



*Journal of Fish Biology* (2009) **75**, 2509–2526

doi:10.1111/j.1095-8649.2009.02451.x, available online at [www.interscience.wiley.com](http://www.interscience.wiley.com)

## Small-scale demographic variation in the stoplight parrotfish *Sparisoma viride*

M. J. PADDACK\*, S. SPONAUGLE AND R. K. COWEN

*Rosenstiel School of Marine and Atmospheric Science, Division of Marine Biology and Fisheries, 4600 Rickenbacker Causeway, Miami, FL 33149, U.S.A.*

(Received 30 September 2008, Accepted 13 August 2009)

Age-based analysis of the stoplight parrotfish *Sparisoma viride* was used to examine whether observed differences in their abundance and size structure among reefs in a cross-shelf portion of the upper Florida Keys could be explained by variation in demographic rates. Annual and daily sagittal otolith increments were enumerated for 176 individuals collected from replicates of reefs in two strata, inshore and offshore reefs (2–6 m depth). von Bertalanffy growth functions fitted to size-at-age plots for each site were similar between reefs within each stratum (inshore and offshore), but differed between strata. *Sparisoma viride* on offshore reefs attained greater average standard length ( $L_S$ ) at age, greater mean asymptotic size and were longer lived than fish from inshore reefs. Fish on inshore reefs attained only half the maximum age observed on offshore reefs (4 v. 8 years, respectively). No terminal phase fish >4 years of age were found on either reef type. Estimates of mortality rates from age-frequency data of collected fish revealed higher mortality on inshore reefs. Demographic variables obtained in this study were similar to published values for *S. viride* from Caribbean reefs but differed significantly from published values from reefs at a similar latitude (Bahamas), reflecting high demographic plasticity on both local and regional scales.

© 2009 The Authors

Journal compilation © 2009 The Fisheries Society of the British Isles

Key words: demographic plasticity; growth rate; mortality; otoliths; Scaridae; spatial variation.

### INTRODUCTION

Demographic plasticity is an important adaptation to potentially highly variable environments experienced by reef fishes and is a widespread phenomena both within and across reef fish taxa (Warner & Downs, 1977; Pauly, 1998; Gust *et al.*, 2002; Robertson *et al.*, 2005). For example, large-scale trends, such as latitudinal variation in size and growth, have been noted in fish populations and suggested to be a counter-gradient adaptation to temperature regimes (Yamahira & Conover, 2002). Variation in the abundance and size structure of reef fishes, however, can occur across several scales, and small-scale variation can be strong (Kingsford & Hughes, 2005; Núñez Lara *et al.*, 2005; Ruttenberg *et al.*, 2005). If this multiscale aspect of demographic rates is not recognized and accounted for, broad-scale interpretations may be

\*Author to whom correspondence should be addressed at present address: Santa Barbara City College, Biology Department, 721 Cliff Drive, Santa Barbara, CA 93109, U.S.A. Tel.: +1 805 9650581, ext. 2328; fax: +1 805 7303050; email: [michelle.paddack@gmail.com](mailto:michelle.paddack@gmail.com)

compromised. Unfortunately, the source and magnitude of small-scale variation in population structure is not well documented, particularly because it can be impossible to determine from the observational data whether population structure is shaped by intrinsic variation in demographic rates (e.g. growth and mortality) or by extrinsic factors such as habitat quality or recruitment rates. To understand patterns in population structure, it is therefore necessary to properly identify and partition sources of variation in demographic rates. Age-based approaches enable the estimation of vital rates such as growth and mortality, providing a means of determining whether variation in population structure is due to variation in demographic rates and lending insight into the importance and magnitude of small-scale variation. While still relatively scarce, recent age-based studies indicate that growth rates and longevity can vary across a range of spatial scales including latitudinal (22°, Choat *et al.*, 2003), cross-shelf (20 km, Gust *et al.*, 2002) and both within and between neighbouring reefs (Clifton, 1995; van Rooij *et al.*, 1995).

Reef fish population size and structure can have important ramifications for the benthic ecosystem. Herbivorous fishes in particular have received increasing attention in recent years due to their strong role in shaping the distribution, community structure, standing crop and production rates of benthic algae on coral reefs (Carpenter, 1986; Bellwood & Choat, 1990; Russ, 2003). By moderating algal growth on coral reefs, herbivorous fishes increase the ability of reefs to resist or recover from loss of live coral cover, an increasing problem on coral reefs across the globe (Gardner *et al.*, 2003; Bellwood *et al.*, 2004; Mumby *et al.*, 2006; Bruno & Selig, 2007). Variation in the abundance and size structure of herbivorous coral-reef fishes is thus an important ecological feature that can drive variation in benthic community structure. Despite the fact that variation in abundance and size structure of herbivorous fishes has been noted on both large and small spatial scales (Lewis & Wainwright, 1985; Gust *et al.*, 2001; Russ, 2003; Paddack *et al.*, 2006), knowledge of the underlying factors driving these patterns is limited (Gust *et al.*, 2001; Floeter *et al.*, 2005).

Amongst herbivorous fishes in the Caribbean, the stoplight parrotfish *Sparisoma viride* (Bonnaterre), is arguably the most ecologically important due to its abundance, excavating grazing mode and rapid growth to relatively large sizes (Gygi, 1975; Bruggemann *et al.*, 1994a; van Rooij *et al.*, 1996a; Mumby *et al.*, 2006). A comparison of the demographic rates of *S. viride* at four locations across the Caribbean found broad-scale variation indicative of latitudinal variation, with more rapid initial growth and greater maximum length in the Bahamas compared with three lower latitude Caribbean locations (Choat *et al.*, 2003). Although adaptive increases in growth rate at higher latitudes have been demonstrated in other fishes (Yamahira & Conover, 2002), such processes have not been documented in tropical reef fishes. Age-based analyses of Indo-Pacific parrotfishes, however, indicate that variation on smaller scales can be considerable and suggest that local processes, such as density dependence, may be more important than large-scale processes in structuring these fish populations (Gust, 2004). Small-scale variation in population structure of *S. viride* is evident: the abundance, size frequency distribution and grazing rates of *S. viride* differ significantly between inshore and offshore reefs in the upper Florida Keys (Table I; Paddack, 2005). This pattern is not due to fishing pressure because herbivorous fishes have been unfished in that region for >28 years, but it is unknown whether these patterns are a result of underlying variation in demographic rates or other factors such as ontogenetic migration.

TABLE I. Numerical density (mean  $\pm$  s.d. number of fish per 100 m<sup>2</sup>), colour phase ratio and fork length ( $L_F$ , mm) data for *Sparisoma viride* on offshore and inshore reefs in the upper Florida Keys from *in situ* surveys (ten 25 m  $\times$  2 m transects at each site each summer) conducted during 2001–2003 by Paddock (2005)

	Offshore			Inshore		
	Pickles	Sand Island	Mean	Algae	White Banks	Mean
Number of fish per 100 m <sup>2</sup>	7.10 $\pm$ 3.28	8.37 $\pm$ 3.46	7.73 $\pm$ 0.90	8.37 $\pm$ 8.78	9.77 $\pm$ 3.58	9.07 $\pm$ 0.99
Maximum $L_F$ , TP	40	40	40	42	39	40.50
Maximum $L_F$ , IP	33	35	34	33	30	31.50
Adult mean $L_F$ , TP	33.53	34.74	34.14	32.04	29.67	30.86
Adult mean $L_F$ , IP	22.11	24.14	23.13	18.26	19.33	18.80

IP, initial phase; TP, terminal phase.

