

# Protection of functionally important parrotfishes increases their biomass but fails to deliver enhanced recruitment

Shay O'Farrell<sup>1,2,3,\*</sup>, Alastair R. Harborne<sup>2,4</sup>, Yves-Marie Bozec<sup>1,2</sup>,  
Brian E. Luckhurst<sup>5</sup>, Peter J. Mumby<sup>1,2,4</sup>

<sup>1</sup>College of Life and Environmental Sciences, University of Exeter, Stocker Rd, Exeter, EX4 4QD, UK

<sup>2</sup>School of Biological Sciences, Goddard Building, University of Queensland, Brisbane, QLD 4072, Australia

<sup>3</sup>Smithsonian Marine Station, 701 Seaway Drive, Fort Pierce, Florida 34949, USA

<sup>4</sup>Australian Research Council Centre of Excellence for Coral Reef Studies, Goddard Building, The University of Queensland, Brisbane, QLD 4072, Australia

<sup>5</sup>2-4 Via della Chiesa, 05023 Acquafredda, Umbria, Italy

**ABSTRACT:** Burgeoning threats to coral reefs have prompted calls for management actions that can enhance ecosystem resilience, such as restoring herbivore populations whose grazing is critical to maintaining ecological function. However, lack of longitudinal datasets has hindered objective assessment of strategies aimed at recovering herbivory. Addressing this gap, we investigated the response of the Bermuda fish assemblage to a trapping ban that amounted to de facto protection of herbivorous parrotfishes (Scaridae). Hook-and-line fishing for piscivores continued during the ban, creating a natural experiment that freed scarids from both fishing mortality and adult-stage predation. Over the 9 yr study period, biomass of piscivores remained low because of the hook-and-line fishery, with the exception of trumpetfish *Aulostomus maculatus* whose biomass increased more than 6-fold. Although scarid post-recruit biomass increased by a factor of 3.7, there was no increase in recruits (<5 cm), contrary to our expectation of observing a stock–recruitment relationship (SRR) in a demographically closed system such as Bermuda. Although the unavoidable lack of a before–after–control–impact design in our study precludes making strong mechanistic inferences, we hypothesize that the observed increase in scarid biomass may indeed have driven a commensurate increase in larval settlement within this closed system, but density of settlers was subsequently regulated by *A. maculatus*, a predator of small fish that was free to respond to prey enrichment owing to the absence of large predators. Our results provide compelling evidence that scarid populations can rapidly recover from overfishing once protected, even if any SRR is decoupled.

**KEY WORDS:** *Aulostomus maculatus* · Coral reefs · Fisheries · Fish traps · Population regulation · Post-settlement mortality · Prey enrichment · Stock recruitment · Trumpetfish

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## INTRODUCTION

Fisheries science has traditionally been concerned with maximizing the yield from individual populations, but in recent years the research focus has shifted towards ecosystem-based management, where-

in the ecological contribution of species is considered when formulating management strategies (Francis et al. 2007, Hilborn 2011). This approach is particularly apposite in systems such as coral reefs, where fish contribute directly to processes that are vital in maintaining ecosystem function and the supply of eco-

\*Corresponding author: shay.ofarrell.ac@gmail.com

system services. For instance, the process of grazing plays a pivotal role in controlling the growth of reef macroalgae (Williams et al. 2001) that otherwise may negatively affect the ability of corals to maintain benthic dominance and of reefs to recover from disturbance (Mumby et al. 2006).

Until the early 1980s, the most important grazer in the wider Caribbean was the long-spined sea urchin *Diadema antillarum*, but the abrupt region-wide decline of the species (Lessios 1988) has left herbivorous fishes of the family Scaridae (parrotfishes) in the role of dominant grazers (Mumby et al. 2006). However, region-wide overfishing has driven declines in populations of most fishes (Jackson et al. 2001), including scarids (Hawkins & Roberts 2004). Limiting or banning fishing for scarids thus has the potential to be a locally achievable and low-cost management strategy to improve reef resilience to disturbances (Mumby et al. 2012).

Releasing scarids (or any taxon) from heavy fishing would be expected to drive an increase in local population biomass owing to a reduction in adult mortality rates, regardless of whether the population is self-recruiting (closed) or seeded from upstream (open). In a closed system, population recovery rate may be further amplified through a positive feedback, whereby an increase in local breeding biomass drives a commensurate increase in local settler density; this is known as the stock–recruitment relationship (SRR). In practice, coral reef fish SRRs have proven extremely difficult to quantify (Haddon 2011), and post-settlement processes, especially early-stage predation, heavily modify or decouple any numerical relationship between adult density and recruit den-

sity in model species such as pomacentrids (damselfishes; e.g. Hixon & Carr 1997) and chaetodontids (butterflyfishes; e.g. Webster 2002).

