Rapid Recovery of Parrotfish (Scaridae) and Surgeonfish (Acanthuridae) Populations Following the Fish Pot Ban in Bermuda

Recuperación Rapida de las Poblaciones de Loros (Scaridae) y Navajones (Acanthuridae) Luego de la Prohibición del Uso de Nasas en Bermuda

Rétablissement Rapide des Populations de Poisson Perroquet (Scaridae) et Chirurgien (Acanthuridae) Suite à L'interdiction des Nasses à Poisson aux Bermudes

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ABSTRACT

This paper analyzes the response of the Bermuda coral reef fish assemblage to a fish pot ban that amounted to *de facto* protection of herbivorous parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) after years of heavy fishing pressure. Hook-and-line fishing continued following the fish pot ban, and the differential impact of the two gear types on scarids and their predators created a 'natural' experiment that provides valuable insight into community recovery dynamics. We found that post-recruitment (> 5 cm FL) parrotfish biomass increased by a factor of 3.72 and abundance by a factor of 2.46. The asymptote in scarid biomass was attained in 5 - 6 years. The biomass of the dominant acanthurid increased by a factor of 3.5 and reached an asymptote in only 4 years. However, there was no increase in abundance of scarid recruits (< 5 cm FL) in this same time period, contrary to our expectation of observing a stock-recruitment relationship (SRR) in a demographically closed system such as Bermuda. As expected, biomass of most mesopredators remained low or decreased over the nine-year study period in those species susceptible to the ongoing hook-and-line fishing pressure. The changes in abundance of large predators e.g. black grouper (*Mycteroperca bonaci*), could not be properly assessed with the stationary census technique used due to their large home range and diver avoidance. Our study provides a rare insight into coral reef community recovery dynamics and demonstrates that when extirpated populations of herbivores are protected, the recovery of their biomass – and by inference their grazing function – can be rapid.

KEY WORDS: Coral reef fish, logistic growth, mesopredator, recovery, trap fishery, trapping ban

INTRODUCTION

Concerns about the capacity of coral reefs to endure an increasing number of threats has focused attention on identifying mechanisms to enhance ecosystem resilience, such as restoring overfished herbivore populations. Grazing by herbivores is critical to maintaining reef ecological function and plays a pivotal role in controlling the growth of reef macroalgae (Williams et al. 2001) that otherwise may impact negatively on the ability of corals to maintain benthic dominance and of reefs to recover from disturbance (Mumby et al. 2006). Until the early 1980s, the primary 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 parrotfishes (Scaridae) in the role of paramount grazers (Mumby et al. 2006). However, region-wide overfishing has driven declines in populations of most fishes (Jackson et al. 2001) including grazers (Hawkins and Roberts 2004). Restoring overfished populations of parrotfishes thus has the potential to be a locally achievable and low-cost management strategy to improve reef resilience to disturbances. However, a lack of longitudinal datasets detailing the response of coral reef fish communities to effective fishing gear restrictions has impeded the development of evidence-based strategies to help managers achieve their intended objectives.

Here we present an analysis of a nine-year fishery-independent dataset from underwater visual surveys to investigate the responses of herbivores (Scaridae, Acanthuridae) and a common mesopredator (Serranidae) to a trapping ban on Bermuda's reefs. Traps are one of the most commonly used fishing gears on Caribbean reefs (Gobert 1998) and their depletory effects on fish populations are well documented (e.g., Ferry and Kohler 1987, Wolff et al. 1999, Hawkins et al. 2007). In an attempt to reverse the severe decline in grouper stocks that had occurred in the late 1970s and 1980s, Bermuda implemented a total ban on the use of fish pots in April 1990 but allowed hook-and-line fishing to continue (Luckhurst, 1996). The Bermuda trapping ban is of particular interest to management science as it amounted to an ecosystem-scale 'natural' experiment. Traps are a relatively non-selective gear type 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 (Trott and Luckhurst 2007) meant that most predator populations continued to be controlled after herbivore populations were released, amounting to a *de facto* ban on fishing for herbivores while controlling predation on their adult stages. In addition, the family Scaridae was added to Bermuda's Fisheries Protected Species list in 1993, only three years after the fish pot ban, to ensure that these important grazers could not be taken by any gear type including spearfishing (Luckhurst, personal observation).

