. John	27.6	Nil	1960s	184 (189)	nd nd	4
		<b>Moderate</b>	<b>1993–1994</b>	<b>244 (189)</b>	<b>172 (71)</b>	5 <sup>a,b</sup>
Barbados	27.6	<b>Moderate</b>	<b>1996</b>	<b>142 (186)</b>	<b>113 (80)</b>	6 <sup>a,b</sup>
		Low (marine reserve)	1996	152 (186)	127 (83)	6 <sup>a,b</sup>
		<b>Moderate</b>	<b>2000</b>	<b>142 (186)</b>	<b>119 (71)</b>	1
Los Roques	27.1	Nil	2000–2002	169 (190)	132 (78)	1
Las Aves	27.1	Nil	2002	174 (190)	140 (80)	1
Bahamas	26.9	Nil	2000	183 (191)	141 (77)	1
Colombia	26.8	Nil	1984–2005	221 (193)	140 (64)	7
Ascension	26.0	Nil	1997	210 (199)	173 (82)	1
Cabo Frio	24.3	Nil	1997	228 (213)	172 (75)	1
Bermuda	22.9	Nil	2001–2002	227 (223)	161 (71)	1
St. Helena	22.6	Nil	1997	220 (227)	183 (83)	1

<sup>a</sup>Calculated from SL = 0.84 (fork length), the measurement used in sources  
<sup>b</sup>Values from diver estimates of size; all other values are based on collections

### Variation in body size relative to fishing

The proportions of high-trapping and low-trapping site locations at which maximum size was less than that predicted by a size/temperature relationship were essentially the same: 3 of 7 high-trapping locations versus 6 of 13 low-trapping locations (Table 1). Relative median sizes in high-trapping populations did not consistently differ from those in low-trapping populations (Table 1): median values were 71 and 76%, respectively (Mann-Whitney *U*-test:  $p = 0.42$ ). The slightly larger maximum and relative median sizes (3 and 2%, respectively) of ocean surgeonfish at Las Aves than at Los Roques are consistent with a fishing effect. However, maximum sizes at both localities were less than that predicted by temperature (Table 1), indicating that some factor in addition to temperature and fishing affects size at both those islands.

Chapman (1997) made underwater visual estimates of size-frequency distributions of *Acanthurus bahianus* in shoreline habitat inside and adjacent to a reserve at

Barbados in 1996. His data show that maximum and median sizes were greater in the reserve than outside. Individuals that we collected at Barbados in 2000 across a broader range of non-reserve habitats had a larger maximum size than both reserve and non-reserve fish in 1996, but a smaller relative median size than either of those groups (Table 1). In all 3 cases (i.e. including the reserve) maximum size was less than that predicted by temperature.

Randall (1963) collected *Acanthurus bahianus* at St. Johns in the 1960s, before trap-fishing began in the area where he worked, but after selective fishing had greatly reduced the abundances of carnivorous reef-fishes (J. E. Randall pers. comm. 2003). About 30 yr later, after many years of intensive trap-fishing (see Rogers & Beets 2001), Garrison et al. (1998) visually estimated sizes of fish in traps in the general vicinity of Randall's (1963) study area. The maximum size of *A. bahianus* in the pre-fishing population (18.4 cm standard length, SL) was slightly less than that expected from the size/temperature relationship (Table 1). In

contrast, the 24.4 cm SL maximum length reported by Garrison et al. (1998) was considerably larger not only than that given by Randall (1963), but also than that predicted by local temperature, and than that we obtained in any collection elsewhere in this species' range (Table 1).

### Variation in adult abundance relative to fishing

Although densities varied considerably among locations, *Acanthurus bahianus* was a common species on reefs at all 12 locations that we censused: average

adult densities ranged from the equivalent of 100 to ~1600 fish ha<sup>-1</sup>, and maximum densities from 183 to 2400 ha<sup>-1</sup> (Table 2). The average density of adult *A. bahianus* varied 16.5-fold among 9 low-trapping locations (Table 2), and was not related to temperature ( $r = 0.04$ , not significant). Levels of variation between habitats at the same location ranged from 1.2- to 34.5-fold (median 3.1-fold) among locations, and, at the 5 locations at which we surveyed the greatest number of habitats, the level of between-habitat variation in density was similar to that among locations (Table 2).