The opportunity to tease apart the recovery dynamics of a heavily fished community and to quantify an SRR for scarids was presented by the existence of a unique dataset documenting a natural experiment on predator-depleted reefs in Bermuda. In an attempt to reverse the severe decline in fish stocks that had occurred in the 1970s and 1980s, Bermuda implemented a total ban on the use of fish traps in April 1990 but allowed hook-and-line fishing to continue (Luckhurst 1996, 1999), creating an ecosystem-scale experiment. Traps are relatively non-selective gears and retain species from all guilds, including large numbers of herbivores (Koslow et al. 1994, Hawkins et al. 2007). Hook-and-line fishing, on the other hand, tends to select for piscivores (Dalzell 1996). The continuation of Bermuda's hook-and-line fishery after the trapping ban took effect meant that predator populations continued to be suppressed after herbivore populations were released (Trott & Luckhurst 2007), amounting to a de facto ban on fishing for herbivores while continuing to control their putative predators.

Our Bermuda dataset has a number of advantages for investigating scarid recovery dynamics. The archipelago lies nearly 1000 km from its nearest neighbour (Fig. 1), which is an order of magnitude greater than the maximum distance over which demographically relevant recruitment of reef fish is likely to take place (Cowen et al. 2006). As a result, local population dynamics are likely to be more tightly coupled than in open systems into which larvae are

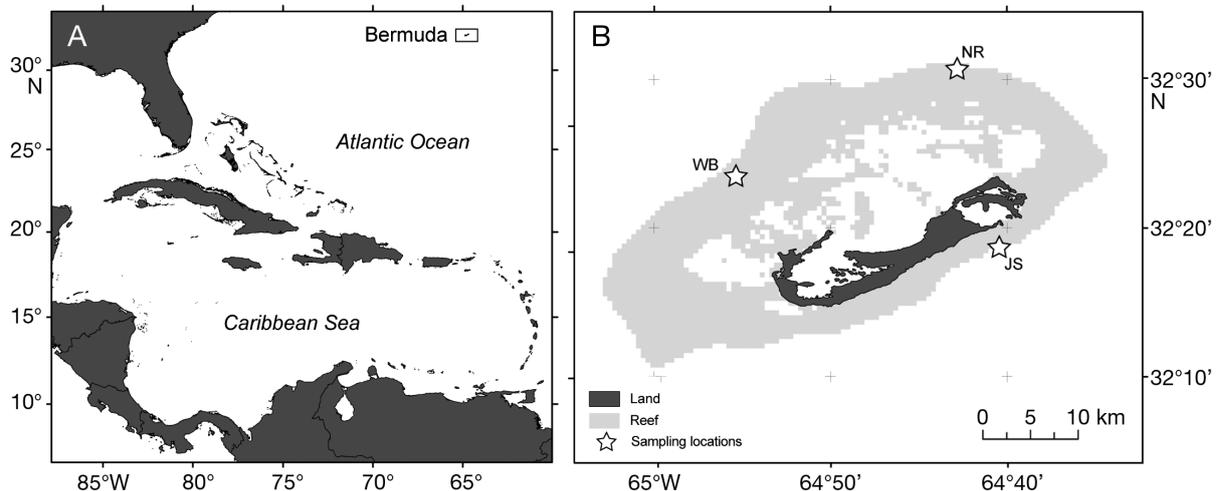


Fig. 1. (A) Position of Bermuda in the western Atlantic Ocean and (B) the 3 sampling locations on the Bermuda reef platform. NR: North Rock; JS: John Smith's Bay; WB: West Blue Cut. National political boundaries from Wessel & Smith (1996); coral reef locations from World Resources Institute (2011)

imported and out of which they are exported. Our data were gathered during a large number (984) of visual census surveys conducted by the same surveyor (B. E. Luckhurst) over a 9 yr period following the imposition of the ban, meaning that our results are not confounded by shifting observer bias. The data were gathered across all 4 seasons (although not necessarily in every year, Table 1), and so seasonal effects are also likely to be minimal.

Taking advantage of the natural experimental setup, we investigated the responses to the trapping ban of Bermuda's scarids and also the most abundant predators, comprising the families Serranidae (groupers), Sphraenidae (barracudas), Lutjanidae (snappers), Carangidae (jacks) and Aulostomidae (trumpetfishes). We hypothesized that: (1) the biomass of predators would remain constant or decline owing to the hook-and-line fishery; (2) the biomass of scarids would increase because of the release from heavy trap-fishing mortality; and if so, then (3) the abundance of scarid recruits (<5 cm fork length, FL) should also increase, as Bermuda is a demographically closed system, and a numerical SRR may be detectable.

## MATERIALS AND METHODS

### Study site and survey protocol

Bermuda is a sub-tropical archipelago in the North Atlantic, consisting of 7 principal islands that lie along the southeast edge of an extensive reef platform. The archipelago is located approximately 1000 km east of the continental USA (Fig. 1). Prior to the imposition of the trapping ban in 1990, traps were the major source of fishing mortality in scarids, which were commonly the most abundant species group in trap landings from the reef platform (Luckhurst 1999). Other methods of fishing for scarids, including spearfishing, were minimal in Bermuda following the trapping ban (B. E. Luckhurst pers. obs.), and fishing for scarids using any gears was completely banned in 1993 (Luckhurst 1999).

