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Addressing life history information gaps for Caribbean parrotfishes: queen parrotfish *Scarus vetula* and stoplight parrotfish *Sparisoma viride*

Jesús M. Rivera Hernández · Virginia R. Shervette

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Abstract Queen parrotfish *Scarus vetula* and stoplight parrotfish *Sparisoma viride* are widely distributed throughout the subtropical/tropical regions of the northwestern Atlantic, play important ecological roles in reef ecosystems, and contribute to small-scale commercial landings within several Caribbean management jurisdictions. Prior to this work, no comprehensive life history information existed for either species that combined otolith analysis and gonad histology. Queen parrotfish (n = 390) and stoplight parrotfish (n = 1801) were sampled throughout the U.S. Caribbean from 2013 to 2023. Queen parrotfish range in size from 82 to 402 mm FL and age from 0 to 16 years; stoplight parrotfish ranged from 73 to 433 mm FL and 0 to 20 years. Growth parameter estimates for queen parrotfish were L_∞ = 347 mm FL and K = 0.42, when t_0 was fixed to −0.06; for stoplight parrotfish, L_∞ = 332 mm FL and K = 0.39, with a fixed t_0 of −0.06. All female queen parrotfish transitioned to males by a maximum length and age of 322 mm FL and 14 years. In contrast, not all female stoplight parrotfish transitioned to males since the largest and oldest individuals sampled were females. Spawning capable queen parrotfish females were collected from November to August indicating a protracted spawning season of 10 months. Stoplight parrotfish exhibited year-round spawning with >50% of mature females in the spawning capable phase during all months of the year. Based on our overall findings related to life history, queen parrotfish and stoplight parrotfish in the U.S. Caribbean did not appear to exhibit signs of overexploitation which may in part relate to U.S. Caribbean management efforts currently in place that limit the minimum mesh size for traps (which ensures that smaller fish can escape from the traps), a ban on using gillnets to target parrotfish species, and the market driven targeting of "plate-size" fish by commercial spearfishers. The life history information documented in the current study will provide essential information for stock assessments and informed management in the U.S. Caribbean for these two important parrotfish species.

Keywords Scarinae · Population demography · Age structure · Fish reproduction

Introduction

Parrotfishes in the genera *Scarus* and *Sparisoma* (family Labridae, subfamily Scarinae) are ubiquitous members of coral reef communities and are widely

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J. M. Rivera Hernández (✉) · V. R. Shervette
Marine Science Program, School of Earth, Ocean
and the Environment, University of South Carolina,
Columbia, SC 29208, USA
e-mail: jriverahernandez.pr@gmail.com

J. M. Rivera Hernández · V. R. Shervette
Fish/Fisheries Conservation Lab, Department
of Biological, Environmental & Earth Sciences, University
of South Carolina Aiken, Aiken, SC 29801, USA

distributed across tropical regions of the western Atlantic Ocean (Robertson and Warner 1978; Robertson and Van Tassell 2019). Collectively they represent a major component of artisanal/small-scale reef fisheries in many island and territorial jurisdictions of the Caribbean Sea (CFMC 1985; Causey et al. 2002; NOAA 2009; Jackson et al. 2014). Parrotfishes play several important ecological roles within reef ecosystems; as a dominant group of fishes in abundance and biomass, they aid in reef ecosystem health and resilience through their consumption of algal resources and production of sediment (Bruggemann et al. 1996; McAfee and Morgan 1996; Mumby 2006; Francini et al. 2010; Dromard et al. 2015).

Queen parrotfish *Scarus vetula* and stoplight parrotfish *Sparisoma viride* are relatively common in reef fish landings throughout much of their geographic range (Mumby 2006; SEDAR 2016; CFMC 2019c). Both species are broadly distributed in the northern tropical/subtropical zone of the western Atlantic (Robertson and Van Tassell 2019) and considered important herbivores. Bruggemann et al. (1994) reported that queen parrotfish and stoplight parrotfish graze preferentially around dead coral and coral rubble substrates, but sometimes stoplight parrotfish consumes live coral. Queen parrotfish feed mainly on turf algal communities and crustose coralline algae, but also consume mat-forming cyanobacteria from sediment and hard surface substrates (Bruggemann et al. 1994; Bruggemann et al. 1996; Manning and McCoy 2023). Stoplight parrotfish forage on a combination of macroalgae, turf algae, mat-forming cyanobacteria, and to a lesser extent, live corals (Bruggemann et al. 1994; Bruggemann et al. 1996; Manning and McCoy 2023).