MATERIALS AND METHODS

Study Site and Survey Protocol

Bermuda is a sub-tropical archipelago in the north Atlantic, consisting of seven principal islands that lie along the southern edge of an extensive reef platform. The archipelago is located approximately 1000 km east of the continental USA (Figure 1A).

A total of 984 underwater fish surveys were conducted by the same surveyor (B.E.L.) between June 1991 and December 1999 at three sites, Western Blue Cut, North Rock and John Smith's Bay (Figure 1B and Table 1) using the stationary visual census method of Bohnsack and Bannerot (1986). The reef area at each survey site (Figure 1B) was larger than 1,200 m² and the habitat was considered to be relatively homogenous. All censuses were conducted at depths between 9 and 12 m and between 1000 and 1500 hours. Stationary surveys were located haphazardly at each site. Using a tape measure to define a radius of 7.5 m, the diver visualized a cylinder extending from the substrate to the surface. Rotating slowly within the cylinder, the diver initially listed the species observed within the cylinder, and then recorded the abundance and estimated the fork length (FL) of individuals to the nearest centimeter. The diver then searched for small fishes sheltering within or near the substrate at the base of the cylinder. Total survey time taken ranged between 10 and 15 minutes. To minimize identification error, the data for scarids smaller than 5 cm FL were pooled. Further details of the survey protocols and site description are given in Luckhurst (1999).

Study Species

The scarid species included in our analysis were: *Scarus taeniopterus* (princess parrotfish, the most abundant scarid in the surveys), *Scarus vetula* (queen), *Sparisoma viride* (stoplight), *Sparisoma aurofrenatum* (redband) and *Scarus iseri* (striped), the least abundant species. Only two species of acanthurids were included, the Ocean surgeon (*Acanthurus bahianus*) and the blue tang (*A. coeruleus*). For the scarids and acanthurids, both individual and family biomass and abundance data were examined. One of the most common mesopredators on Bermuda's reefs, the Coney *Cephalopholis fulva*, subjected to heavy line fishing pressure (Trott and Luckhurst 2007) was also assessed. We use the term 'recruits' to mean post-settlement individuals (~2 - 5 cm FL) that are still vulnerable to predation from most mesopredators but are small enough to be capable of taking refuge within much of the reef matrix. All individuals larger than 5 cm FL we term as 'post-recruits'.

Data Analysis

Biomass was calculated using empirical length-to-weight conversion parameters (Froese and Pauly 2013). As duration varied among surveys, biomass data were standardized to one-minute periods, hereafter referred to as standardized biomass. Models were fitted using nonlinear least squares (NLS) regression, which assumes Gaussian error distribution. However, our zero-bounded data were right-skewed, so the response variable underwent log+1 transformation and residuals were subsequently checked

Table 1. Total number of surveys conducted on the reefs of Bermuda in each year. The fish pot ban was imposed in 1990.

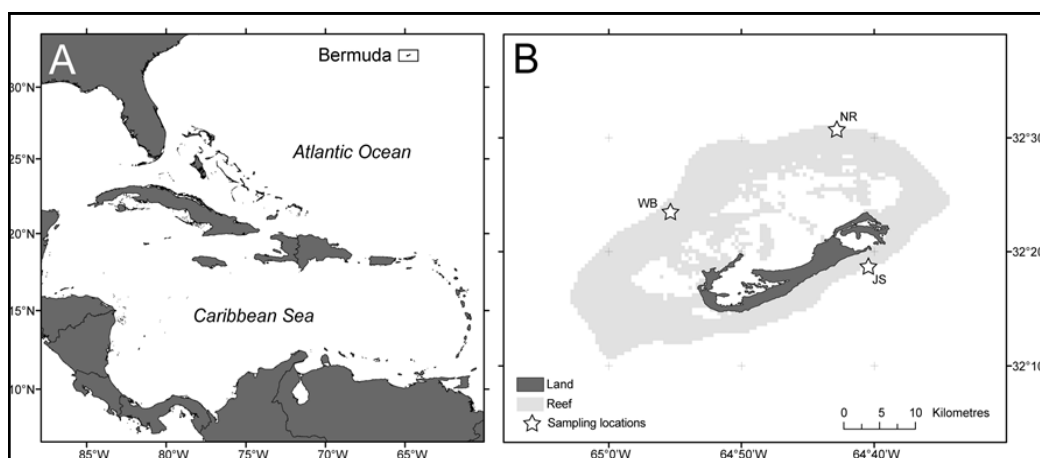| Year	1991	1992	1993	1994	1995	1996	1997	1998	1999
Surveys	193	110	61	284	144	112	24	8	48

Total = 984

Figure 1. Position of Bermuda in the western Atlantic Ocean (A) and the three sampling locations on the Bermuda reef platform (B). NR, North Rock; JS, John Smith's Bay; WB, West Blue Cut. Coral reef locations from World Resources Institute (2011).

for normality using quantile-quantile plots of standardized residuals versus fitted values (Crawley 2007).