To assess whether maximum and/or median size might be related to density (e.g. through an effect of competition) we examined 2 relationships between size and abundance at 8 low-trapping locations: density vs. % deviation from the temperature-predicted maximum, and density vs. relative median size. In neither case was there a significant relationship:  $r = -0.33$ ,  $p = 0.42$ ; and  $r = 0.47$ ,  $p = 0.24$ , respectively.

We have data from too few high-trapping locations to allow statistically rigorous assessments of the possible effect of intensive trapping on density. However, there is no suggestion that abundances were consistently low at high-trapping locations: average and maximum densities at 3 high-trapping locations ranged from 11.6 to 25.2 fish 300 m<sup>-2</sup> (median 14.4) and 13.8 to 31.7 fish 300 m<sup>-2</sup> (median 19.5), respectively vs. 3.0 to 49.4 fish 300 m<sup>-2</sup> (median 12.5) and 5.5 to 72.2 fish 300 m<sup>-2</sup> (median 17.8), respectively, at 9 low-trapping locations (Table 2). Further, the average density of ocean surgeonfish at Los Roques was 2.7 times that at Las Aves (Table 2), which is the reverse of the difference expected due to heavy selective fishing at Las Aves.

At Panamá, the abundance of adult *Acanthurus bahianus* varied 2.6-fold with an average of 25.5% deviation from the median over 19 yr. Although adult abundances were at the low end of the range in the last (1997) census, there was no persistent trend of change in numbers over that period (Fig. 3). Annual juvenile recruitment varied by an amount similar to adult abundances (range 3.9-fold, average = 28.3% deviation from the median value), and without any long-term trend of change (Fig. 3).

Table 2. *Acanthurus bahianus*. Density (no. fish 300 m<sup>-2</sup>) in relation to fishing pressure at 12 locations (high pressure locations in bold at top, low pressure locations at bottom). Densities derived from 10 × 30 m transects except where indicated

Location	Relative fishing pressure		Fish density		
	General	On <i>A. bahianus</i>	Habitat mean (SE)	n	Location avg.
<b>Barbados</b>	<b>High</b>	<b>High</b>	9.3 (1.9)	4	11.6
			13.8 (3.6)	5	
<b>St. Croix</b>	<b>High</b>	<b>High</b>	18.7 (5.8)	4	25.2
			31.7 (12.8)	4	
<b>St. Thomas</b>	<b>High</b>	<b>High</b>	19.5 (5.4)	4	14.4
			9.2 (1.9)	4	
Panamá	Moderate	Low	5.5 (2.3)	11	3.0
			0.5 (0.2)	10	
			2.9 (0.6)	22	
Las Aves	High	Nil	13.8 (3.2)	11	7.1
			0.4 (0.2)	10	
Bermuda	High	Nil	4.6 (1.0) <sup>a</sup>	8	8.6
			8.5 (1.6) <sup>a</sup>	8	
			16.3 (6.9) <sup>a</sup>	8	
			17.8 (1.4) <sup>a</sup>	8	
			4.0 (1.1) <sup>a</sup>	8	
			10.0 (3.5) <sup>a</sup>	8	
			7.7 (2.1)	28	
			10.2 (0.9)	26	
Cabo Frio	High	Nil	17.8 (0.3) <sup>b</sup>	105	17.8
Curaçao	High	Nil	52.4 (19.1)	6	49.4
			23.5 (11.5)	7	
			72.2 (11.7)	7	
Bahamas	Moderate	Nil	11.2 (2.3)	6	12.5
			13.7 (1.9)	5	
Bonaire	Moderate	Nil	12.2 (5.4)	5	13.5
			6.7 (1.2)	5	
			21.7 (8.3)	3	
Belize	Moderate	Nil	12.0 (3.0)	14	9.6
			7.1 (0.6)	7	
Los Roques	Very low	Nil	3.7 (1.0)	4	19.4
			34.5 (12.9)	6	
			37.7 (10.6)	16	
			1.6 (0.4)	10	

<sup>a</sup>Counts in 15 m diameter circles monitored for 12 mins: J. Pitt (unpubl. data)

<sup>b</sup>2 × 20 m transects censused by C. Ferreira (pers. comm. 2002)