The aim of this study was to measure growth and mortality rates of *S. viride* at small (reef to reef, <3 km) and medium (cross-shelf, 3 km) spatial scales at unfished sites in the upper Florida Keys and to use this information to evaluate factors influencing the observed spatial variation in population structure. In addition, these results will help to resolve the question of whether latitudinal variation can be documented for a tropical marine fish by providing demographic data on *S. viride* at multiple sites at similar latitude to the outlying Bahamian data of the Choat *et al.* (2003) study. By expanding the spatial scope of age-based studies of this species, the present study provides an opportunity to evaluate the degree of demographic plasticity on both large and small spatial scales and explore the mechanisms that determine differential demographic rates.

## MATERIALS AND METHODS

### STUDY SPECIES

*Sparisoma viride* is protogynous (female first) and fully dichromatic (Robertson & Warner, 1978). Initial phase (IP) fish are females or secondary males and are dark red with white splotches and red fins. Terminal phase (TP) fish are male and are green with a distinct yellow spot on the upper edge of the gill cover and yellow colouration on the caudal fin. Size ranges of the two phases overlap considerably, with phase transition occurring at 130–200 mm standard length ( $L_S$ ) (Robertson & Warner, 1978), and reach a maximum recorded total length ( $L_T$ ) of 64 cm (Froese & Pauly, 2006). They occur in aggregations of either a single TP defending a territory consisting of up to 14 IPs or in variably sized roving groups of non-reproductive TP (van Rooij *et al.*, 1996b).

TABLE II. Sample sizes, size ranges, von Bertalanffy growth function parameters and maximum age observed for *Sparisoma viride* at four sites in the upper Florida Keys (see Fig. 1)

Site	<i>n</i>	$L_S$ (mm)	$L_{S\infty}$ (mm)	<i>K</i>	$t_0$	$r^2$	Maximum age (year)
SI	57	12–303	267.1	1.04	–0.06	0.93	7
PI	41	12–300	273.7	0.96	–0.06	0.96	8
Offshore	98	12–303	269.9	1.00	–0.06	0.95	
AL	24	112–236	236.3	0.96	–0.06	0.51	3
WB	54	11–254	249.4	0.89	–0.06	0.90	4
Inshore	78	11–254	246.2	0.90	–0.06	0.86	
Overall	176	11–303	269.2	0.84	–0.06	0.90	8

$L_{S\infty}$ , mean asymptotic standard length; *K*, the rate at which fish reach  $L_{\infty}$ ;  $t_0$ , age at theoretical  $L_S$  of 0.

## STUDY SITES AND FIELD SAMPLING

All data were collected from two offshore reefs and two inshore patch reefs in the upper Florida Keys (Fig. 1). The offshore reefs (Pickles, PI, and Sand Island, SI) were representative of many reefs along the upper Florida Keys: highly eroded relict spur and groove reefs with extensive hard-bottom punctuated by sand channels. These reefs were located *c.* 8 km offshore and varied in-depth from 2 to 7 m. The inshore patch reefs (Algae, AL, and White Banks, WB) were *c.* 5 km offshore, located between Hawk Channel and the reef break, and consisted of patchy coral heads and hard bottom, ranging in-depth from 2 to 5 m, and surrounded by seagrass.

Prior to this study, as part of a broader effort, size-specific density of *S. viride* was measured at each site by counting fish and estimating fork length ( $L_F$ ) along ten 25 m × 2 m long transects at each site during three summers (2000, 2001 and 2003; Paddock, 2005). To clarify comparisons of visual-based data with the age-based data from the present study,  $L_F$  (mm) from these visual-based surveys were converted to  $L_S$  (mm) using a conversion obtained by a least-squares linear regression of the 220 collected fish ( $L_S = 0.877; L_F = 6.128; r^2 = 0.997, P < 0.001$ ).

As they were encountered by divers, *S. viride* were collected by spear and net from the same four sites in the upper Florida Keys in 2005 (sample sizes in Table II). *Sparisoma viride* has not been commercially or recreationally targeted in Florida since 1981 when a ban on fish traps was implemented (Sutherland & Harper, 1983). Currently, exploitation is restricted to ornamental fish trade, which is minimal for this species (<400 fish per year for the entire Florida Keys; H. Molina-Ureña, pers. com.) and by-catch from commercial fisheries is negligible (Matthews & Donahue, 1997).

## OTOLITH PROCESSING

Collected fish were kept on ice and immediately transported to the laboratory where  $L_S$  was recorded and sagittal otoliths removed. Otoliths were cleaned in ethanol, dried and weighed ( $M_S$ ) to the nearest 0.1 mg. In order to prevent shattering, sagitta were embedded in epoxy resin before being sectioned transversely with a low-speed saw (IsoMet 1000 precision saw; www.buehler.com) using a diamond edge blade. Each section was affixed to a glass slide with thermoplastic cement (Crystalbond; www.crystalbond.com). Sections were lightly sanded by hand with P400 grit abrasive paper until the nucleus was reached. Both sides of the sections were then polished using a polishing cloth and 0.3 µm alumina powder. Sectioned otoliths were examined under compound and dissecting microscopes using transmitted light at × 20–100. Each otolith was read three times for annuli and discarded if assigned ages differed in more than one of the replicate reads. Presumed annuli were readable in sectioned sagitta but increments were often difficult to discern; 28% were rejected because of

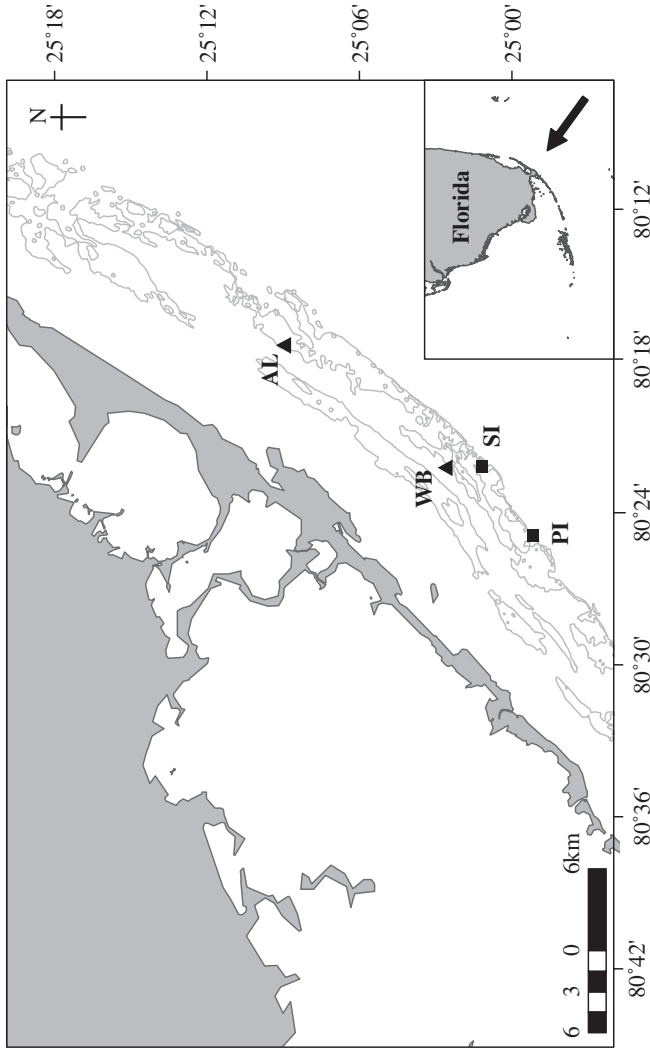


FIG. 1. Sampling sites for *Sparisoma viride* in the upper Florida Keys. Inshore, patch reefs (▲): Algae Reef (AL) and White Banks (WB). Offshore, low-relief reefs (■): Sand Island (SI) and Pickles (PI).

inconsistent reads or lack of distinct increments. About half of these (15% of the total) were fish <150 mm  $L_F$  and probably <1 year of age.