Between June 1991 and December 1999, the same surveyor (B. E. Luckhurst) conducted a total of 984 underwater fish surveys at 3 sites, viz. John Smith's Bay, North Rock and West Blue Cut (Fig. 1B, Table 1).

Table 1. Underwater visual censuses (n = 984) of fish in forereef habitats conducted in Bermuda following a trap-fishing ban imposed in 1990, detailed here by year and by month. All data (species, abundance, life phase and body size) were collected by the same surveyor

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Sum
1991	-	-	-	-	-	27	36	30	30	30	30	10	193
1992	30	20	10	40	-	-	-	-	-	-	-	10	110
1993	-	-	24	-	-	23	-	-	14	-	-	-	61
1994	24	24	24	24	24	24	24	24	24	20	24	24	284
1995	-	8	8	24	16	8	24	-	16	16	24	-	144
1996	8	-	24	24	-	16	-	-	24	-	8	8	112
1997	-	-	-	-	-	-	24	-	-	-	-	-	24
1998	-	-	-	-	-	-	-	-	-	-	-	8	8
1999	16	8	-	-	-	16	-	-	-	-	-	8	48

The study sites were chosen to represent a wide geographical range of similar reef platform habitat. All 3 sites were on the seaward side of the breaking reefs that line the perimeter of the Bermuda platform, and contained over 10 000 m<sup>2</sup> of relatively homogenous habitat with a depth range of 9 to 12 m. We selected survey locations haphazardly at each site.

The surveyor conducted stationary underwater visual censuses between 10:00 and 15:00 h, following the method of Bohnsack & Bannerot (1986). Using a tape measure for calibration, the surveyor visualized a cylinder of radius 7.5 m extending from the substrate to the surface. Each census consisted of 3 stages: (1) identification of species, (2) quantification of larger individuals and (3) quantification of cryptics. (1) Rotating slowly within the cylinder, the surveyor first identified all of the species he could observe within the cylinder, taking as long as necessary to do so. (2) He then spent a subsequent period of approximately 10 min quantifying the abundance and body size of all individuals within the cylinder. (3) Finally, he spent approximately 2 min quantifying small individuals within and near the substrate at the base of the cylinder. To account for varying survey duration, the surveyor recorded the time taken to conduct the quantification stages of each census so that metrics could be later standardised per unit time. The surveyor recorded body size as FL to the nearest centimetre. Further details of the survey protocols and site description are given by Luckhurst (1999).

### Study species and data analysis

We aggregated the species biomass data at family level for the most abundant piscivores, with the exception of serranids, which we subdivided into

2 groups by body size. The piscivore groups (with species in parentheses) were: (1) large Serranidae/groupers (*Mycteroperca bonaci*, *M. interstitialis*); (2) Sphyraenidae/barracudas (*Sphyraena barracuda*); (3) Carangidae/jacks (*Seriola rivoliana*, *S. dumerili*, *Caranx ruber*); (4) Lutjanidae/snapper (*Lutjanus griseus*, *L. synagris*); (5) Aulostomidae/trumpetfishes (*Aulostomus maculatus*); and (6) small Serranidae/groupers (*Cephalopholis fulva*, *C. cruentata*, *Epinephelus guttatus*). For the scarids, we examined both family biomass and abundance data. We use the term 'recruits' to mean scarid individuals <5 cm FL and 'post-recruits' to mean all larger individuals. The scarid species (with common names in parentheses) we investigated were *Scarus vetula* (queen), *S. taeniopterus* (princess), *S. iseri* (striped), *Sparisoma viride* (stoplight) and *Sparisoma aurofrenatum* (redband). To minimize identification error, the data for all scarid individuals <5 cm FL were pooled as 'scarid recruits'.

During data analysis, we converted observed length to estimated biomass using empirical length-to-weight conversion parameters, using mean values calculated from multiple studies for each species (Froese & Pauly 2013). Duration varied among surveys, and so we standardised the biomass data to 1 min periods, which we refer to as 'standardised biomass'. To accommodate varying survey effort among sites and to avoid pseudo-replication resulting from site effects, the data were pooled and averaged separately for each site in each year. Models were then fitted using the 3 site means as replicates in each year.

We assessed changes over time in the population recovery variables of interest (e.g. biomass, abundance) for the species groups, using nonlinear least squares (NLS) regression (NLS2 package in R; Grothendieck 2013). NLS fitting assumes Gaussian error distribution, and because our 0-bounded data were right-skewed, we transformed the response variable using  $\log(x+1)$  transformation. We checked residuals for homogeneity of variance using plots of residuals versus fitted values to confirm that no error structure was visible, and for approximate normality using quantile-quantile plots of standardised residuals versus fitted values (Crawley 2007).