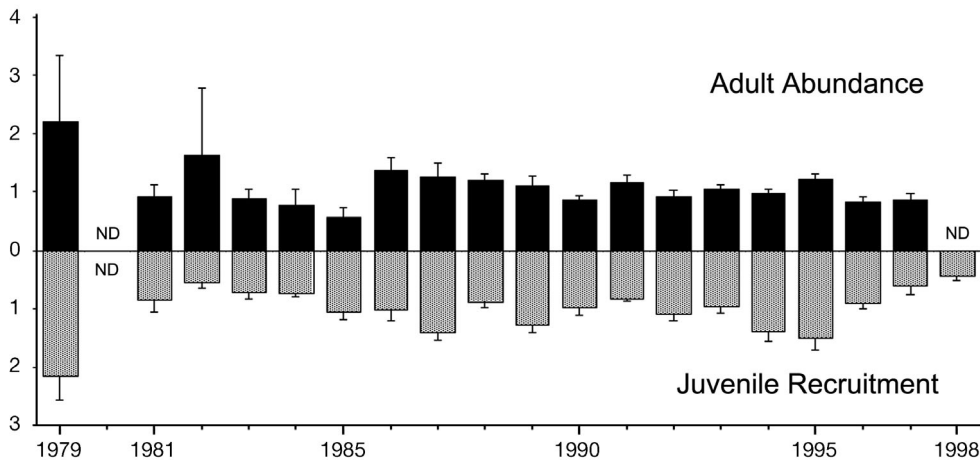


Fig. 3. *Acanthurus bahianus*. Interannual variation in adult abundance and juvenile recruitment at Panamá. ND: no data

## DISCUSSION

Intensive trap-fishing should lead to reduced longevity, size and abundance of *Acanthurus bahianus*. Selective fishing on predatory fishes that eat small reef-fishes, on the other hand, should reduce mortality on the ocean surgeonfish and lead to increased longevity and abundance. In a regional-scale comparison across a wider range of types of sites with greatly varying fishing conditions we found no consistent patterns of variation in those demographic features of the ocean surgeonfish that are attributable to these differing fishing effects. Choat et al. (2003) obtained similar results in a comparison of variation in the demography of a NW Atlantic parrotfish across 4 of the locations used in the present study.

### Longevity

The small amount of the 3.2-fold variation in the longevity of the ocean surgeonfish that was not explained by latitudinal variation in temperature did not follow patterns consistent with fishing effects. Longevity was neither unduly low at a location with heavy trap-fishing nor overly high at localities with heavy fishing on predatory reef-fishes. Similarly, variation in average adult survivorship was related to temperature, but not (in any consistent manner) to fishing. Longevity and survivorship were not greater at Las Aves (heavy fishing on predators) than in the Los Roques reserve.

### Size

Maximum and median length varied 1.4- and 1.6-fold, respectively, among localities. Maximum size of *Acanthurus bahianus* was related to temperature, although

less strongly so than was longevity (Robertson et al. 2005). The pattern of divergence from the temperature-predicted maximum size among heavy-trapping localities did not differ from that at low-trapping locations. Relative median size at heavily trapped locations also did not consistently differ from that at low-trapping sites. Change in size following several decades of intensive trap-fishing at St. John did not follow a clear pattern. At Las Aves the ocean surgeonfish reached a slightly larger size than at Los Roques, the only indication of an expected fishing effect on 3 demographic characteristics (size, longevity/survivorship, and abundance).

### Abundance

There was considerable (16-fold) variation in the average density of adult ocean surgeonfish among locations, but abundance was not consistently lower at heavily-trapped localities than at those with little or no trapping. We also found no relationship between size and average abundance in low-trapping areas, indicating that they vary independently and without mutually confounding effects that could obscure fishing effects. Contrary to expectations from a fishing effect, abundance was not greater at Las Aves than at Los Roques. Finally, there was no trend of change in the abundance of *Acanthurus bahianus* at the Panamá site over an 18 yr period during which juvenile recruitment rates remained fairly stable and the fisher population gradually increased by ~70%.

### Results of other studies

As an abundant, and conspicuous member of Caribbean reef-fish assemblages, the ocean surgeonfish has been included in various studies of effects of fishing in different parts of that area.