Reading of daily increments on fish <1 year was attempted, but increments were difficult to resolve and reads were inconsistent. To include some fish <1 year old, newly settled recruits (<30 mm  $L_F$ ) collected from the same sites as part of another study (Paddock & Sponaugle, 2008) were added to the age analysis. Recruits were available for all sites with the exception of AL. Otoliths were removed from recruits and immediately placed in immersion oil for 2 to 4 days. Whole sagittae were read under an oil-immersion compound microscope lens at  $\times 250$ . Images were captured and transferred to ImagePro-Plus 4.5 image analysis software (Media Cybernetics; www.mediacy.com) to enumerate daily increments. Each sagitta was read twice and samples were rejected if values differed by >10%. The first value of all acceptable samples was used. Age of fish <1 year old was recorded as the fraction of the year (number of rings per 365).

Although fish were initially collected as they were encountered, the high number of otoliths rejected required additional collections. During these collections, larger size classes were targeted due to a lack of older individuals in the collected samples. To ensure that the additional targeted collecting efforts did not cause an overrepresentation of older age classes in the catch curves (the frequency distribution of ages of fish collected), sampled age distributions were compared with published distributions of *S. viride* taken on a first-encounter basis (Choat *et al.*, 2003).

## DATA ANALYSES

To validate the use of sagittal otoliths for determining annual age and to cross-validate age, the best-fit relationship was identified between  $M_S$  and age ( $t$ ). The  $M_S$  and  $t$  relationship was also used as additional check of assigned age data by examining whether age obtained *via* increment analysis matched the expected age based on  $M_S$ .

Fish size-at-age data were then described by the von Bertalanffy growth curve function (VBGF):  $L_{St} = L_{S\infty}[1 - e^{-K(t-t_0)}]$ , where  $L_{St}$  is the estimated  $L_S$  at age  $t$ ,  $L_{S\infty}$  is the mean asymptotic  $L_S$ ,  $K$  is the curvature parameter and  $t_0$  is the age at theoretical length of 0 year. Best-fit parameters were obtained using non-linear regression with the Marquardt function in SAS (www.sas.com). Estimates were derived for  $K$ ,  $L_{S\infty}$  and  $t_0$  using an initial estimate from each site. Initial estimates of  $L_{S\infty}$  were determined for each site by taking the mean of  $L_S$  of the oldest age class divided by 0.95. Initial estimates of  $K$  were obtained by ln-transforming the VBGF and determining the linear regression parameters ( $K = -b_1$ ). To be comparable with other published values (Choat *et al.*, 2003), non-linear regressions were run with  $t_0$  constrained to -0.06 (approximating values obtained by constraining  $L_S$  intercepts). VBGF models were run for each site using IP data only, TP data only and data for all life-history phases combined. Parameters were fitted for each site, for inshore and offshore reefs combined and for all sites combined. Model fits were determined using  $r^2 = 1$  minus residual sum of squares divided by corrected total sum of squares. Growth curves generated by VBGF were compared by generating 95% confidence regions around the parameter estimates of  $K$  and  $L_{S\infty}$  (Kimura, 1980). Non-overlapping confidence regions indicate differences in growth parameters and were used to compare growth functions among individual sites and between inshore and offshore reefs.

Mortality rates ( $M$ ) were estimated as the slope of the log-linear regression of age-frequency data from collected fish and compared among sites with ANCOVA. Fishes younger than 2 years were excluded from this analysis to limit bias due to larger sample sizes of juveniles and to maintain comparability with previously published mortality rates of *S. viride* (Choat *et al.*, 2003).

## RESULTS

The  $L_S$  distributions of *S. viride* from three summers of visual surveys were roughly similar between inshore and offshore reefs (Kolmogorov–Smirnov,  $P > 0.05$ ;

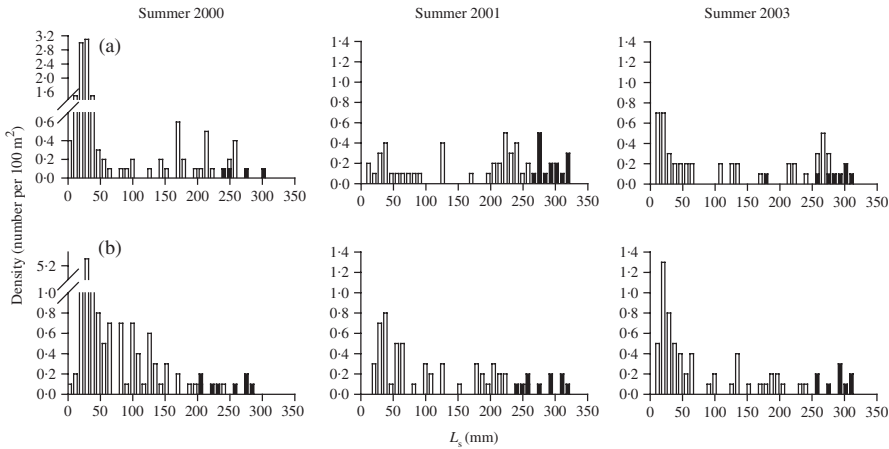


FIG. 2. Standard length ( $L_S$ ) frequency distributions of initial (□) and terminal (■) phase *Sparisoma viride* from visual transects conducted during 2000–2003 in (a) offshore and (b) inshore reefs. Note that a strong recruitment event in summer 2000 resulted in unusually high densities of fish <50 mm  $L_S$  for that sample period.

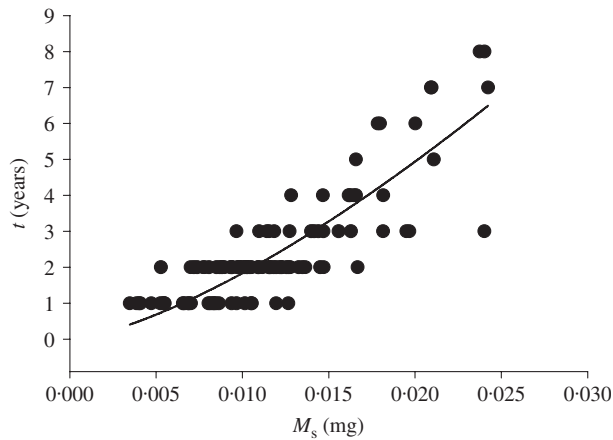


FIG. 3. Power function of age ( $t$ ) (sagittal increments) and sagittal mass ( $M_S$ ) in *Sparisoma viride* for all sample reefs combined. The curve was fitted by:  $y = 1306x^{1.43}$  ( $n = 130$ ).

Fig. 2). Although maximum sizes of *S. viride* recorded in visual surveys were similar between inshore and offshore reefs, the proportion of *S. viride* >200 mm  $L_S$  was higher on offshore reefs compared with inshore reefs (32.2 and 18.4%, respectively). The largest size classes on all reefs consisted of only TPs and there was little overlap in the size distribution of IP and TP fish (Fig. 2).

A strong relationship between  $M_S$  and  $t$ , defined by a power function ( $r^2 = 0.71$ ; Fig. 3), validated that annual increments were deposited throughout the life of the fish (although otolith accretion slowed slightly with age) and supports the use of sagittal otoliths for ageing *S. viride*.

Age-at- $L_S$  plots revealed a typical growth pattern, with fish quickly reaching an asymptotic length (Fig. 4). The age distributions of fish collected in this study (Fig. 5) and the similarity of these age distributions with that of Choat *et al.* (2003) from San Blas, where fish were collected on a first-encounter basis, indicate that older age classes were not overrepresented despite the necessary deviation from randomly collected samples in the present study. Parameters estimated from von Bertalanffy growth functions fitted to the age-at-length data from each site are presented in Table II. Overlapping 95% confidence regions around VBGF parameters  $K$  and  $L_{S\infty}$  allowed pooling of data within each strata (Fig. 6). Non-overlapping 95% confidence regions intervals around pooled inshore and offshore data indicate significant differences in the VBGF parameter estimates between strata (Fig. 7).