Three growth models (Table 2) were assessed to determine which best fit the data, and were fitted to the field data using nonlinear least squares regression (Grothendieck 2013). First, a simple linear model was fitted, followed by a Ricker model 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 non-linear models, likelihood ratio tests (Ritz and Streibig 2008) were carried out, whereby the likelihood of each candidate model was tested against that of a null model, here a straight line with a slope of zero whose intercept is the general mean of the response variable. When multiple models were deemed to be 'likely' at a 95% confidence level, the optimal model was chosen using Akaike's Information Criterion (AIC, Crawley 2007).

RESULTS

Time Series of Scarid Population Data

The biomass data for the most abundant scarid species, *Scarus taeniopterus* (princess parrotfish), was well described by a logistic curve ($r^2 = 0.85$) with the population reaching an asymptote by year 5 (Figure 2A). The growth in *Sc. vetula* (queen parrotfish) biomass was also best described by a logistic curve (Figure 2B) but the fit was not as good ($r^2 = 0.68$). This species curve reached an asymptote in year 6. *Sparisoma viride* (stoplight parrotfish) was also best described with a logistic curve ($r^2 = 0.79$) reaching an asymptote in year 6 (Figure 2C) while *Sp. aurofrenatum* (redband parrotfish) biomass reached an asymptote (logistic, $r^2 = 0.88$) in year 5 (Figure 2D). The least common scarid species in our analysis, the striped parrotfish *Sc. iseri*, did not show any significant change in biomass and the data are not plotted. When the biomass data from all five scarid species are pooled (Figure 2E), the logistic model provides an exceptionally good fit to the data ($r^2 = 0.94$). The aggregate biomass of all post-recruitment parrotfish increased by a factor of 3.7 (Figure 2E) and abundance increased by a factor of 2.5.

Time Series of Acanthurid Population Data

With respect to acanthurids, only two species were included in our analysis. The most abundant species was *Acanthurus bahianus* (ocean surgeon) whose biomass increase was also best described by the logistic model ($r^2 = 0.85$). The population reached an asymptote in year 5 (Figure 2F). The other acanthurid *A. coeruleus* (blue tang) was patchy in the surveys and change in biomass was best described by a Ricker model suggesting an initial increase and then subsequent decline in biomass (Figure 2G), although the fit is poor ($r^2 = 0.40$). However, when these two datasets were combined, the resulting aggregate biomass was best described by the logistic model ($r^2 = 0.84$) with the asymptote being reached at year 4 to 5 (Figure 2H), increasing by a factor of 3.27 between 1991 and 1999.

Time Series of Coney Population Data

The coney is an abundant mesopredator on Bermuda's reefs and was subjected to substantial line fishing pressure following the fish pot ban (Trott and Luckhurst 2007). One year before the ban (1989), coney comprised over 20% of total grouper landings as it replaced the larger species whose populations had declined dramatically (Luckhurst 1996). One year after the fish pot ban (1991), coney comprised almost 50% of total grouper landings (Trott and Luckhurst 2007) with all landings coming from hook-and-line fishing alone. When examining biomass data from coney, we see that there is no significant change ($F_{[1,22]} = 0.526$; $p = 0.476$) in biomass over the nine-year study period (Figure 2I).

DISCUSSION

Following the trap-fishing ban in Bermuda, the biomass of post-recruitment (> 5 cm FL) parrotfishes (Scaridae) increased by a factor of 3.7 and abundance by a factor of 2.5 over a period of only nine years. The parrotfishes in our study are all relatively fast-growing species, and even the larger-bodied species such as *Sparisoma viride* achieve sexual maturity within around one year (vanRooij et al. 1996), reach half their asymptotic body size within two years (vanRooij et al. 1995) and have a maximum life span of nine years (Choat et al. 2003).