We assessed 3 biomass growth models (Table 2) to determine which best fit the data. First, we fitted a simple linear model, followed by a Ricker model

Table 2. Growth models fitted to Bermuda time series data for fish populations

Model	Equation	Parameters
Linear	$a + bt$	$a$ is the intercept, $b$ is the slope, and $t$ is time, expressed as years since fishery closure
Ricker	$N_0 + (bt)e^{-kt}$	$N_0$ is initial population size, $b$ is the slope of the curve at $t_0$ , $e$ is the base of the natural logarithm, and $k$ is the initial rate of decline
Logistic	$a + \left( \frac{b-a}{1 + e^{r(d-t)}} \right)$	$a$ and $b$ are the left and right hand asymptotes, $r$ is the growth rate, and $d$ is the inflexion point of the curve

which allows for an initial peak followed by a subsequent decline (Ricker 1954), and finally a logistic model which reaches an asymptote at carrying capacity, achieving its maximum growth rate at half that capacity (Verhulst 1845).

To assess the goodness of fit of the models, we performed likelihood ratio tests (Ritz & Streibig 2008), whereby the likelihood of each candidate model was tested against that of a null model, here a straight line with a slope of 0 whose intercept is the general mean of the response variable. When multiple models were deemed to be 'likely' at a 95% confidence level, we chose the optimal model using Akaike's information criterion (AIC, Akaike 1974).

## RESULTS

### Time series of piscivore data

The biomass of large serranids (Fig. 2A) and sphyraenids (Fig. 2B) did not decrease significantly over the study period (Table 3). Carangid biomass increased for the first 4 yr and then declined over the rest of the time series (Fig. 2C), eventually dropping to below its initial value. Lutjanids (Fig. 2D) showed no significant change. It is not possible to select between the linear and Ricker model fits for small serranids (Fig. 2E) based on the AIC value ( $\Delta < 2$ ), but the likelihood ratio ( $Q = 0.672$ ) implies that the linear model is unlikely to fit better than a null model, and we conclude that no change in biomass occurred. The biomass of *Aulostomus maculatus* increased slowly at first, then rapidly increased for the remainder of the study (Fig. 2F), growing by a factor of 6.6 between Years 1 and 9. The best fitting model (logistic, Table 3) predicts that the biomass had not reached carrying capacity by the end of the time series and may have continued to grow.