The major difference in *S. viride* population structure among inshore and offshore reefs in the upper Florida Keys was in maximum age obtained. Fish on inshore reefs were no older than 4 years of age, whereas those on offshore reefs reached 7–8 years of age (Fig. 4). No terminal phase fish, however, were found to be >4 years of age on any of the reefs studied, despite the fact that the largest fish sampled were terminal phase (Fig. 5). Age structure of terminal phase fish differed between inshore and offshore reefs (Figs 4 and 5). While the majority of terminal phase fish were 2 years of age on both inshore and offshore reefs (60 and 64%, respectively), offshore reefs had no terminal phase fish <2 years of age, whereas 23% of terminal phase fish on inshore reefs were 1 year of age. A higher proportion of terminal phase fish in the maximum age class (4 years) occurred on offshore reefs (13%) compared with inshore reefs (5%).

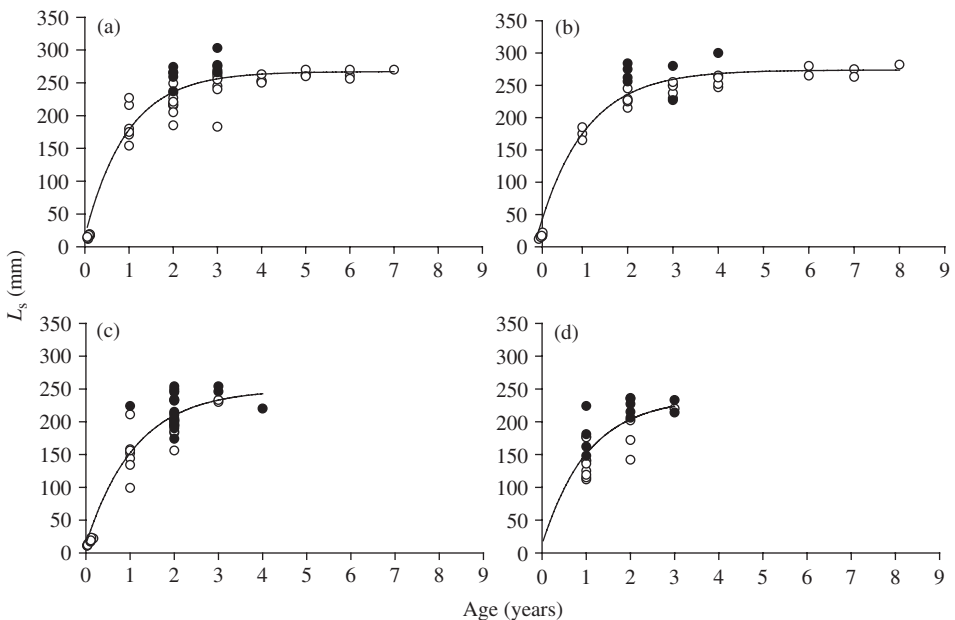


FIG. 4. Standard length ( $L_S$ )-at-age plots for initial (○) and terminal (●) phase *Sparisoma viride* from four reefs in the upper Florida Keys. (a) Sand Island, (b) Pickles, (c) Algae Reef and (d) White Banks (see Fig. 1) Otolith-derived ages were fitted von Bertalanffy growth function (VBGF) curves (—) for combined life-history phases. VBGF parameters are listed in Table II.

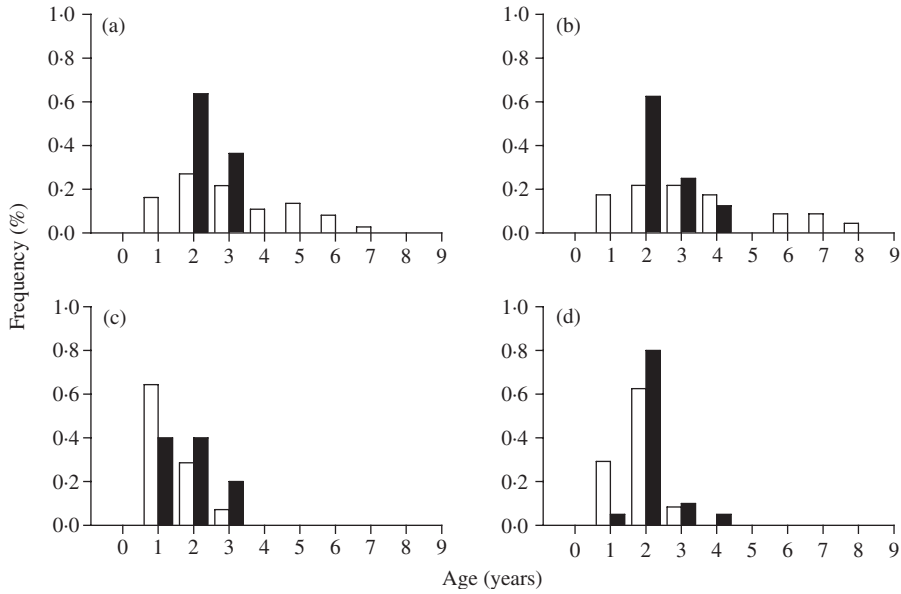


FIG. 5. Age-frequency histograms of *Sparisoma viride* for initial (□) and terminal (■) phases at (a) Sand Island, (b) Pickles, (c) Algae Reef and (d) White Banks (see Fig. 1). Fish <1 year were excluded because of the biased sampling of new recruits.

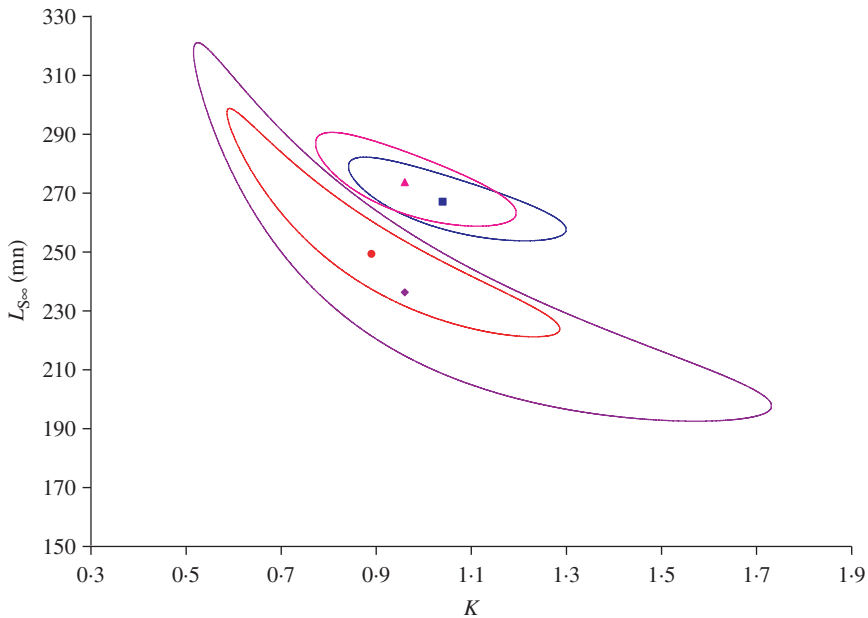


FIG. 6. Comparison of VBGF parameters,  $L_{S_{\infty}}$  and  $K$ , with 95% confidence regions estimated for *Sparisoma viride* at each study site for combined life-history phases [offshore sites: Sand Island (■, -) and Pickles (▲, -); inshore sites: Algae Reef (◆, -) and White Banks (●, -)].