### Barbados

Chapman & Kramer (1999) compared sizes and abundances of 26 reef-fishes in areas of the same general habitat type inside and outside a reserve at Barbados. Densities of the ocean surgeonfish did not differ in these 2 areas. Although the average length of *Acanthurus bahianus* was 10% greater inside the reserve, Chapman & Kramer (1999) found that that difference was reduced to 1% when differences in microhabitat structure of the 2 areas were taken into account. Overall, when microhabitat differences were factored out, the number of species with higher densities in the reserve was reduced from 6 to 0, and the number with larger sizes inside the reserve from 12 to 1 (the latter being *A. bahianus*). This dissection of microhabitat effects on size and density, plus the fact that maximum size in the reserve is less than that predicted by temperature, make it difficult to definitely attribute any of the size characteristics of *A. bahianus* at Barbados to fishing effects. Chapman & Kramer's (1999) study is the only one to date in the Caribbean that has assessed reserve effects while controlling for variation in microhabitat characteristics among areas of equivalent habitat. It provides a clear demonstration that it is essential to take such microhabitat effects into account in studies of fishing effects on abundant, small, sedentary reef-fishes.

### Belize

Polunin & Roberts (1993) compared abundances, average sizes and biomass of fished reef-fishes in 1 reserve site vs. 4 nearby non-reserve sites on a section of the main barrier reef with intense commercial fishing plus heavy subsistence fishing that involved traps. They found more and larger individuals of ~25% of 40 species (including 2 *Acanthurus* spp, but not *Acanthurus bahianus*) inside the reserve, but no differences in the abundance and biomass of surgeonfishes (all species combined) in and out of the reserve. McClanahan et al. (2001) compared abundances of reef-fishes inside and outside a small no-take reserve in the lagoon of a ~300 km<sup>2</sup> oceanic atoll. The atoll, which is ~45 km off the mainland coast, had only ~20 resident subsistence fishers, but experiences selective commercial fishing for carnivorous reef-fishes (McClanahan et al. 2001). They found that abundances of 15 of 29 reef-fishes were higher inside the reserve. These included not only species commonly targeted by commercial and subsistence fishers (snappers and grunts), but also *A. bahianus* and several other species that were unlikely to be fished on that atoll. Greater abundances of non-target as well as target species in the reserve suggest

that a habitat effect was involved in producing some of the differences in density in and out of the reserve.

### Jamaica

Reef-fisheries at Jamaica are intense, and based on traps (Munro 1983, Koslow et al. 1989, 1994, Sary et al. 1997). Koslow et al. (1989) found large declines in catches of acanthurids (all species combined, no separate information on *Acanthurus bahianus*) in heavily fished areas of southern Jamaica between 1969 to 1973 and 1986. Sary et al. (1997) found that, following 4 yr of use of traps with an increased mesh size (which reduced catchability of small fish) at northern Jamaica, catch rates (biomass) of acanthurids (all species combined) increased, but without a consistent pattern of change in the mean size of *A. bahianus*. Those results and our analysis provide no clear indications of whether fishing affects the size of *A. bahianus* at Jamaica, although Koslow et al.'s (1989) results indicate a likely effect in the abundance of this species.

### Saba

Polunin & Roberts (1993) compared abundances of commercially fished reef-fishes (which include *Acanthurus* spp.) in and out of a reserve 4 yr after protection began. About a 25% of 34 species had more and larger individuals inside the reserve than outside. There was a higher biomass (but not numbers) of *A. bahianus* inside the reserve. When Roberts (1995) re-censused the same areas 2 yr later he found no differences in biomass or abundance of *A. bahianus* inside and outside the reserve.

### St. John

Beets (1997) found that the mean length of ocean surgeonfish trapped at this island declined by ~16% between 1982 to 1983 and 1993 to 1994. A range of other species showed much the same pattern. However, as indicated in 'Results' (second subsection), Garrison et al.'s (1998) data indicate that maximum size of ocean surgeonfish did not decline in that area between the 1960s and 1990s. Garrison et al. (1998) found that, in 1992 to 1994 the density of *Acanthurus bahianus* was higher inside a reserve than outside. However, catch rates of acanthurids (all species combined) actually increased between 1991 and 1994. Thus while some data from St. John do indicate adverse fishing effects on size and abundance of *A. bahianus*, others show unclear relationships with fishing.