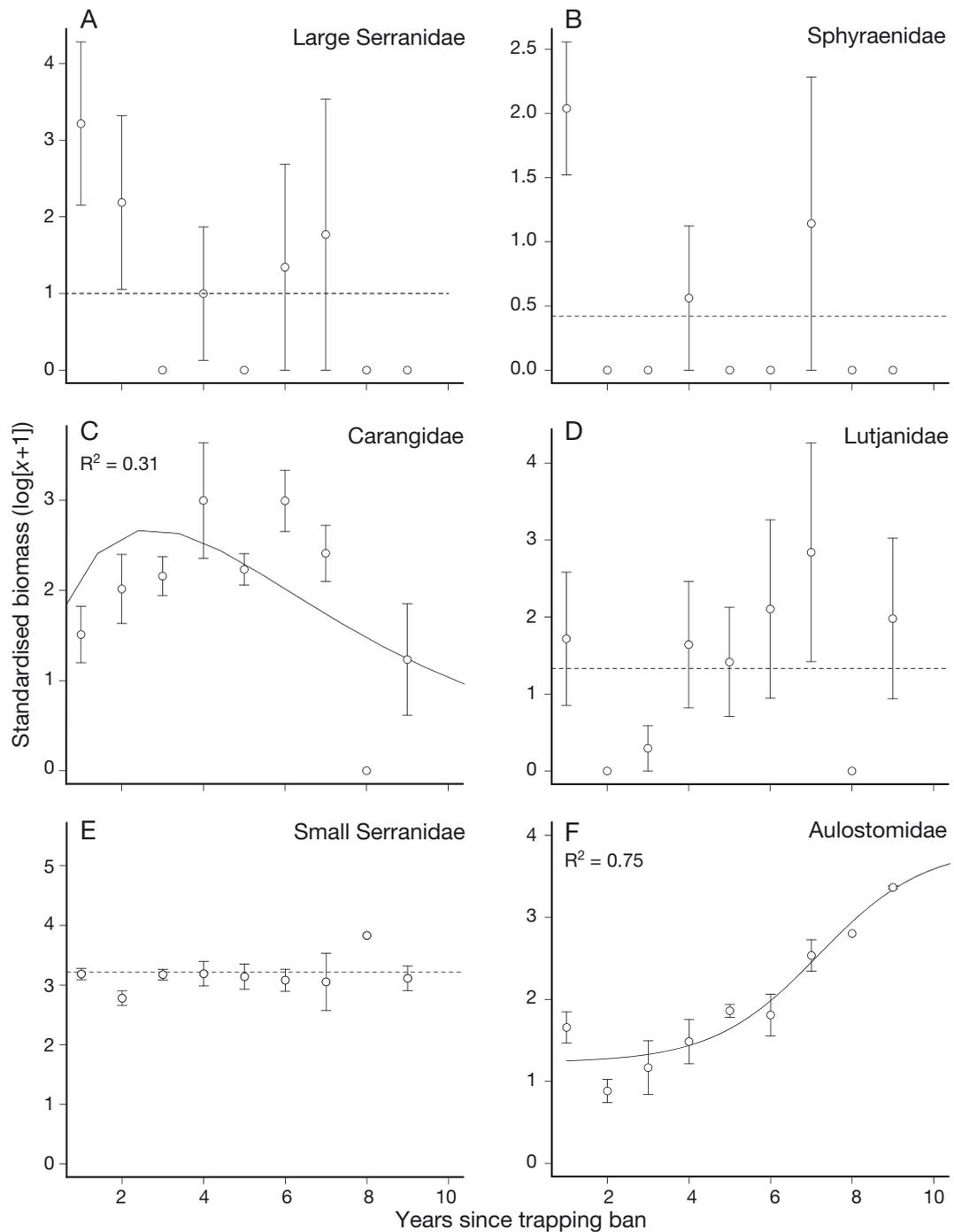


Fig. 2. Time series of biomass data ( $\pm 95\%$  CI) for the most abundant predator families in the Bermuda dataset. Solid lines indicate best model fits to  $\log(x+1)$  transformed field data, and nonlinear  $R^2$  approximations are given in the panels. Dashed lines represent mean values of field data and indicate no detectable trend. Fitted parameter values, log-likelihood ratio test results and Akaike's information criterion (AIC) values are given in Table 3

To provide a more detailed investigation of the biomass growth observed in *A. maculatus*, we analysed data for body size and abundance separately. Mean  $\pm$  SE body size grew linearly across the study period (Fig. 3A), increasing significantly from  $42 \pm 2$  cm FL

in Year 1 to  $56 \pm 3$  FL in Year 9 ( $t_{35} = -4.1951$ ;  $p < 0.001$ ). The change in *A. maculatus* abundance (Fig. 3B) lagged behind the change observed in biomass (Fig. 2F) and did not begin to increase until near the end of the study period.

Table 3. Population growth models and fitted parameter values for the Bermuda piscivore data plotted in Figs. 2 & 3. Log-likelihood ratio tests were performed to determine whether the data were more likely under each candidate model than under a null model, which was a line whose intercept was the overall mean of the data and whose slope was 0. Where the data were deemed likely (i.e.  $p \leq 0.05$ ) for multiple models, Akaike's information criterion (AIC) values were used to select the best fitting models (in **bold**). Equations for the growth models are shown in Table 2. Blank cells indicate non-convergence of the fitting algorithm (i.e. no good fit)

Estimated parameters	Null		Linear		Ricker			Logistic									
	a	AIC	a	b	$N_0$	b	k	a	b	r	d	p	AIC				
Large serranid biomass	<b>1.05</b>	<b>108.48</b>	2.35	-0.26	0.115	110.16											
Sphyraenid biomass	<b>0.42</b>	<b>77.42</b>	0.95	-0.21	0.296	76.98											
Carangid biomass	1.95	82.6	2.51	-0.11	0.342	82.5	<b>0.11</b>	<b>2.09</b>	<b>0.3</b>	<b>0.017</b>	<b>76.5</b>						
Lutjanid biomass	<b>1.33</b>	<b>103.62</b>	0.78	0.11	0.622	104.67											
Small serranid biomass	<b>3.15</b>	<b>26.24</b>	3.01	0.02	0.281	25.7	3.01	0.02	0.01	0.468	27.7						
<i>Aulostomus maculatus</i> biomass	1.62	75.74	0.69	0.25	<0.001	36.9	0.69	0.24	0	<0.001	38.7	<b>3.86</b>	<b>-2.63</b>	<b>-0.77</b>	<b>7.18</b>	<b>&lt;0.001</b>	<b>31.1</b>
<i>A. maculatus</i> mean size	47.23	1580	<b>37.86</b>	<b>2.39</b>	<b>&lt;0.001</b>	<b>1530</b>	37.6	2.5	0.1	<0.001	1541	<b>0.05</b>	<b>0.16</b>	<b>1.58</b>	<b>8.59</b>	<b>&lt;0.001</b>	<b>-1485</b>
<i>A. maculatus</i> abundance	0.16	-3756	0.04	0.01	0.914	-1431	0.04	0.03	0.01	<0.001	-1429						

Table 4. Population growth models and fitted parameter values for Bermuda scarid data plotted in Fig. 4. See details in Table 3 legend

Estimated parameters	Null		Linear		Ricker			Logistic									
	a	AIC	a	b	$N_0$	b	k	a	b	r	d	p	AIC				
Post-recruit biomass	5.83	44.4	4.93	0.18	<0.001	3.1	4.27	0.62	0.11	<0.001	-17.7	<b>4.77</b>	<b>1.42</b>	<b>1.29</b>	<b>2.87</b>	<b>&lt;0.001</b>	<b>-22.8</b>
Post-recruit abundance	1.03	-104	0.76	0.06	<0.001	-592	0.64	0.16	0.09	<0.001	-650	<b>0.71</b>	<b>0.49</b>	<b>0.93</b>	<b>2.78</b>	<b>&lt;0.001</b>	<b>-654</b>
Recruit abundance	0.6	738	<b>0.77</b>	<b>-0.04</b>	<b>0.007</b>	<b>730</b>											