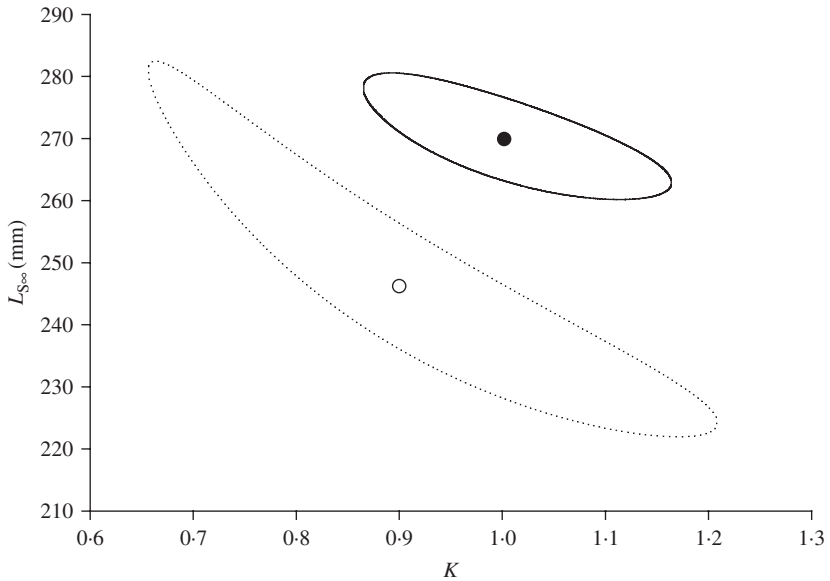


FIG. 7. Comparison of VBGF parameters,  $L_{S\infty}$  and  $K$ , with 95% confidence regions estimated for *Sparisoma viride* on inshore (○) and offshore (●) reefs of the upper Florida Keys.

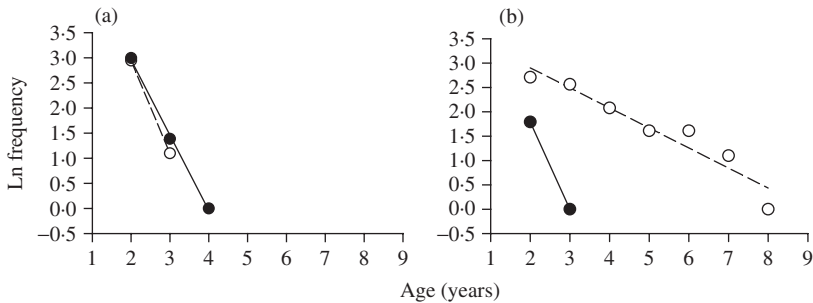


FIG. 8. Catch curves and estimates of mortality rates ( $M$ ) of initial (○) and terminal (●) phase *Sparisoma viride* on (a) inshore and (b) offshore reefs in the upper Florida Keys.

Mortality rates calculated from fish  $\geq 2$  years were significantly higher on inshore than offshore reefs (ANCOVA, d.f. = 1, 6,  $P < 0.001$ ). Mortality rates also differed significantly between IP and TP fish on offshore reefs (ANCOVA, d.f. = 1, 7,  $P < 0.05$ ), but not on inshore reefs (ANCOVA, d.f. = 1, 2,  $P > 0.05$ ; Fig. 8).

## DISCUSSION

Previous surveys of *S. viride* revealed significant variation in density and size structure between inshore and offshore reefs (Paddack, 2005), with density and the ratio of TP:IP fish greater on offshore reefs (Table I). Results of the present study

show that this cross-shelf variation was driven by several key demographic rates. *Sparisoma viride* attains a greater size at age, larger mean asymptotic size, and two-fold longer maximum life span on offshore reefs relative to inshore reefs. These results indicate that small-scale variation in demographic rates of *S. viride* can be considerable and should not be ignored when evaluating large-scale patterns. Variation in growth, maximum size and mortality across-shelf as well as between reef systems of similar latitude (Bahamas, Choat *et al.*, 2003) suggests that demographic rates can be strongly controlled by local conditions. Differential growth rates of scarids have been noted on a variety of spatial scales and have been attributed to food and shelter availability (Jones, 1986; Clifton, 1995; Gust, 2004), water temperature (Choat *et al.*, 2003), community structure (Gust *et al.*, 2002) and social factors (Warner & Downs, 1977; van Rooij *et al.*, 1995; Munday *et al.*, 2004).

Among the environmental variables known to influence demographic variables, there is some evidence suggesting that differing growth rates and sex ratios found between strata in the upper Florida Keys are due to variation in food availability and quality. Although water temperature can strongly influence growth rates of fishes (Houde, 1989; Atkinson, 1994; Sponaugle *et al.*, 2006), no notable cross-shelf temperature differences were found among the sampled reefs within a 3-year period (M. J. Paddack, unpubl. data). Instead, higher density, biomass and individual grazing rates of *S. viride* on offshore reefs *v.* inshore reefs (Paddack *et al.*, 2006) suggest that availability and quality of food differs between strata. *Sparisoma viride* have been shown to have higher grazing rates, assimilation efficiencies and exhibit more territorial defence in areas of high-quality food (Bruggemann *et al.*, 1994*b, c*), occur in higher densities in areas of higher algal production (Lewis & Wainwright, 1985; Russ, 2003) and exhibit increased growth rates coincident with higher food availability (Jones, 1986; Clifton, 1995; Gust *et al.*, 2002). Basic variables of benthic community composition, algal per cent cover and algal turf productivity do not vary significantly between inshore and offshore reefs in the upper Florida Keys (Paddack *et al.*, 2006), suggesting that finer-scale food quality variables may be important. Two potential variables are the density of the substratum and the presence of crustose coralline algae, as both have been shown to influence algal intake in *S. viride* (Bruggemann *et al.*, 1994*b*). In addition, detritus associated with the epilithic algal community may be an important food resource for herbivorous fishes (Crossman *et al.*, 2001; Wilson *et al.*, 2003). A positive correlation between scarid growth rates and detrital availability has been documented in the Great Barrier Reef (GBR) (Crossman *et al.*, 2001; Gust *et al.*, 2002), but a causal and widespread relationship has yet to be determined.

Spatial variation in resource (food or habitat) quality may also underlie unequal sex ratios onshore and offshore (1.7 and 2.9, respectively). *Sparisoma viride* is a harem-forming fish with territorial TP males defending areas that are shared with one to 14 IP with whom they mate (van Rooij *et al.*, 1996*b*). A stronger bias in the sex ratio, as found on offshore reefs, can occur in more resource-rich areas; harem behaviour appears to be stronger in areas of higher food quality (Bruggemann *et al.*, 1994*c*), possibly because the higher quality of the territory increases the number of conspecifics that can optimally coexist. Such variation in social structure might be expected to influence estimated growth rates overall on inshore and offshore reefs due to differences in growth rates among life-history phases. Territorial TP have been shown to have higher growth rates than IP and bachelor TP (non-reproductive

individuals that school in shallow water away from territorial areas) (van Rooij *et al.*, 1995; Choat *et al.*, 2003). Therefore, the proportion of the population that is IP *v.* TP fish and the proportion of the TP population made up by territorial *v.* bachelor males could influence the estimated overall growth rate. Social status of collected TP was not recorded; however, bachelor male groups were less common on inshore reefs than offshore reefs, probably due to the restricted amount of reef area available for non-territorial TP on inshore patch reefs (M. J. Paddack, pers. obs.). More importantly, the 60% higher proportion of IP to TP *S. viride* on offshore reefs would lead to reduced growth offshore, in contrast to the present observations.