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	$a + \left(\dfrac{b-a}{1 + e^{r(d-t)}} \right)$	*a* and *b* are the left and right hand asymptotes, *r* is the growth rate and *d* is the inflexion point of the curve

Table 3. Population growth models and fitted parameter values for Bermuda scarid data (Figure 4).

Response variable	Linear		Ricker			Logistic			
	a	b	N_0	b	k	a	b	r	d
Post-recruit biomass	4.93	0.18	4.27	0.62	0.11	4.77	1.42	1.29	2.87
	(AIC = 3.1)			(AIC = -17.7)			(AIC = -22.8)		
Post-recruit abundance	0.76	0.06	0.64	0.16	0.09	0.71	0.49	0.93	2.78
	(AIC = -592)			(AIC = -650)			(AIC = -654)		
Recruit abundance	0.77	-0.04	NC			NC			
	(p = 0.03)								

NC, Non-convergence of the fitting algorithm – no good fit

These life history characteristics collectively suggest that parrotfishes are strong candidates to make a rapid recovery from a perturbation such as the cessation of trap fishing. Indeed, our data show that the populations reach new equilibria in only 5 - 6 years after the ban. However, given that piscivore populations continued to be depleted during the study period, the magnitude of the recovery seems modest in comparison to that observed on Kenyan reefs, where McClanahan et al. (2007) conducted a space-for-time study of the recovery of reef fish communities from decades of overfishing.

Using the model parameters presented in McClanahan et al. (2007), we can broadly compare the recovery of scarid biomass in Bermuda and Kenya, standardizing the values for both countries by expressing them as proportional increases from their respective initial conditions. The two recovery trajectories closely track each other for the first four years after fishery closure, by which time scarid biomass has recovered by a factor of 2.75 in Bermuda and 2.64 in Kenya (Figure 5 in McClanahan et al. 2007). What is strikingly different is that scarid biomass in Bermuda then rapidly slows to reach an asymptote by year six, achieving a total recovery factor of only 3.7, whereas Kenyan scarid biomass continues to increase until around year 20 with a total recovery factor of 10.6. That the recovery of scarids was so much greater in Kenya is particularly noteworthy given that predation would also be expected to increase over time within recovering no-take areas (Micheli et al. 2004), contrasting with the situation in Bermuda.

Although it is difficult to robustly compare Bermudian reefs with Kenyan reefs, both are historically productive reef systems that had supported large fisheries for many decades. Even so, alternative hypotheses could be formulated to explain the difference in scarid recovery between the countries. For example, initial conditions may have been markedly different, with Kenyan populations having been more heavily depleted prior to the fishery closure than Bermudian populations, thereby having greater recovery potential. Although reliable data on scarid abundance do not exist for Bermuda for the period prior to the ban, traps are known to have impacted heavily on parrotfishes throughout the wider Caribbean (Hawkins and Roberts 2004). There is anecdotal evidence of declines in scarid abundance in the 1980s (Luckhurst, personal observation) and it is not plausible that decades of intensive trap fishing in Bermuda did not substantially deplete local parrotfish populations as occurred elsewhere in the Caribbean region.

Another hypothesis explaining the difference between Kenyan and Bermudian scarid recovery factors is that parrotfish carrying capacity differs between the systems. However, to explain the magnitude of the observed difference would require that Kenyan reefs have three times the scarid carrying capacity of Bermudian reefs, which is unconvincing even without considering biomass losses to recovering piscivore populations in Kenyan no-take zones .

After the fish pot ban, it is clear that black grouper (*Mycteroperca bonaci*) abundance started to increase as this species was taken almost entirely by fish pots before the ban (Luckhurst 1996). However, this increase would have been little detected in the visual census data as these large groupers tend to avoid divers. Limited stomach contents data from black grouper (Luckhurst, unpublished data) indicates that this species does prey on scarids as large groupers are primarily ambush predators. Predation attempts on scarids by black grouper at a multi-species scarid spawning aggregation site in Bermuda are detailed in Luckhurst (2011).