Despite their important roles in coral reef ecosystems and importance to local fisheries, no prior comprehensive research effort has characterized the population demographics, growth, and reproductive biology of either queen parrotfish or stoplight parrotfish. As protogynous hermaphrodites, most parrotfish species exhibit complex sexual ontogenies and reproductive strategies (Robertson and Warner 1978; van Rooij et al. 1995a; 1995b; van Rooij et al. 1996a; van Rooij et al. 1996b; DeMartini et al. 2018; Jones 2020). Both queen parrotfish and stoplight parrotfish utilize reef-associated habitats at depths up to at least 42 m; in the U.S. Caribbean, spearfishers typically encounter both species at depths ranging from 2 to 23 m (Rivera Hernández and Shervette 2024a). Visual reef fish surveys at sites ranging in depth from 28 to 42 m in the Marine Conservation District south of St. Thomas, USVI, ranked queen parrotfish and stoplight parrotfish as the first and second most abundant fisheries species observed (Nemeth and Quandt 2005).

Previously published age-based studies do not exist for queen parrotfish. A few limited studies have reported on age-structure and growth for stoplight parrotfish, but these studies did not incorporate sex-specific information. Maximum age estimates for stoplight parrotfish varied among studies and regions; work in the Florida Keys sampled stoplight parrotfish at shallow depths (< 15 m) and reported a maximum age of 8 years based on increment counts from otoliths (Paddack et al. 2009). Another study sampled stoplight parrotfish at shallow depths (≤ 15 m), from waters of Panama, Barbados, Venezuela, and Bahamas, and documented a maximum age of 9 years, also based on otolith increment counts (Choat et al. 2003). A study from Bonnaire utilized repeated visual censuses that included marked fish to estimate mortality rates and noted that 10% of stoplight parrotfish > 250 mm FL attain an estimated age of 17 years and older (van Rooij and Videler 1997).

Aspects of the reproductive biology of queen parrotfish and stoplight parrotfish were reported for individuals sampled from Panama; both species exhibit protogyny and are fully dichromatic (Robertson and Warner 1978). Three ontogenetic color phases were observed in both species: juvenile color phase consisted of immature fish; initial color phase (IP) consisted of mostly female individuals, but a few males were present; and terminal color phase (TP) was composed of only males. Clavijo (1983) observed two types of territorial spawning for queen parrotfish. The first type consisted of TP males defending large (>1000 m^2) foraging and spawning territories in back reef habitat at depths of 17–21 m. Each TP male defended its territory containing 2–4 IP females by chasing away intruding TP and IP fish. A territorial male would consecutively pair-spawn with IP females residing within his territory from 9:20 to 11:40 am; this territorial spawning was described as a harem strategy (Clavijo 1983). The second type of territorial spawning observed was described as a lek-like strategy and occurred only along the shelf edge where TP males would establish and defend small (25–50 m^2) temporary territories only during the peak spawning morning period (Clavijo 1983). IP females were not stationary in this area, but rather moved continuously along the shelf edge and as an IP fish passed a territory, the defending TP male would follow her and initiate courtship. A successful spawning rush consisted of the pair swimming into deeper water ~2 m from the small temporary territory (Clavijo 1983). Detailed reproductive behavior observations for stoplight parrotfish were reported from Bonnaire (van Rooij et al. 1995a; van Rooij et al. 1995b; van Rooij et al. 1996a; van Rooij et al. 1996b). That research indicated that stoplight parrotfish also exhibited the two types of territorial spawning strategies and noted year-round spawning for territorial TP males with each female in its harem. Stoplight parrotfish females within a harem spawned at least once daily, year-round, and some females spawned two or more times a day, once with their territorial TP male and then additional times with males in deeper water temporary territories (van Rooij et al. 1995a; van Rooij et al. 1995b; van Rooij et al. 1996a; van Rooij et al. 1996b). Additionally, a study from Bermuda documented spawning aggregations of queen parrotfish and stoplight parrotfish in June and July and observed pair-spawning events for both species (Luckhurst 2011).

Territorial and federal waters of the U.S. Caribbean are among the most highly regulated fisheries jurisdictions in the Caribbean. The U.S. Caribbean is located in the western portion of the Caribbean archipelago (Fig. 1) and includes the territories of Puerto Rico (PR) and the U.S. Virgin Islands (USVI). Mainly, seven parrotfish species are landed in the reef fish fisheries of PR and USVI: stoplight parrotfish, redtail parrotfish *Sparisoma chrysopterum*, redband parrotfish *Sp. aurofrenatum*, yellowtail parrotfish *Sp. rubripinne*, princess parrotfish *Scarus taeniopterus*, striped parrotfish *Sc. iseri*, and queen parrotfish (Rivera Hernández and Shervette 2024a). The U.S. Caribbean is divided into three fisheries management platforms that reflect ecological, cultural (e.g., traditional fishing practices), and market preference distinctions specific to each platform island system (CFMC 1985; CFMC 2019a; CFMC 2019b; CFMC 2019c). The largest island management platform is PR in the west. Waters of PR are characterized by extensive coral reef ecosystems that occur across approximately 3400 km^2. In PR, commercial landings of parrotfishes are reported as an aggregate group ("parrotfishes – unspecified") (Matos-Caraballo 2018). From 2011 to 2019, annual reported landings parrotfishes for PR averaged 16,899 lbs. USVI contains two fisheries management platforms: in the north is St. Thomas/St. John (STT/J) and St. Croix (STX) in the south (NOAA Fisheries, Commercial