The timing of sex change can vary as a function of population density, growth and mortality rates (Cowen, 1990; Gust, 2004). Early sex change may occur if sexually active individuals suffer higher mortality or reduced growth rates (Cowen, 1990; Iwasa, 1991; Gust, 2004). It is possible that sex change is occurring earlier and at smaller sizes on inshore reefs: the youngest TP on offshore reefs were 2 years old and an average of 266 mm  $L_S$ , whereas the youngest on inshore reefs were 1 year old and 201 mm  $L_S$ . Because total mortality rate is higher inshore and growth rates are reduced, however, the relative importance of these two processes in mediating the timing of sex change cannot be differentiated, as has been the case in other populations of hermaphroditic fishes (Cowen, 1990; Gust, 2004).

#### CROSS-SHELF DIFFERENCES IN LONGEVITY

An unexpected finding was the two-fold difference in maximum age between inshore and offshore reefs. Because this study encompassed a limited number of sites and a fairly small sample size, it is possible that older fish exist on the inshore reefs but were not sampled. Choat *et al.* (2003) found that *c.* 10% of the *S. viride* population at each of four areas in the Caribbean and Atlantic Ocean were >4 years old, a trend reflected in the age distributions on offshore reefs in the upper Florida Keys. Thus, even if fish attain greater ages on inshore reefs, their absence in the present samples indicates that the proportion of older fish on inshore reefs is substantially less than reefs offshore and those reported by Choat *et al.* (2003). The sex differences observed in maximum age within strata also do not appear to be ubiquitous, as TP fish >4 years have been noted at a number of other Caribbean reefs (van Rooij & Videler, 1997; Choat *et al.*, 2003).

One possible explanation for the difference in maximum age between inshore and offshore reefs is that *S. viride* migrate offshore from inshore reefs with age. There is no evidence, however, of ontogenetic migration for this species. Although seagrass beds and nearshore areas have been shown to be nursery areas for several species of fishes, including scarids in the Caribbean (Nagelkerken *et al.*, 2001; Gillanders *et al.*, 2003; Heck *et al.*, 2003; Mumby *et al.*, 2004), monthly surveys of seagrass beds surrounding nearshore patch reefs and mangrove habitats over 2.5 years in the same region of the upper Florida Keys have found that the use of habitats other than reefs is uncommon for *S. viride* (unpubl. data). In addition, *S. viride* recruits are abundant in adult habitats and recruitment rates of *S. viride* are higher on offshore reefs (Tolimieri, 1998; Paddack & Sponaugle, 2008). Thus, nearshore areas do not appear to be serving as nurseries from which large-scale emigrations of this species would occur.

As adults, *S. viride* have been shown to be site-attached with limited home ranges (up to 820 m<sup>2</sup>; van Rooij *et al.*, 1996b). Relocation of territory or home range area has been observed and adults are known to occasionally roam over long distances within continuous reef habitat (McAfee & Morgan, 1996; van Rooij *et al.*, 1996b; Corless *et al.*, 1997; Chapman & Kramer, 2000). The TP fish occasionally swim down the reef slope to deeper reef areas in Bonaire (>30 m), but only for short-term spawning events or feeding forays (van Rooij *et al.*, 1996b). *Sparisoma viride* have been observed on deeper reefs of the upper Florida Keys (30–40 m) in moderate abundance and as larger individuals than shallow reefs (Jameson, 1981), but their presence and persistence in this habitat has not been quantified. The slope in the Florida Keys, however, is gradual and deeper reefs generally are not continuous with shallow water hard-bottom habitat (Jameson, 1981). This reduces the likelihood of *S. viride* migration to these reefs. Furthermore, a tagging study in Barbados found that *S. viride* occasionally moves between reefs separated by 10 m of sand, but that they rarely cross even modest expanses of sand (20–300 m; Chapman & Kramer, 2000). Elsewhere, limited longer range adult movement has been documented: a small proportion (9.7%) of *S. viride* was found 3–16 km away from a nearshore tagging area in Jamaica (Munro, 1998). Thus, although *S. viride* tends to be fairly site attached, adults can and do move among reefs (Corless *et al.*, 1997; Munro, 1998). Numerous small reef patches and coral heads scattered throughout the inshore areas of the Florida Keys also may provide a stepping-stone habitat for fishes traversing to offshore reefs. Nonetheless, if *S. viride* are moving onto offshore reefs, either the input is too diffuse to be detectable (length distributions over time on all reefs are stable; Paddack *et al.*, 2005) or they are moving into unsampled habitats (*e.g.* deeper reef areas).

A disparity in maximum age has also been documented for scarids in the GBR, albeit with an opposite pattern of fishes from offshore reefs being shorter-lived (Gust *et al.*, 2002). The shorter life span of GBR scarids offshore is associated with higher growth rates and higher mortality rates, a relationship that holds for many fish species (Pauly, 1998). Mortality *via* fishing, collecting or as by-catch is negligible for *S. viride* in the Florida Keys. Vulnerability to predation mortality may be enhanced due to the lower relief and limited size of inshore patch reefs (Caley & St John, 1996; Beukers & Jones, 1997).

## DEMOGRAPHIC PLASTICITY

A comparison of *S. viride* growth rates obtained in this study with published values (Choat *et al.*, 2003) reveals that the growth rates in the upper Florida Keys are similar to those of fish at lower latitude Caribbean reefs but are lower than those of fish from the Bahamas (an area only 1° lower in latitude; Fig. 9). The present results are therefore counter to the hypothesis put forth by Choat *et al.* (2003) that the higher growth rates and maximum size of *S. viride* in the Bahamas are due to latitudinal compensatory growth as found in other species (Yamahira & Conover, 2002). There are no immediately obvious factors that would cause such different growth rates between Florida and the Bahamas. Although predator biomass can be locally very high in the Bahamas, predator biomass in the study area of Choat *et al.* (2003) is similar to that in the upper Florida Keys (M. J. Paddack, unpubl. data) and mortality rates estimated for the Bahamas are similar to those of offshore reefs

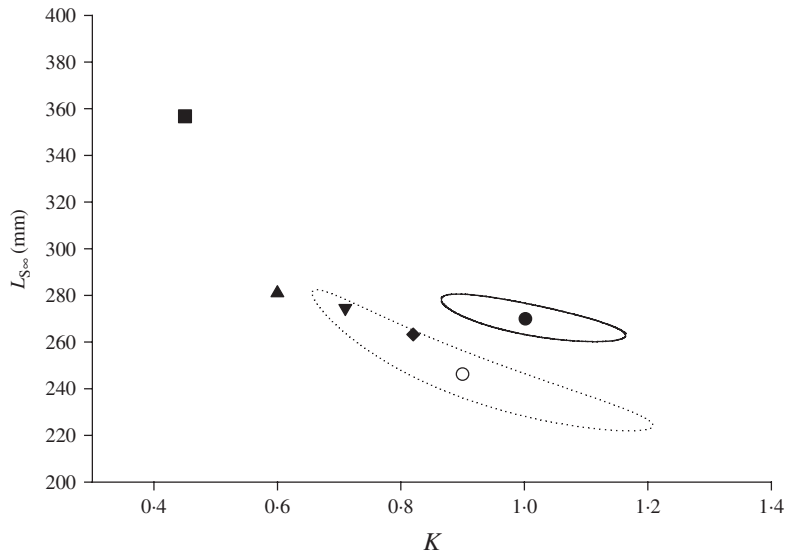


FIG. 9. Comparison of VBGF parameters,  $L_{S_{\infty}}$  and  $K$ , estimated for *Sparisoma viride* at each site from the present study [Florida offshore (●) and Florida inshore (○)] and from four sites [Bahamas (■), Los Roques (▲), Barbados (▼) and San Blas (◆)] sampled by Choat *et al.* (2003).

in Florida (Florida, 0.26–0.35 year<sup>-1</sup>; Bahamas, 0.33 year<sup>-1</sup>; Choat *et al.* 2003). Furthermore, algal consumption rates of *S. viride* are similar between the Bahamas and the upper Florida Keys (M. J. Paddack, unpubl. data). Further investigation of the degree of demographic plasticity within latitude (by expanding the number of reefs sampled) and causal factors (*e.g.* assessment of food and habitat quality) are needed.