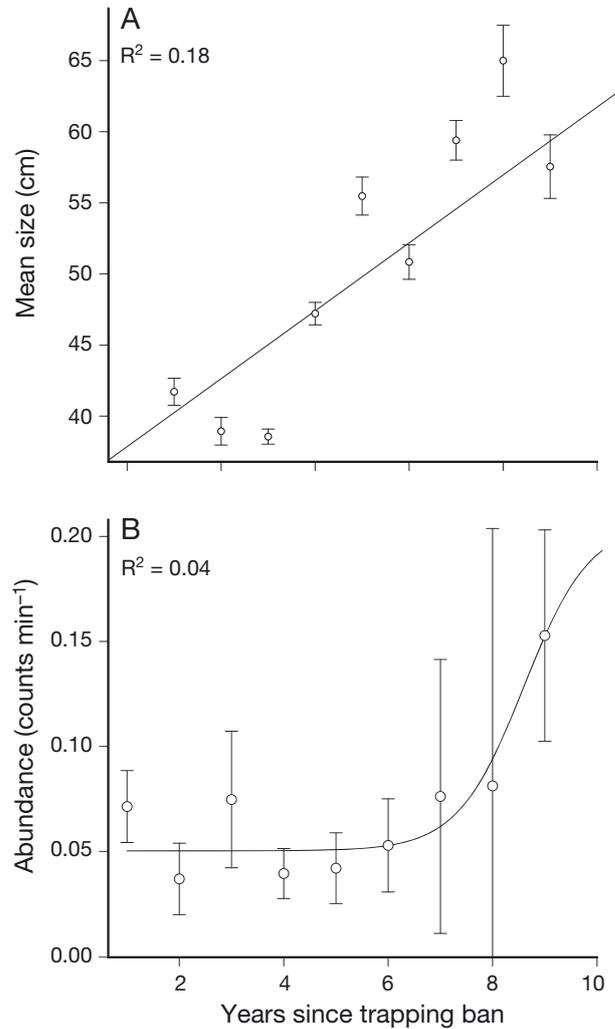


Fig. 3. Model fits to time series data ( $\pm$  95% CI) for *Aulostomus maculatus* mean (A) body size (fork length) and (B) abundance in Bermuda. Solid lines indicate best model fits to  $\log(x+1)$  transformed field data, and nonlinear  $R^2$  approximations are given in the panels. Fitted parameter values, log-likelihood ratio test results and Akaike's information criterion (AIC) values are given in Table 3

### Time series of Scaridae data

The aggregated biomass of post-recruitment (>5 cm FL) individuals for all scarid species increased (Table 4) by a factor of 3.7 (Fig. 4A), and abundance increased by a factor of 2.5 (Fig. 4B). Recruit abundance decreased significantly ( $F_{1,330} = 5.35$ ;  $p = 0.03$ ), although the negative slope is influenced disproportionately by exceptionally high values in Year 3 (Fig. 4C) and was not significant in the absence of this outlier.