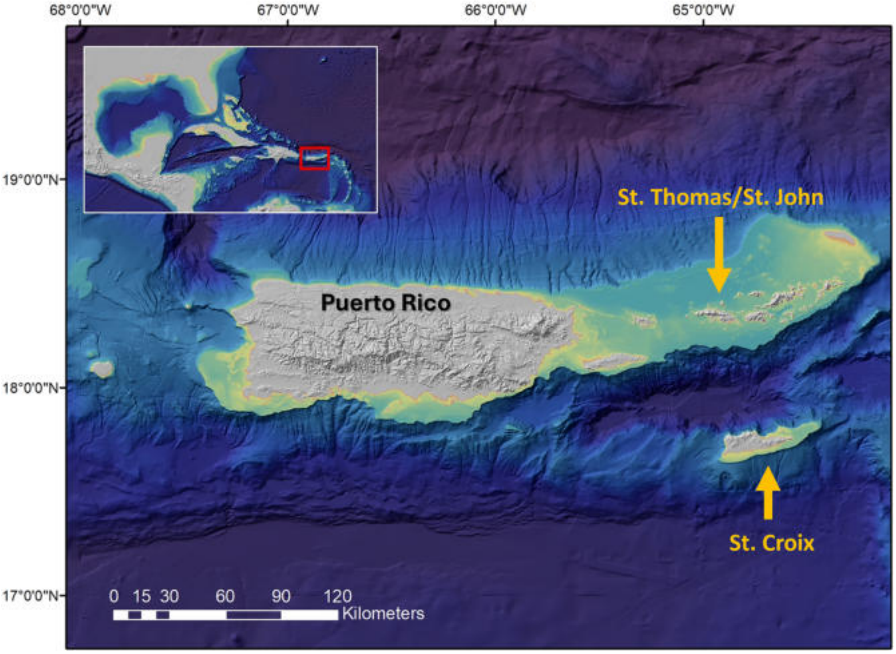

Fig. 1 Map of the U.S. Caribbean sampling region

Fisheries Landings Database accessed June 2021). STT/J occurs on a large shelf platform containing a fishable area of approximately 1500 km^2 and consists of a complex network of reef ecosystems (Kadison et al. 2017). “Parrotfishes” are mainly caught commercially in STT/J using traps and are primarily fished in shelf waters at depths > 25 m (CFMC 2019c). Reported annual commercial landings of parrotfishes in STT/J for 2011–2019 averaged 9127 lbs (NOAA Fisheries, Commercial Fisheries Landings Database accessed June 2021). The management platform of STX is located approximately 60 km south of STT/J. STX sits on a narrow platform surrounded by approximately 300 km^2 of continental shelf waters containing a system of coral reefs and associated habitats. Over 85% of the fishable area is at depths < 25 m (Kadison et al. 2017). Commercial fishers in STX target parrotfishes mainly using traps and spearfishing. Reported annual landings of parrotfishes in STX from 2011 to 2019 averaged 32,380 lbs (NOAA Fisheries, Commercial Fisheries Landings Database accessed June 2021).

Several fisheries management tools are currently in use within the U.S. Caribbean that regulate the commercial harvest of reef-associated species (CFMC 2019a; CFMC 2019b; CFMC 2019c). Within each management platform, many federal and territorial protected areas were established that are closed to fishing activities. In PR, an annual catch limit (ACL) caps the total landing of “parrotfishes” (CFMC 2019a). In the USVI, a moratorium on issuance of commercial licenses for harvesting reef fishes via traps and spearfishing has been in place since 2001 (CFMC 2019b; CFMC 2019c). STT/J has a minimum mesh size limit for traps and ACLs for parrotfish species (CFMC 2019c). St. Croix banned the use of gillnets to harvest parrotfishes, has a minimum mesh size limit for traps, and ACLs for parrotfish species (CFMC 2019b). Additionally, market-driven, self-imposed slot-limits exist for reef-associated species in the USVI which results in the selection of mostly mature individuals and minimizes targeting of fish in the largest size groups (Rivera Hernández and Shervette 2024b).

Past attempts to conduct stock assessments for parrotfish species populations in the U.S. Caribbean were incomplete due to the lack of basic life history information (SEDAR 2016). The overall goal of the current study was to fill in critical life history information gaps for queen parrotfish and stoplight parrotfish in U.S. Caribbean waters. The specific objectives of our study were to (1) determine size/age structure and growth rates for each species; (2) define spawning seasonality in the U.S. Caribbean for the two species; and (3) document size and age at sexual maturity and at sexual transition for queen parrotfish and stoplight parrotfish.