Similarity in growth rate between *S. viride* the Caribbean and Florida is surprising given the colder water temperatures experienced in Florida during winter months. Higher growth rates in relation to higher water temperatures have been observed in many fish taxa (Houde, 1989; Atkinson, 1994; Sponaugle *et al.*, 2006). van Rooij *et al.* (1995) noted seasonal patterns of growth in *S. viride* in Bonaire, with higher growth rates during warmer summer months. Given the wider range in seasonal water temperatures, even stronger seasonal variation might be expected in Florida. Although the three parameter VBGF utilized in this study provided a good fit to the data, it may be useful to explore modifications of the model designed to reflect seasonal variability in growth (Porch *et al.*, 2002) as well as those designed to accommodate the two phases of growth, the rapid initial growth and slower growth later in life (Craig *et al.*, 1997; Craig, 1999). A more detailed analysis of growth during the initial growth phase (up to age 2 years) may provide a better understanding of the observed differences in the population structure of *S. viride* on inshore and offshore reefs in the upper Florida Keys, as there is evidence that differences in growth of scarids during the first year of life determine which individuals become TP (Munday *et al.*, 2004). For a fish that spawns year-round and has a complex social structure such as *S. viride*, the season in which a fish recruits may be an important determinant of the growth rate and thus the timing of maturation, sex change and the ability to compete for high-quality territories and mates.

Variation in demographic rates can result in differences in the population size and structure of organisms across small and large spatial scales. This can ultimately influence the ecological functioning of key organisms, particularly if their ecological impact increases with size, age and abundance. The effect of grazing by *S. viride* on the benthos is dependent upon the sizes of individuals since larger fish are not only able to consume more algae per bite, but are also able to shift into an excavating mode of grazing, which promotes coral recruitment (Bruggemann *et al.*, 1994b; Mumby, 2006). This is a critical process on coral reefs, given the unprecedented rates of decline in live corals and expansion of macroalgal cover (Côté *et al.*, 2005; Bruno & Selig, 2007). *Sparisoma viride* may therefore be instrumental in halting and possibly reversing this trend in the Caribbean (Mumby *et al.*, 2006). Management of these fish requires knowledge of the processes that shape populations. The small-scale demographic variation revealed here provides a better context from which to delineate natural and human-caused drivers and to understand the processes that shape reef communities.

Sincere thanks are extended to J. H. Choat for his valuable help in validating ages and providing helpful feedback and resources. J. Tunnell at Florida Marine Research Institute (FMRI) and J. Schull of NOAA graciously provided training on otolith preparation and reading. T. Rankin, C. Faunce, N. Coroneos, K. Grorud-Colvert, S. Trbovich, A. Miyake, L. Buhmaster, E. D'Alessandro, J. Llopiz, A. Ortiz, M. Crossland and J. Kool provided much needed assistance in the laboratory and in the field. Funding for this study was provided by the National Center for Caribbean Coral Reef Research (NCORE) through EPA Grant #R828020. Collections were permitted under Florida Fish and Wildlife Conservation Commission Permit #04SR-533. Comments of two anonymous reviewers improved an earlier version of the manuscript.

## References

- Atkinson, D. (1994). Temperature and organism size: a biological law for ectotherms? *Advances in Ecological Research* **25**, 1–58.
- Bellwood, D. R. & Choat, J. H. (1990). A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environmental Biology of Fishes* **28**, 189–214.
- Bellwood, D. R., Hughes, T. P., Folke, C. & Nyström, M. (2004). Confronting the coral reef crisis. *Nature* **429**, 827–833.
- Beukers, J. S. & Jones, G. P. (1997). Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* **114**, 50–59.
- Bruggemann, J. H., Kuyper, M. W. M. & Breeman, A. M. (1994a). Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). *Marine Ecology Progress Series* **112**, 51–66.
- Bruggemann, J. H., Begeman, J., Bosma, E. M., Verburg, P. & Breeman, A. M. (1994b). Foraging by the stoplight parrotfish *Sparisoma viride*. II. Intake and assimilation of food, protein and energy. *Marine Ecology Progress Series* **106**, 57–71.
- Bruggemann, J. H., van Oppen, M. J. H. & Breeman, A. M. (1994c). Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different, socially determined habitats. *Marine Ecology Progress Series* **106**, 41–55.
- Bruno, J. F. & Selig, E. R. (2007). Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One* **2**, e711. doi:10.1371/journal.pone.0000711.
- Caley, M. J. & St John, J. (1996). Refuge availability structures assemblages of tropical reef fishes. *Journal of Animal Ecology* **65**, 414–428.
- Carpenter, R. C. (1986). Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* **56**, 345–363.

- Chapman, M. R. & Kramer, D. L. (2000). Movements of fishes within and among fringing coral reefs in Barbados. *Environmental Biology of Fishes* **57**, 11–24.
- Choat, J. H., Robertson, D. R., Ackerman, J. L. & Posada, J. M. (2003). An age-based demographic analysis of the Caribbean stoplight parrotfish *Sparisoma viride*. *Marine Ecology Progress Series* **246**, 265–277.
- Clifton, K. E. (1995). Asynchronous food availability on neighboring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish *Scarus iserti*. *Marine Ecology Progress Series* **116**, 39–46.
- Corless, M., Hatcher, B. G., Hunte, W. & Scott, S. (1997). Assessing the potential of fish for fish migration from marine reserves to adjacent fished areas in the Soufriere Marine Management Area, St. Lucia. *Proceedings of the Gulf and Caribbean Fisheries Institute* **49**, 71–98.
- Côté, I. M., Gill, J. A., Gardner, T. A. & Watkinson, A. R. (2005). Measuring coral reef decline through meta-analyses. *Philosophical Transactions of the Royal Society B* **360**, 385–395.
- Cowen, R. K. (1990). Sex change and life history patterns of the labrid, *Semicossyphus pulcher*, across an environmental gradient. *Copeia* **1990**, 787–795.
- Craig, P. C. (1999). The von Bertalanffy growth curve: when a good fit is not good enough. *Naga* **22**, 28–29.
- Craig, P. C., Choat, J. H., Axe, L. M. & Saucerman, S. (1997). Population biology and harvest of the coral reef surgeonfish *Acanthurus lineatus* in American Samoa. *Fishery Bulletin* **95**, 680–693.
- Crossman, D. J., Choat, J. H., Clements, K. D., Hardy, T. & McConochie, J. (2001). Detritus as food for grazing fishes on coral reefs. *Limnology and Oceanography* **46**, 1596–1605.
- Floeter, S. R., Behrens, M. D., Ferreira, C. E. L., Paddock, M. & Horn, M. H. (2005). Geographical gradients of marine herbivorous fishes: patterns and processes. *Marine Biology* **147**, 1435–1447.
- Gardner, T. A., Côté, I. M., Gill, J. A., Grant, A. & Watkinson, A. R. (2003). Long-term regional declines in Caribbean corals. *Science* **301**, 958–960.
- Gillanders, B. M., Able, K. W., Brown, J. A., Eggleston, D. B. & Sheridan, P. F. (2003). Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Marine Ecology Progress Series* **247**, 281–295.
- Gust, N. (2004). Variation in the population biology of protogynous coral reef fishes over tens of kilometers. *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 205–218.
- Gust, N., Choat, J. H. & McCormick, M. I. (2001). Spatial variability in reef fish distribution, abundance, size, and biomass: a multi-scale analysis. *Marine Ecology Progress Series* **214**, 237–251.
- Gust, N., Choat, J. H. & Ackerman, J. L. (2002). Demographic plasticity in tropical reef fishes. *Marine Biology* **140**, 1039–1051.
- Gygi, R. A. (1975). *Sparisoma viride* (Bonnaterre), the stoplight parrotfish, a major sediment producer on coral reefs of Bermuda. *Ecologiae Geologicae Helveticae* **68**, 327–359.
- Heck, K. L., Hays, G. & Orth, R. J. (2003). Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series* **253**, 123–136.
- Houde, E. D. (1989). Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fishery Bulletin* **87**, 471–495.
- Iwasa, Y. (1991). Sex change evolution and cost of reproduction. *Behavioral Ecology* **2**, 56–68.
- Jameson, S. C. (Ed.) (1981). *Key Largo Coral Reef National Marine Sanctuary Deep Water Resource Survey*. Washington, DC: Office of Coastal Zone Management.
- Jones, G. P. (1986). Food availability affects growth in a coral reef fish. *Oecologia* **70**, 136–139.
- Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin* **77**, 765–774.
- Kingsford, M. J. & Hughes, J. M. (2005). Patterns of growth, mortality, and size of the tropical damselfish *Acanthochromis polyacanthus* across the continental shelf of the Great Barrier Reef. *Fishery Bulletin* **103**, 561–573.