The combination of our results and those described above indicate fishing has few strong and consistent effects on *Acanthurus bahianus* across a wide range of locations that might be expected to provide clear signs of such effects. Hence, fishing effects on *A. bahianus* may be likely to become universally evident only under catastrophic levels of fishing, i.e. where there are sustained, widespread, intensive trap-fisheries, such as have existed at Jamaica. However, even in such extreme situations, effects on the size of the ocean surgeonfish are unclear and data are lacking that would allow any rigorous assessment of effects on its abundance. The lumping of 3 *Acanthurus* species together during analyses in many studies hinders rather than facilitates assessment of fishing effects.

### CONCLUSIONS

Why should consistent and widespread fishing effects on *Acanthurus bahianus* not be readily evident? Both the demographic characteristics of this species and the extent of natural spatial variation in its demography likely are involved: populations of small, rapidly growing, early maturing, short-lived and abundant species are among those most resilient to fishing mortality (Adams 1980, Roff 1984, Musick 1999, Pope et al. 2000). *A. bahianus* exhibits such demographic characteristics, and most strongly so in the more tropical part of its range (Robertson et al. 2005), where fishing pressure on this species is highest it: is one of the most abundant small herbivores on reefs throughout its range, and is shorter-lived than other Caribbean members of its genus. This species has the most rapid growth to asymptotic size yet known for any acanthurid, and grows very little during its adult life. For a species with such growth characteristics it may not be surprising to find that fish size is unrelated to fishing pressure, at least across the gradient of fishing intensity we examined. The growth rate of this species varies inversely with temperature in a gradient that is sufficiently strong to enable all populations to reach ~90% of asymptotic size by 2 yr, even though there is 3-fold variation in terminal size among locations. Further, habitat variation in growth and terminal size at a single site can not only largely span the regional range of variation in both characteristics, but also follow different patterns at different locations. Abundance also varies greatly both among habitats at the same site and among locations. Hence strong habitat and latitudinal effects on growth, size and abundance may well overpower effects due to fishing in the sort of large-scale, regional comparisons that are commonly used to assess fishing effects.

Published studies of effects of fishing on reef-fishes that relied on comparisons of subpopulations in and out of reserves at the same location largely failed to demonstrate clearcut, consistent fishing effects on the size and abundance of *Acanthurus bahianus*. Chapman & Kramer's (1999) careful analysis of the situation at a single location, together with our results at a much larger spatial scale, indicate how detection of fishing effects is likely to be confounded by effects of habitat variation on size, growth and abundance across a range of spatial scales. Results of other investigations of (1) the degree of natural variation in the demography of reef-fishes among neighbouring reefs (Newman et al. 1995, Hart & Russ 1996, Gust et al. 2002, Kritzer 2002, Williams et al. 2003) and (2) the extent of habitat variation in growth, size and abundance within the same location (Kritzer 2002) reinforce the conclusion that it is essential to take habitat effects into account in future assessments of fishing effects (see also Willis & Millar 2005).

For large, mobile, wide-ranging, reef-fishes that occur at low densities, inter-reef comparisons similar to that we employed may be essential. Small-scale habitat effects such as those found by Chapman & Kramer (1999) are probably less relevant for such species than for small, common, sedentary species. However, larger-scale (among reef) location effects on natural variation in abundance, size and demography of large, mobile species cannot be ignored. For species with population and demographic characteristics like those of *Acanthurus bahianus*, assessments of fishing effects must involve comparisons of adjacent subpopulations in and out of no-take reserves (e.g. Willis et al. 2003a,b, Willis & Millar 2005) that control for both between- and within-habitat effects (cf. Chapman & Kramer 1999, and see also Willis et al. 2003b). No-take marine reserves are essential for determination of fishing effects because they allow the defining of (relatively) natural patterns of not only size and abundance but also longevity, survivorship, and growth of reef-fishes. All these characteristics may be affected by fishing and influence the ability of populations to cope with fishing (Berkeley et al. 2004). As Choat et al. (2003) pointed out, and our data on *Acanthurus bahianus* show, populations of abundant, short-lived, rapidly growing species are sufficiently resilient to fishing to be able to easily withstand the small amounts of sampling needed to establish demographic characteristics of populations within reserves.