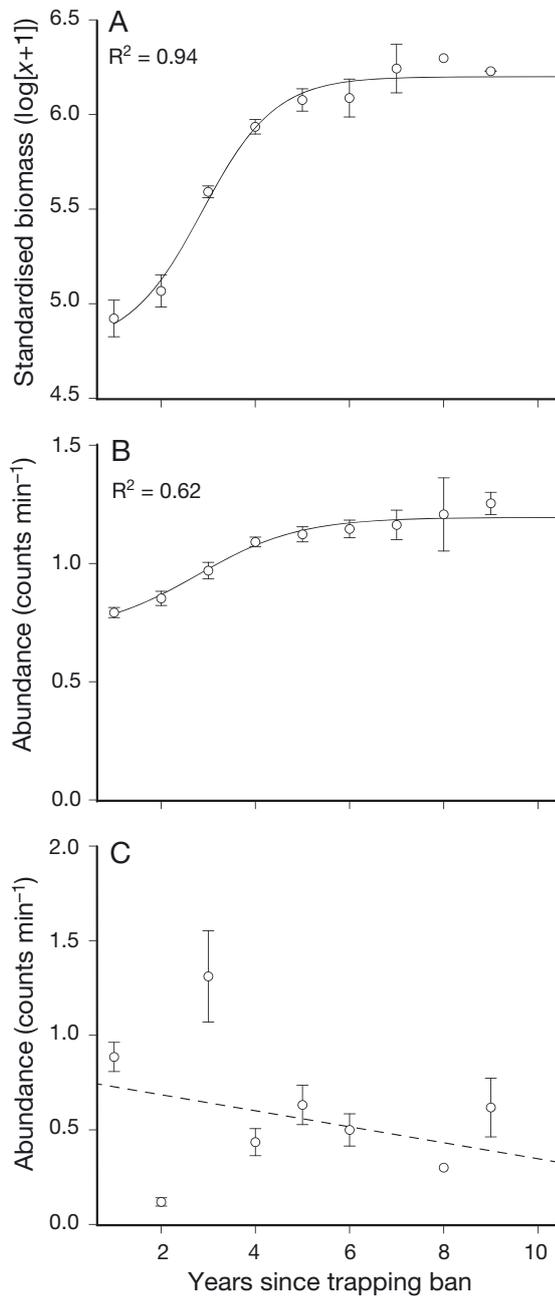


Fig. 4. Model fits to time series data ( $\pm 95\%$  CI) for (A) scarid post-recruit biomass, (B) post-recruit abundance and (C) recruit abundance in Bermuda. Solid lines indicate best model fits to field data, and nonlinear  $R^2$  approximations are given in the panels. Fitted parameter values, log-likelihood ratio test results and Akaike's information criterion (AIC) values are given in Table 4. Although the negative slope of the linear model fitted to the recruit abundance data is statistically significant, the model is heavily influenced by extreme values recorded in Year 3, which are statistical outliers. As a result, we have illustrated the fit using a dashed line as we do not interpret the data to mean that recruitment was decreasing, but rather that the overall pattern across the 9 yr dataset is one of fluctuating recruitment with no strong trend

## DISCUSSION

Our analysis showed that Bermuda piscivore biomass decreased or remained constant over the 9 yr study period following the trap-fishing ban, with the exception of the trumpetfish *Aulostomus maculatus*. The biomass of *A. maculatus* increased by a factor of 6.6, and the best-fitting model indicated that biomass growth might have continued after the data-gathering period. However, there was a marked lag before any change in *A. maculatus* abundance was observed, and the biomass growth was initially driven by the observed increase in mean body size. The biomass of post-recruit ( $>5$  cm FL) scarids increased by a factor of 3.7 and abundance increased by a factor  $\sim 2.5$ . However, the abundance of scarid recruits ( $<5$  cm FL) did not increase, despite our expectation of observing a positive SRR in Bermudan scarids. We discuss our results, focusing on (1) the lack of a scarid SRR, and (2) the startling growth in aulostomid biomass. Although the lack of a before-after-control-impact (BACI) design in our dataset precludes making strong inferences about ecological mechanisms, we speculate from our results that these 2 unexpected findings may be connected.

Although it is notoriously difficult to find empirical evidence for the existence of SRRs in reef fishes (Haddon 2011), we expected that fishes which can spawn on a daily basis (scarids), in a demographically isolated reef system such as Bermuda (Cowen et al. 2006), with depleted predator populations, that experiences a large increase in adult breeding stock, would provide an excellent opportunity to observe an SRR. However, this was not the case, and the observed increase in post-recruit biomass must have been driven solely by release from fishing mortality without the positive feedback of an SRR.

There are at least 4 mechanisms that could explain a lack of increase in the supply of juveniles despite an increase in post-recruitment biomass within a closed system. First, reef habitat quality could have deteriorated during the study, leading to increased juvenile mortality. However, a recent meta-analysis of benthic data by Colella et al. (2014) determined that Bermudan coral cover has not declined, and may even have increased, over the past few decades at a wide range of study sites across the reef platform, including sites close to our own. As a result, we assume that habitat quality did not decline over the course of our study and therefore the lack of SRR cannot easily be explained by systematic loss of habitat quality.

Secondly, processes in the larval planktonic phase may have regulated the abundance of scarids settling to the reef such that larval supply remained relatively unaffected by a nearly 4-fold rise in post-recruitment biomass. Although we cannot rule out this mechanism completely, we feel that it is unlikely because previous studies have shown that the abundance of settling scarids displays an extremely high degree of temporal fluctuation (Vallès et al. 2008), implying that planktonic regulation is not strong prior to arrival at the reef.

Thirdly, post-settlement mortality may have decoupled the SRR through intraspecific competition for food or habitat. In terms of food, scarids are primarily algal grazers, and the extremely high productivity of their food resources (Bruggemann et al. 1994) means that food availability is unlikely to be limiting on most reefs. Although habitat quality does not appear to have declined in Bermuda (Colella et al. 2014), it would still be plausible that an increase in scarid settler density would intensify competition for refuges within the structurally complex habitat (Hixon et al. 2002, 2012), and individuals near the habitat periphery would be more vulnerable to predators of early life stage fish.

Finally, responses to prey enrichment by the predators themselves could have regulated scarid recruit abundance. Of the piscivore data we examined, the only species to increase following the fishing ban was *A. maculatus*. Aulostomids have to date attracted scant interest from applied or theoretical ecologists, and little is known about them. *A. maculatus* prey on small and/or settlement-stage fishes (Randall 1967), and their presence induces classic anti-predator responses in small fishes, including juvenile scarids (Wolf 1985).