Methods

Field collection and processing

Samples of queen parrotfish and stoplight parrotfish were collected monthly from 2013 to 2023 through (1) fishery-dependent (FD) sampling via purchase of fish from local fishers; and (2) opportunistic fishery-independent (FI) sampling. Fishery-dependent samples were obtained directly from fishers and divided into two FD sample types: FD-random were collected by randomly selecting all parrotfish individuals for a particular species from one side of a cooler containing the day’s catch or by purchasing all parrotfish individuals for a particular species landed by a fisher on the day of sampling; FD-nonrandom were collected by haphazardly selecting a subsample of individuals for a particular species from a fisher at market which meant that catch may have been combined from multiple trips and an unknown portion of fish may have been sold prior to our sampling. Opportunistic FI sampling consisted of working collaboratively with fishers to collect individuals encountered in traps or during spearfishing, from the smallest and largest length classes, but that fishers would not typically retain from traps or target while spearfishing. This was to ensure that individuals smaller and larger than the size range (“plate-size” fish) typically retained/targeted by fishers for sale to locals were represented in the samples. Additional FI samples were collected via spearfishing and with a castnet by fish biologists. Fish samples were kept on ice (maximum of 48 h) until processing occurred.

Fish samples were measured for length (standard length [SL], fork length [FL], total length [TL]) to the nearest mm and whole weight to the nearest g. Gonads were removed, weighed (to the nearest 0.01 g), and then preserved for sex determination and reproductive phase characterization via histological processing in the lab (Rivera Hernández et al. 2019; Jones et al. 2021). Sagittal otoliths were extracted and stored dry after gently cleaning with water to remove tissue and other biological debris.

Population demographics—size and age trends

Length and weight measurements were used for exploring species-specific trends related to population demographics. Regression analyses were used to establish length-length and length-weight relationships for each species using combined fish length and weight data from FD and FI samples. For each species, we used separate ANOVAs to test for significant differences in mean FL among the three sexes (female, transitioning, and male). Separate Kolmogorov-Smirnov (K-S) tests were used to determine if significant differences occurred in length frequency distributions between sexes (female versus transitioning; female versus male; transitioning versus male) for each species.

Parrotfish sagittal otoliths were processed for age estimation as described in the Caribbean parrotfishes bomb radiocarbon age validation study (Rivera Hernández and Shervette 2024a). Briefly, one sagittal otolith from each fish sample was embedded in epoxy, then otoliths were sectioned transversely through the nucleus to a thickness of ~ 0.3 mm using a low-speed saw using a diamond-edged blade. Otolith sections were mounted on glass slides and covered with a clear mounting media. Ages for all otoliths were determined based on the number of increments counted independently by two readers with 10+ years of fish age estimation experience using a stereoscope with transmitted light at a magnification of 20–40×. Each increment consisted of a set of one translucent band and one opaque band. Increment counts were assessed without knowledge of fish size or the time of year that the sample was collected. Average percent error (APE) was calculated to assess between-reader precision (Beamish and Fournier 1981). In cases of between-reader increment count disagreements, the two readers concurrently evaluated the otolith section together and reached a final consensus age.

For each species, we used separate ANOVAs to test for significant differences in mean age among the three sex categories (female, transitioning, and male). Separate pairwise K-S tests were used to compare the age frequency distributions between sexes (female versus transitioning; female versus male; transitioning versus male).

Growth parameters for each species were estimated by fitting size-at-age data to the von Bertalanffy growth function (VBGF) represented by:

$$L_i = L_\infty 1 - e^{-K(i-t_0)}$$

where L_i is the estimated size at age i, L_∞ is the asymptotic length (FL mm), K is the growth coefficient, and t_0 is the age at which fish have a theoretical length of zero. We computed VBGF for each species as follows: (1) length type FL; (2) length type FL; fixed t_0 value of −0.06 following the recommendations from previous parrotfish growth studies (Paddack et al. 2009; Taylor and Choat 2014). Length type SL (for comparison with other studies that used SL); (4) Length type SL; fixed t_0 value of −0.06 following the recommendations from previous parrotfish growth studies (Paddack et al. 2009; Taylor and Choat 2014).

Reproductive biology

Gonads were removed from each parrotfish sample and fixed in 11% seawater-buffered formalin or polyethylene glycol–ethyl alcohol–glycerol–acetic acid (PAGA) fixative for up to 2 weeks and then transferred to 70% isopropanol. Gonad samples were processed for histological assessment by the University of South Carolina Fish Reproductive Histology Lab in Aiken, SC (Rivera Hernández et al. 2019; Shervette et al. 2020; Jones et al. 2021; Zajovits 2021; Shervette and Rivera Hernández 2022). Gonad tissue samples were vacuum-infiltrated and embedded in paraffin wax. At least three transverse sections (~7-μm thick) were cut using a rotary microtome, mounted on glass slides, stained with double strength Gill hematoxylin, and counter-stained with eosin-y. Coverslips were applied after gonad sections were fully dry from the staining process.