- Lewis, S. M. & Wainwright, P. C. (1985). Herbivore abundance and grazing intensity on a Caribbean coral reef. *Journal of Experimental Marine Biology and Ecology* **87**, 215–228.
- Matthews, T. R. & Donahue, S. (1997). By-catch abundance, mortality and escape rates in wire and wooden spiny lobster traps. *Proceedings of the Gulf and Caribbean Fisheries Institute* **49**, 280–298.
- McAfee, S. T. & Morgan, S. G. (1996). Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. *Marine Biology* **125**, 427–437.
- Mumby, P. J. (2006). The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecological Applications* **16**, 747–769.
- Mumby, P. J., Edwards, A. J., Arias-Gonzales, J. E., Lindeman, K. C., Blackwell, P., Gall, A., Gorczyńska, M. I., Harborne, A. R., Pescod, C. L., Renken, H., Wabnitz, C. C. C. & Llewellyn, G. (2004). Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* **427**, 533–536.
- Mumby, P. J., Dahlgren, C. P., Harborne, A. R., Kappel, C. V., Micheli, F., Brumbaugh, D. R., Holmes, K. E., Mendes, J. M., Broad, K., Sanchirico, J. N., Buch, K., Box, S., Stoffle, R. W. & Gill, A. B. (2006). Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* **311**, 98–101.
- Munday, P. L., Hodges, A. L., Choat, J. H. & Gust, N. (2004). Sex-specific growth effects in protogynous hermaphrodites. *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 323–327.
- Munro, J. L. (1998). Outmigration and movement of tagged coral reef fish in a marine fishery reserve in Jamaica. *Proceedings of the Gulf and Caribbean Fisheries Institute*. **51**, 557–568.
- Nagelkerken, I., Kleijnen, S., Klop, T., van den Brand, R. A. C. J., Cocheret de la Moriniere, E. & van der Velde, G. (2001). Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. *Marine Ecology Progress Series* **214**, 225–235.
- Núñez Lara, E., Arias-Gonzales, J. E. & Legendre, P. (2005). Spatial patterns of Yucatan reef fish communities: testing models using a multi-scale survey design. *Journal of Experimental Marine Biology and Ecology* **324**, 157–169.
- Paddack, M. J. (2005). Herbivorous coral reef fishes in a changing ecosystem. PhD Thesis, University of Miami, Miami, FL, U.S.A.
- Paddack, M. J. & Sponaugle, S. (2008). Recruitment and habitat selection of newly settled *Sparisoma viride* to reefs with low coral cover. *Marine Ecology Progress Series* **369**, 205–212.
- Paddack, M. J., Cowen, R. K. & Sponaugle, S. (2006). Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. *Coral Reefs* **25**, 461–472.
- Pauly, D. (1998). Tropical fishes: patterns and propensities. *Journal of Fish Biology* **53**, 1–17. doi: 10.1111/j.1095-8649.1998.tb01014.x
- Porch, C. E., Wilson, C. A. & Nieland, D. L. (2002). A new growth model for red drum (*Sciaenops ocellatus*) that accommodates seasonal and ontogenetic changes in growth rates. *Fishery Bulletin* **100**, 149–152.
- Robertson, D. R. & Warner, R. R. (1978). Sexual patterns in the labroid fishes of the Western Caribbean, II: The parrotfishes (Scaridae). *Smithsonian Contributions to Zoology* **255**, 26 pages.
- Robertson, D. R., Ackerman, J. L., Choat, J. H., Posada, J. M. & Pitt, J. (2005). Ocean surgeonfish *Acanthurus bahianus*. I. The geography of demography. *Marine Ecology Progress Series* **295**, 229–244.
- van Rooij, J. M. & Videler, J. J. (1997). Mortality estimates from repeated visual censuses of a parrotfish (*Sparisoma viride*) population: demographic implications. *Marine Biology* **128**, 385–396.
- van Rooij, J. M., Bruggemann, J. H., Videler, J. J. & Breeman, A. M. (1995). Plastic growth of the herbivorous reef fish *Sparisoma viride*: field evidence for a trade-off between growth and reproduction. *Marine Ecology Progress Series* **122**, 93–105.
- van Rooij, J. M., de Jong, E., Vaandrager, F. & Videler, J. J. (1996a). Resource and habitat sharing by the stoplight parrotfish, *Sparisoma viride*, a Caribbean reef herbivore. *Environmental Biology of Fishes* **47**, 81–91.

- van Rooij, J. M., Kroon, F. J. & Videler, J. J. (1996b). The social and mating system of the herbivorous reef fish *Sparisoma viride*: one-male versus multi-male groups. *Environmental Biology of Fishes* **47**, 353–378.
- Russ, G. R. (2003). Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. *Coral Reefs* **22**, 63–67.
- Ruttenberg, B. I., Haupt, A. J., Chiriboga, A. I. & Warner, R. R. (2005). Patterns, causes and consequences of regional variation in the ecology and life history of a reef fish. *Oecologia* **145**, 394–403.
- Sponaugle, S., Grorud-Colvert, K. & Pinkard, D. (2006). Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish *Thalassoma bifasciatum* in the Florida Keys. *Marine Ecology Progress Series* **308**, 1–15.
- Sutherland, D. L. & Harper, D. E. (1983). The wire fish-trap fishery of Dade and Broward counties, Florida: December 1979–September 1980. *Florida Marine Research Publication* **40**, 1–21.
- Tolimieri, N. (1998). The relationship among microhabitat characteristics, recruitment and adult abundance in the stoplight parrotfish, *Sparisoma viride*, at three spatial scales. *Bulletin of Marine Science* **62**, 253–268.
- Warner, R. R. & Downs, I. F. (1977). Comparative life histories: growth vs. reproduction in normal males and sex-changing hermaphrodites of the striped parrotfish, *Scarus croicensis*. In *Proceedings of the 3rd International Coral Reef Symposium* (Taylor, D. L., ed.), pp. 275–281. Miami, FL: Rosentiel School of Marine and Atmospheric Science.
- Wilson, S. K., Bellwood, D. R., Choat, J. H. & Furnas, M. J. (2003). Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanography and Marine Biology Annual Review* **41**, 279–309.
- Yamahira, K. & Conover, D. O. (2002). Intra- vs. interspecific latitudinal variation in growth: adaptation to temperature or seasonality? *Ecology* **83**, 1252–1262.

### Electronic Reference

- Froese, R. & Pauly, D. (Eds). (2006). *FishBase*. Available at [www.fishbase.org](http://www.fishbase.org) (version July 2006).