Characterized by an exceedingly slender body and elongate mouth, *A. maculatus* can occasionally be seen hovering within traps on the seabed, but they are not retained when the trap is hauled, as they easily swim through the mesh (S. O'Farrell pers. obs.). Furthermore, they were not considered to be taken by the Bermuda trap fishery (B. E. Luckhurst pers. obs.) and are rarely, if ever, present in trapping study data (e.g. Wolff et al. 1999). As a result, trap fishing mortality is likely to be negligible for this species, and it likely did not benefit from reduced mortality resulting from the Bermuda trapping ban, leaving the striking increases observed in *A. maculatus* biomass (Fig. 2F), body size and abundance (Fig. 3) unexplained.

Although the unavoidable lack of a BACI design in our study precludes making strong inferences about

mechanisms, we can offer a parsimonious and testable hypothesis to unite our 2 least-expected results, namely (1) that the observed increase in scarid post-recruit biomass did not induce any increase in recruit abundance, and (2) that the *A. maculatus* population grew so strikingly following a trap-fishing ban from which it would not be expected to benefit. We propose that the observed increase in scarid biomass may indeed have induced a commensurate increase in the density of larvae settling from the plankton to Bermuda's reefs, but that *A. maculatus* benefitted from prey enrichment by these settlers, thereby regulating scarid recruit density without the mesopredator itself being regulated owing to the lack of large predators. Interestingly, in a region-wide study of Caribbean predatory fish assemblages, Stallings (2009) found that *A. maculatus* populations appear to thrive on heavily fished reefs where populations of large predators are depleted, hypothetically allowing this relatively unstudied mesopredator to capitalize on larval fluctuations without itself being subjected to top-down regulation.

A predator such as *A. maculatus* may respond to prey enrichment and regulate prey populations through a number of mechanisms, including aggregative (Hassell & May 1974), developmental (Murdoch 1971), behavioural (including functional) and numerical responses (Holling 1959). Although our census data, by their nature, preclude commenting on the first 2 mechanisms, the data may provide some preliminary insight into the latter two. A functional response involves a change in predator food intake as prey availability changes, and numerical response involves a change in predator reproductive rate as prey availability changes (Holling 1959).

The initial increase we observed in *A. maculatus* mean body size, with no change in abundance, is consistent with the scenario of the mesopredator initially responding to prey enrichment by increasing its consumption rate, viz. a functional response. Although we do not have behavioural observations to corroborate that a functional response occurred, the observed increase in mean body size is difficult to explain otherwise. Reproductive output tends to scale with body size in teleost fishes (Muñoz & Warner 2004), so after mean body size had increased, *A. maculatus* would have been in a position to convert the biomass gains from the functional response into a numerical response (Holling 1959), which has never been documented in a wild fish population (White et al. 2010). A lagged numerical response would explain the late increase observed in *A. maculatus* abundance. Although the mean values for body size

increased consistently for the last 6 yr of the study, we emphasize that the final data point heavily influences the model fit.

If our hypothesis is correct in that a lack of large predators in Bermuda allowed the aulostomid to respond without regulation to prey enrichment from juvenile scarids, then this may have implications for management. (1) Wherever populations of large coral reef predators are reduced, as is presently the case in much of the western Atlantic (including inside marine protected areas, MPAs), then recovery of fish populations may presently be dampened by unregulated responses by aulostomids, which usually go unstudied. A useful line of investigation may thus be to determine whether interventions to regulate mesopredators of settlement-stage fish to 'natural' (i.e. pre-fishing) densities are likely to promote the recovery of management target species such as scarids, serranids and lutjanids. (2) In a related point, MPAs are sometimes employed as tools for recovering lost grazing function, based on the reasoning that spillover of adult and larval scarids will repopulate surrounding non-protected areas. Obviously, grazing benefits of adult-stage spillover would be lost if fishing for scarids continued in non-protected areas. However, if our aulostomid-release hypothesis is correct, this would also imply that larval scarid spillover benefits in non-protected areas may be lost if aulostomids can respond unchecked to prey enrichment because of the absence of large predators to control their biomass. On predator-depleted reefs, MPAs may not be as useful for recovering grazing function in the short term as banning fishing for herbivores throughout the reefscape. However, whenever an MPA has been successful in recovering populations of large-bodied predators, then the aulostomid population may be regulated and predation mortality reduced in juvenile scarids, although the demographic benefits would of course trade off against increased predation mortality in adult scarids.

We stress that both of these arguments are speculative, despite arising from our results, and we offer them as points for discussion rather than as recommendations at this time. Our aulostomid-release hypothesis is testable, however, and if correct, experimental manipulation of aulostomid density should have a quantifiable effect on early-life-stage survival in fishes that recruit directly to the reef.

Although our study has produced unanswered questions, it has also provided compelling evidence that banning of traps and other fishing methods that impact scarids may be an effective means of rapidly recovering lost grazing function. That scarid biomass

recovered by a factor of 3.7 within only a few years, despite the lack of a quantifiable SRR, is good news for Atlantic coral reefs and supports managers taking local measures to enhance reef resilience in the face of a changing climate.

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