Stained gonad sections were viewed using a compound microscope to determine sex and reproductive phase, assessed according to the general histological criteria for Caribbean Labridae species (Rivera Hernández and Shervette 2024d) with modifications related to ova shape and size. Sex was determined by the presence of oogenesis or spermatogenesis in the tissue (Sadovy and Shapiro 1987). Samples with gonad tissue that displayed only oogenesis or predominant oogenesis were considered female, and samples with tissue exhibiting only spermatogenesis or predominant spermatogenesis were considered male (Sadovy and Shapiro 1987; Jones 2020; Shervette et al. 2020; Jones et al. 2021). Transitioning individuals were narrowly defined by gonad tissue samples that contained pre-vitellogenic and/or atretic oocytes with intrusion of spermatogenic tissue (McBride and Johnson 2007; Jones 2020; Shervette et al. 2020; Jones et al. 2021).

Two readers independently assigned sex and reproductive phase without knowledge of the capture date, specimen length, or specimen age. If differences in the assignment of reproductive phases occurred, readers examined the slide simultaneously to obtain a consensus reproductive phase assignment. Separately for each species, the proportion of spawning-capable females and males relative to the total number of mature individuals in developing, regressing, and regenerating reproductive phases for each month was plotted to document overall spawning season for the U.S. Caribbean region. To quantify the contribution of immature individuals in the commercial catch, we computed for each species the proportion of immature fish sampled from FD collections.

For each of the two species, length (LM_{50}) and age (AM_{50}) at median sexual maturity were calculated using separate logistic regressions. For each of the two species, size (LT_{50}) and age (AT_{50}) at median sexual transition were computed using separate logistic regressions. Maturity (not mature versus mature) and sex (not male versus male) were treated as binomial response variables in these analyses (Jones et al. 2021). Logistic regressions were conducted using the logit function transformation and the GLM procedure in R (Olge 2016).

Results

Queen parrotfish

A total of 390 queen parrotfish samples ranging in size from 82 to 402 mm FL (mean FL = 294 mm) were collected and processed for this study (Table 1). Linear regression analyses of length-length and length-weight relationships were strongly correlated (Table 2). Initial color phase (IP) queen parrotfish (n = 191) ranged in size from 82 to 327 mm FL (mean FL = 255 mm) and TP fish (n = 199) ranged in size from 264 to 402 mm FL (mean FL = 331 mm). Based on length frequency distributions, TP fish were significantly larger than IP fish with a larger proportion of TP individuals in the larger length-classes (Table 3; Fig. 2).

Queen parrotfish males ranged in size from 169 to 402 mm FL (mean FL = 329 mm) and females ranged in size from 82 to 321 mm FL (mean FL = 254 mm; Table 1). Fish with gonads in sexual transition (n = 20) ranged in size from 140 to 322 mm FL (mean FL = 264 mm). Males were significantly larger than transitioning fish and females (Table 3). Length frequency distributions were significantly different between males and females and between males and transitioning fish with a larger proportion of males in the larger length-classes for both comparisons (Table 4; Fig. 2). Length frequency distributions did not differ significantly between females and transitioning fish.

A total of 387 samples were aged using the validated otolith age estimation method (Rivera Hernández and Shervette 2024a). The APE computed to assess between reader age estimation precision for this species was 3.7%. Queen parrotfish ages ranged from 0 to 16 years with a mean age of 5.2 years (Table 1). IP queen parrotfish ranged in age from 0 to 14 years (mean age = 4.4 years) and TP fish ranged in age from 3 to 16 years (mean age = 5.9 years). Based on age frequency distributions, TP fish were significantly larger than IP fish with a larger proportion of TP individuals in the larger length-classes (Table 3; Fig. 2). Females ranged in age from 0 to 13 years (mean age = 4.3 years) and ages of males ranged from 1 to 16 years (mean age = 5.9 years). Fish with gonads in sexual transition ranged in age from 1 to 14 years (mean age = 5.0 years). Males were significantly older than females (Table 4). Length frequency distributions were significantly different between males and females with a larger proportion of males in the older age-classes (Table 3; Fig. 2). Age frequency distributions did not differ significantly between females and transitioning fish nor between males and transitioning fish (Table 3; Fig. 2).