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#### LITERATURE CITED

- Adams PB (1980) Life history patterns in marine fishes and their consequences for management. *Fish Bull US* 78: 1–12
- Anonymous (1982) Censos nacionales: VIII censo de población y vivienda de 1980. Vol 1. Lugares poblados de la Republica. Contraloría General de la Republica, Direccion de Estadística y Censo, Panama City, Panama
- Anonymous (2002) Censos nacionales: X censo de población y vivienda de 2000. Vol 1. Lugares poblados de la Republica. Contraloría General de la Republica, Direccion de Estadística y Censo, Panama City, Panama
- Beets J (1997) Can coral reef fish assemblages be sustained as fishing intensity increases. *Proc 8th Int Coral Reef Symp* 2:2009–2014
- Berkeley SA, Hixon MA, Larson RJ, Love MS (2004) Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* 29:23–32
- Chapman MR (1997) Coral reef fish movements and the effectiveness of the Barbados marine reserve. MSc thesis, McGill University, Montreal
- Chapman MR, Kramer DL (1999) Gradients in coral reef fish diversity and size across the Barbados marine reserve boundary: effects of reserve protection and habitat characteristics. *Mar Ecol Prog Ser* 181:81–96
- Chiappone M, Sluka R, Sealy KS (2000) Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. *Mar Ecol Prog Ser* 198:261–272
- Choat JH, Robertson DR, Akerman JL, Posada JM (2003) An age-based demographic analysis of the Caribbean stoplight parrotfish *Sparisoma viride*. *Mar Ecol Prog Ser* 246:265–277
- Duarte SA, Acero AP (1992) Ensayo de marcado-recaptura para la estimacion de tasas de crecimiento en peces arrecifales del genero *Acanthurus* en el Caribe Colombiano. *Caldasia* 17:115–120
- Dulvy NK, NVC Polunin, AC Mill, NAJ Graham (2004) Size structural changes in lightly exploited coral reef fish communities: evidence for weak indirect effects. *Can J Fish Aquat Sci* 61:466–475
- Edwards AJ (1990) The fish and fisheries of Saint Helena Island. University of Newcastle on Tyne, Newcastle
- Faunce CH, Lorenz JL, Ley JA, Serafy JE (2002) Size structure of gray snapper (*Lutjanus griseus*) within a mangrove 'no-take' sanctuary. *Bull Mar Sci* 70:211–216
- Froese R, Pauly D (eds) (2004) FishBase. www.fishbase.org
- Garrison VH, Rogers CS, Beets J (1998) Of reef fishes, overfishing and *in situ* observations of fish traps in St. John, U.S. Virgin Islands. *Rev Biol Trop* 46 (Supl 5):41–59
- Graham NAJ, Evans RD, Russ GR (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environ Conserv* 30: 200–208
- Gust N, Choat JH, Ackermann JL (2002) Demographic plasticity in tropical reef fishes. *Mar Biol* 140:1039–1051
- Hart AM, Russ GR (1996) Response of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks. III. Age, growth, mortality and maturity indices of *Acanthurus nigrofuscus*. *Mar Ecol Prog Ser* 136:25–35
- Hawkins JP, Roberts CM (2003) Effects of fishing on sex-changing Caribbean parrotfishes. *Biol Conserv* 115: 213–226
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA and 15 others (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638
- Jennings S, Polunin NVC (1996) Effects of fishing effort and catch rate upon the structure and biomass of Fijian reef fish communities. *J Appl Ecol* 33:400–412
- Koslow JA, Hanley F, Wicklund R (1989) Effects of fishing on reef fish communities of Pedro Bank and Port Royal Cays, Jamaica. *Mar Ecol Prog Ser* 43:201–212
- Koslow JA, Aiken K, Auil S, Clementson A (1994) Catch and effort analysis of the reef fisheries of Jamaica and Belize. *Fish Bull (Wash DC)* 92:737–747
- Kritzer JP (2002) Variation in the population biology of stripey bass *Lutjanus carponotatus* within and between 2 island groups on the Great Barrier Reef. *Mar Ecol Prog Ser* 243: 191–207
- McClanahan TR, McField M, Huitric M, Bergman K and 5 others (2001) Responses of algae, corals and fish to the reduction of macroalgae in fished and unfished patch reefs at Glover's Reef Atoll, Belize. *Coral Reefs* 19: 367–379
- Munro JL (1983) Coral reef fish and fisheries of the Caribbean Sea. *ICLARM Stud Rev* 7:1–9
- Munro JL (2000) Outmigration and movement of tagged coral reef fish in a marine fishery reserve in Jamaica. *Proc Gulf Caribb Fish Inst* 51:557–568
- Musick JA (1999) Criteria to define extinction risk in marine fishes. *Fisheries* 24:6–14
- Newman SJ, Williams DMcB, Russ GR (1995) Variability in the population structure of *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) among reefs in the central Great Barrier Reef, Australia. *Fish Bull (Wash DC)* 94:313–329
- Polunin NVC, Roberts CM (1993) Greater biomass and value of target coral-reef fishes in 2 small Caribbean marine reserves. *Mar Ecol Prog Ser* 100:167–176
- Pope JG, Macdonald DS, Daan N, Reynolds JD, Jennings S (2000) Gauging the vulnerability of non-target species to fishing. *ICES Mar Sci Symp* 57:689–696
- Randall JE (1963) An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. *Caribb J Sci* 3:31–47
- Randall JE (2002) Acanthuridae. In: Carpenter KE (ed) The living marine resources of the western central Atlantic, 3. FAO, Rome, p 1801–1805