Our study contributes to the body of literature supporting the evolving paradigm that fisheries impacts must be considered at an ecosystem level. Even species that are not primary fisheries targets but are generally regarded as bycatch may be severely affected by non-selective gears, e.g. fish traps and when such species perform vital ecological roles such as grazing, fisheries must be managed explicitly to mitigate impacts on their populations.
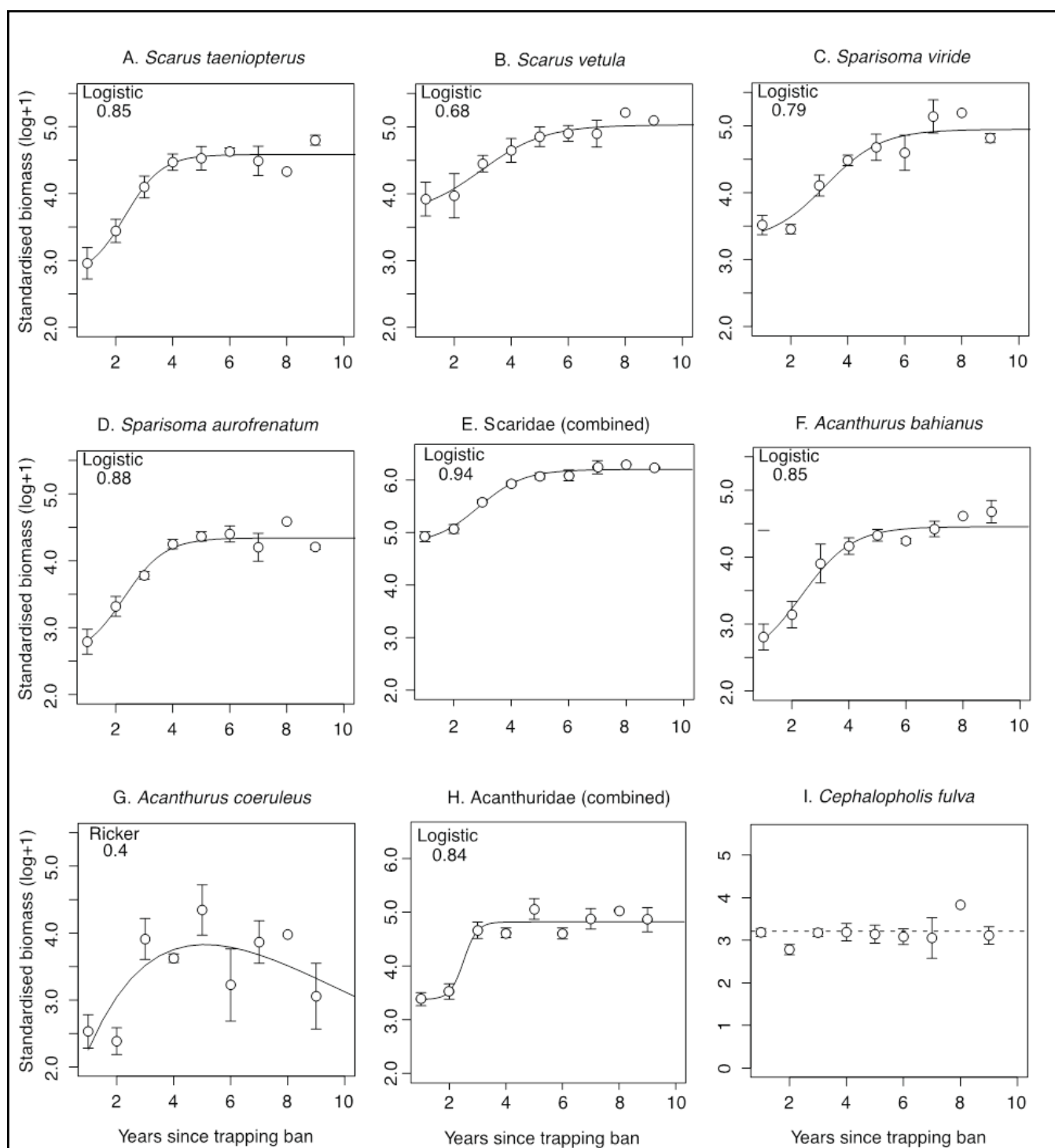
Figure 2. Growth curves fitted to scarid, acanthurid and serranid biomass data gathered across a nine-year period following the imposition of a ban on fish pots (traps) in Bermuda. White markers indicate mean values, and error bars show 95% confidence intervals. The best fitting growth model for each taxon is plotted and identified in the top left of the panels, along with the nonlinear approximation of r^2. As indicated in the vertical axis label, the data were log+1 transformed for model fitting and so the recovery factors reported in the text were calculated using anti-logged values. Note that the vertical scale varies in family level panels, E and H. No significant change over time was found in the coney data (Panel I), and the dashed line plotted is the overall mean of the time series.

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