Fork length and age data fit to a von Bertalanffy growth curve produced an asymptotic length (L_∞) of 347 mm FL and a growth coefficient (K) of 0.32 when t_0 was fixed at −0.06 (Fig. 3; Table 5). When t_0

Table 1 Summary of fork length (FL), standard length (SL), and age information obtained from U.S. Caribbean queen parrotfish and stoplight parrotfish samples overall ("All fish"), by sex, and by color phase * sex. Samples of unknown sex were not included beyond the "All fish" group

Species	Group	*N* measured/aged	FL range (mean) mm	SL range (mean) mm	Age range (mean) y
Scarus vetula	All fish	390/387	82–402 (294)	64–335 (245)	0–16 (5.2)
Sex	Female	167/165	82–321 (254)	64–272 (210)	0–13 (4.3)
	Male	203/202	169–402 (329)	136–335 (275)	1–16 (5.9)
	Transition	20/20	140–322 (264)	115–262 (217)	1–14 (5.0)
Initial phase	All	191/189	82–327 (255)	64–274 (210)	0–14 (4.4)
	Female	167/165	82–321 (254)	64–272 (210)	0–13 (4.3)
	Male	4/4	169–327 (237)	136–274 (197)	1–6 (3.5)
	Transition	20/20	140–322 (264)	115–262 (217)	1–14 (5.0)
Terminal phase	Male	199/198	264–402 (331)	219–335 (277)	3–16 (5.9)
Sparisoma viride	All fish	1801/1714	73–433 (281)	60–376 (240)	0–20 (5.4)
Sex	Female	791/754	73–433 (259)	60–376 (218)	0–20 (5.2)
	Male	917/874	127–399 (304)	103–355 (261)	1–16 (5.7)
	Transition	73/70	183–366 (258)	148–315 (217)	2–15 (4.5)
	Unknown	20/16	135–293 (241)	114–237 (199)	2–9 (5.0)
Initial phase	All	917/869	73–433 (258)	60–376 (217)	0–20 (5.1)
	Female	791/754	73–433 (259)	0–376 (218)	0–20 (5.2)
	Male	34/30	127–298 (238)	103–241 (198)	1–7 (4.2)
	Transition	72/69	183–366 (258)	148–315 (217)	2–15 (4.5)
	Unknown	20/16	135–293 (241)	114–237 (199)	2–9 (5.0)
Transitioning color phase	All	4/4	250–318 (290)	213–282 (247)	4–8 (5.5)
	Male	3/3	291–318 (303)	242–282 (258)	5–8 (6.0)
	Transition	1/1	250	213	4
Terminal phase	Male	880/841	210–399 (306)	175–355 (264)	2–16 (5.7)

Table 2 U.S. Caribbean queen parrotfish and stoplight parrotfish length-length and length-weight conversion relationships derived from regression analyses

Category	*n*	Regression equation	R^2
Scarus vetula			
SL→Wt	387	$Wt = (8\times10^{-5})\ SL^{3.02}$	0.96
FL→Wt	388	$Wt = (1\times10^{-5})\ FL^{3.14}$	0.97
TL→Wt	388	$Wt = (8\times10^{-5})\ TL^{2.73}$	0.96
FL→SL	387	SL = 0.85FL − 6.31	0.98
FL→TL	390	TL= 1.21FL – 44.98	0.98
TL→SL	387	SL= 0.69TL + 29.70	0.98
Sparisoma viride			
SL→Wt	1488	$W= (2\times10^{-4})\ SL^{2.69}$	0.93
FL→Wt	1716	$W= (4\times10^{-5})\ FL^{2.90}$	0.95
TL→Wt	1706	$W= (3\times10^{-4})\ TL^{2.51}$	0.95
FL→SL	1488	SL= 0.90FL − 14.11	0.98
FL→TL	1711	TL= 1.28FL – 47.38	0.97
TL→SL	1488	SL= 0.70TL + 22.33	0.97

was not fixed, L_∞ = 363 mm FL, K = 0.31, and t_0= −0.87 (Table 5).

Spawning capable females, including those that were actively spawning, occurred from November through August (Fig. 4). Over 50% of females were in spawning condition from January to July. For February and March, 100% of mature females were in spawning condition (Fig. 4). Of the 150 queen parrotfish FD samples with gonad histology results, 0% were sexually immature. Queen parrotfish length at median maturity (LM_{50}; fork length at which 50% of the fish were mature) was 192 mm FL (Table 6). The age at median sexual maturity (AM_{50}), or the age at which 50% of the fish were mature, was 1.9 years (Table 6). Length at median sexual transition (LS_{50}; total length at which 50% of the fish were male) was 293 mm FL (Table 5). Age at median sexual transition (AT_{50}), or the age at which 50% of the fish were male, was 4.5 years (Table 6).