- Recksiek CW, Appeldorn RS, Turigan RG (1991) Studies of fish traps as stock assessment devices on a shallow reef in south-west Puerto Rico. *Fish Res* 10:177–197
- Reeson PH (1983) The biology, ecology and bionomics of the surgeonfishes, Acanthuridae. *ICLARM Stud Rev* 7: 178–190
- Roberts CM (1995) Rapid build-up of fish biomass in a Caribbean marine reserve. *Conserv Biol* 9:815–826
- Robertson DR (1988) What determines abundances of adult surgeonfishes on patch reefs in Caribbean Panamá: settlement or post-settlement events? *Mar Biol* 97:495–501
- Robertson DR (1992) Patterns of lunar settlement and early-recruitment in Caribbean reef fishes at Panama. *Mar Biol* 114:527–537
- Robertson DR, Kaufmann KW (1998) Assessing early-recruitment dynamics and its demographic consequences among tropical reef fishes: accommodating variation in recruitment seasonality and longevity. *Aust J Ecol* 23:226–233
- Robertson DR, Swearer S, Kaufmann K, Brothers EB (1999) Settlement vs environmental dynamics in a pelagic spawning reef fish in Caribbean Panama. *Ecol Monogr* 69:195–218
- Robertson DR, Ackerman JL, Choat JH, Posada JM, Pitt J (2005) Ocean surgeonfish *Acanthurus bahianus*. I. The geography of demography. *Mar Ecol Prog Ser* 295:229–244
- Robichaud D, Hunte W, Chapman MR (2000) Factors affecting the catchability of reef fishes in antillean fish traps. *Bull Mar Sci* 67:831–844
- Rocha LA, Bass AL, Robertson DR, Bowen BW (2002) Adult habitat preferences, larval dispersal and the comparative phylogeography of 3 Atlantic surgeonfishes (Teleostei: Acanthuridae). *Mol Evol* 11:243–252
- Roff DA (1984) The evolution of life history parameters in teleosts. *Can J Fish Aquat Sci* 41:989–1000
- Rogers CS, Beets J (2001) Degradation of marine ecosystems and decline of fishery resources in marine protected areas in the US Virgin Islands. *Environ Conserv* 28:312–322
- Russ GR (2002) Yet another review of marine reserves as reef fishery management tools. In: Sale PF (ed) *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, New York, p 421–443
- Sary Z, Oxenford HA, Woodley JD (1997) Effects of an increase in trap mesh size on an overexploited coral reef fishery at Discovery Bay, Jamaica. *Mar Ecol Prog Ser* 154: 107–120
- Spalding MD, Ravilious C, Green EP (2001) *World atlas of coral reefs*. University of California, San Diego, CA
- Williams AJ, Davies CR, Mapstone BD, Russ GA (2003) Scales of spatial variation in demography of a large coral-reef fish—an exception to the typical model? *Fish Bull* (Wash DC) 101:673–683
- Williamson DH, Russ GR, Ayling AM (2004) No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. *Environ Conserv* 31:149–159
- Willis TJ, Millar RB, Babcock RC (2003a) Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *J Appl Ecol* 40:214–227
- Willis TJ, Millar RB, Babcock RC, Tolimieri N (2003b) Burden of evidence and the benefits of marine reserves: putting Descartes before des horses? *Environ Conserv* 30:97–103
- Willis TJ, Millar RB (2005) Using marine reserves to estimate fishing mortality. *Ecol Lett* 8:47–52

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