Table 3 Results from Kolmogorov-Smirnov tests

Comparison	*N*	*D*	*P*
Scarus vetula			
Length (FL mm)			
Initial v terminal	191 +199	7.85	<0.001
Female v transition	167 + 20	1.06	0.211
Female v male	167 + 203	7.59	<0.001
Transition v male	20 + 203	3.26	<0.001
Age (y)			
Initial v terminal	189 + 198	3.27	<0.001
Female v transition	165 + 20	0.45	0.993
Female v male	165 + 202	3.13	<0.001
Transition v male	20 + 202	1.20	0.115
Sparisoma viride			
Length (FL mm)			
Initial v terminal	897 + 880	10.66	<0.001
Female v transition	791 + 73	1.29	0.072
Female v male	791 + 917	9.58	<0.001
Transition v male	73 + 917	4.92	<0.001
Age (y)			
Initial v terminal	853 + 841	4.25	<0.001
Female v transition	754 + 70	1.60	0.062
Female v male	754 + 874	3.53	<0.001
Transition v male	70 + 874	3.03	<0.001

Stoplight parrotfish

A total of 1801 stoplight parrotfish samples ranging in size from 73 to 433 mm FL (mean FL = 281 mm) were collected and processed for this study (Table 1). Linear regression analyses of stoplight parrotfish length-length and length-weight relationships were strongly correlated (Table 2). Stoplight parrotfish IP samples ($n = 917$) ranged in size from 73 to 433 mm FL (mean FL = 258 mm) and TP fish ($n = 880$) ranged in size from 264 to 402 mm FL (mean FL = 331 mm). Based on length frequency distributions, TP fish were significantly larger than IP fish with a larger proportion of TP individuals in the larger length-classes (Table 3; Fig. 5).

Stoplight parrotfish males ranged in size from 127 to 399 mm FL (mean FL = 304 mm) and females ranged in size from 73 to 433 mm FL (mean FL = 259 mm; Table 1). Fish with gonads in sexual transition ($n = 73$) ranged in size from 183 to 366 mm FL (mean FL = 258 mm). Males were significantly larger than transitioning fish and females (Table 3). Length frequency distributions were significantly different between males and females and between males and transitioning fish with a larger proportion of males in the larger length-classes for both comparisons (Table 4; Fig. 5). Length frequency distributions did not differ significantly between females and transitioning fish.

For stoplight parrotfish, 1714 samples were aged using the validated otolith age estimation method (Rivera Hernández and Shervette 2024a). The APE computed to assess between reader age estimation precision for this species was 4.1%. Ages ranged from 0 to 20 years with a mean age of 5.4 years (Table 1). IP stoplight parrotfish ranged in age from 0 to 20 years (mean age = 5.1 years) and TP fish ranged in age from 2 to 16 years (mean age = 5.7 years). Based on age frequency distributions, TP fish were significantly older than IP fish with a larger proportion of TP individuals in the larger length-classes (Table 3; Fig. 5). Females ranged in age from 0 to 20 years (mean age = 5.2 years) and ages of males ranged from 1 to 16 years (mean age = 5.7 years). Fish with gonads in sexual transition ranged in age from 2 to 15 years (mean age = 4.5 years). Males were significantly older than females (Table 4). Length frequency distributions were significantly different between males and females and between males and transitioning fish with a larger proportion of males in the older age-classes (Table 3; Fig. 5). Age frequency distributions did not differ significantly between females and transitioning fish (Table 3; Fig. 5).

Fork length and age data fit to the von Bertalanffy growth model produced an asymptotic length (L_∞) of 332 mm FL and a growth coefficient (K) of 0.39 when t_0 was fixed at −0.06 (Fig. 3; Table 5). When t_0 was not fixed, L_∞ = 338 mm FL, K = 0.33, and t_0= −0.52 (Table 5).

Spawning capable females, including those that were actively spawning, occurred during all months of the year (Fig. 4). Over 50% of mature females were in spawning condition for all months (Fig. 4). A total of 1592 stoplight parrotfish were FD samples and 0% of those were sexually immature. Stoplight parrotfish length at median sexual maturity (LM_{50}) was 153 mm FL (Table 6). The age at median sexual maturity (AM_{50}) was 1.6 years (Table 6). Length at median sexual transition (LS_{50}) was 279 mm FL (Table 5). Age at median sexual transition (AT_{50}), or the age at which 50% of the fish were male, was 4.5 years (Table 6).

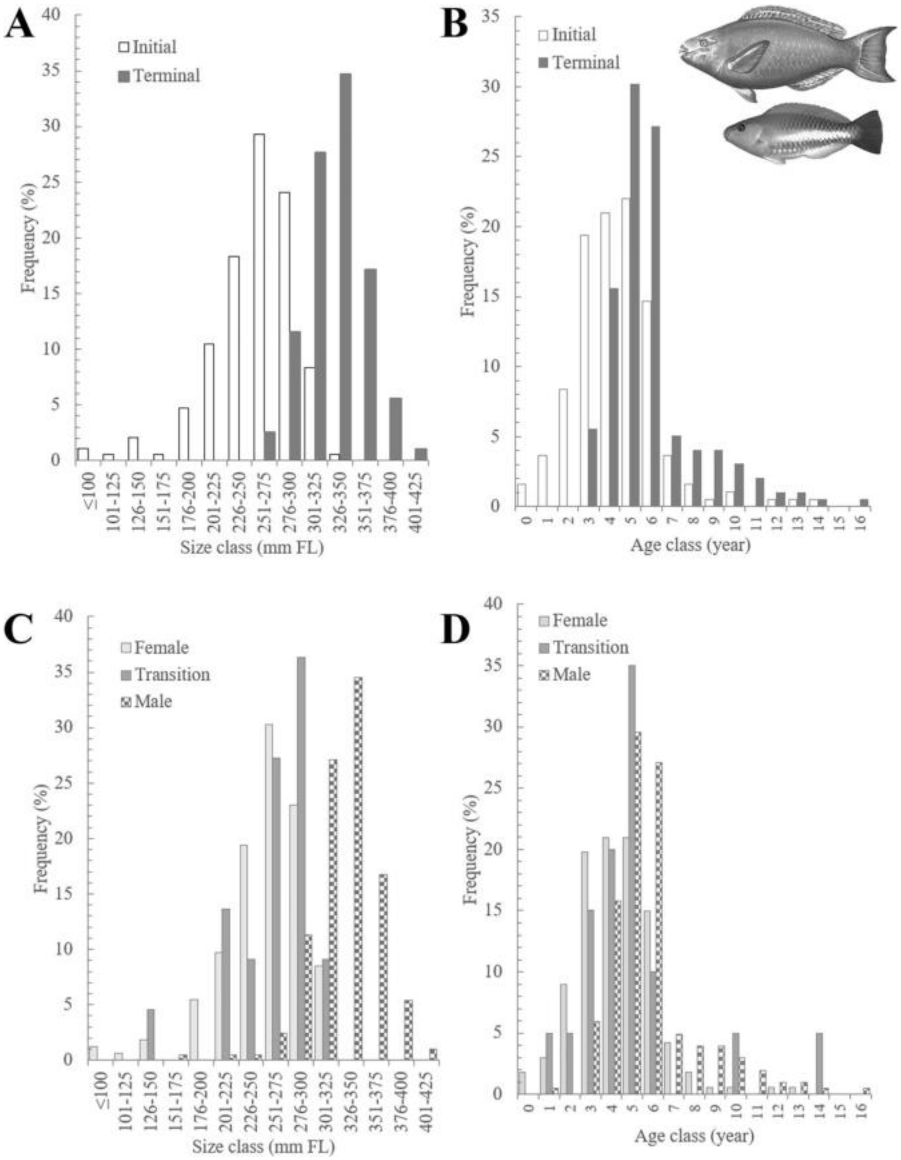

Fig. 2 Length frequency (**A**, **C**) and age frequency (**B**, **D**) comparisons for U.S. Caribbean queen parrotfish initial color phase versus terminal color phase (**A**, **B**) and female, sexually transitioning ("Transition"), and male fish (**C**, **D**)

Discussion

This is the first published study to provide comprehensive documentation of population size and age structure, growth, spawning seasonality, size and age at sexual maturity, and size and age at sexual transition for queen parrotfish and stoplight parrotfish. Previous studies on Caribbean parrotfishes have mainly focused on their important trophic roles in reef ecosystems and their reproductive behavior. But without the critical information on life history parameters, fisheries managers struggled to conduct scientifically robust stock assessments for parrotfish species. Parrotfishes exhibit complex sexual ontogenies which can impact size and sex-specific growth patterns (Robertson and Warner 1978; van Rooij et al. 1995a; van Rooij et al. 1996b; Taylor and Choat 2014; DeMartini et al. 2018). In addition, several studies have documented a decoupling of size and age in some parrotfish species emphasizing a greater importance for incorporating age estimates in documenting demographic patterns related to life history strategies (van Rooij et al. 1995a; van Rooij et al. 1995b; Taylor and Choat 2014; DeMartini et al. 2018). Many studies

Table 4 ANOVA analysis results for mean length and mean age among sexes (female, transitioning, and male)

Source	df	Sum of squares	Mean square	*F*	*P*
Scarus vetula					
Length (FL mm)					
Sex	2	538444	269222	208.03	<0.001
Error	387	500835	1294		
Age (y)					
Sex	2	213	106	23.62	<0.001
Error	384	1729	5		
Sparisoma viride					
Length (FL mm)					
Sex	2	892734	446367	300.29	<0.001
Error	1778	2642932	1486		
Age (y)					
Sex	2	175	87	18.12	<0.001
Error	1695	8176	5		

noted that age estimation in parrotfishes can be difficult, mostly because otolith increments can be relatively difficult to visualize or interpret (Choat et al. 1996; Paddack et al. 2009; Jones et al. 2021). The current study is unique compared to the few past studies that reported on demographic patterns Caribbean parrotfish species because we utilized an age estimation method that we validated as providing accurate ages for our two species via bomb radiocarbon analysis (Rivera Hernández and Shervette 2024a) combined with detailed examination of parrotfish gonads using reproductive histology (Jones et al. 2021).

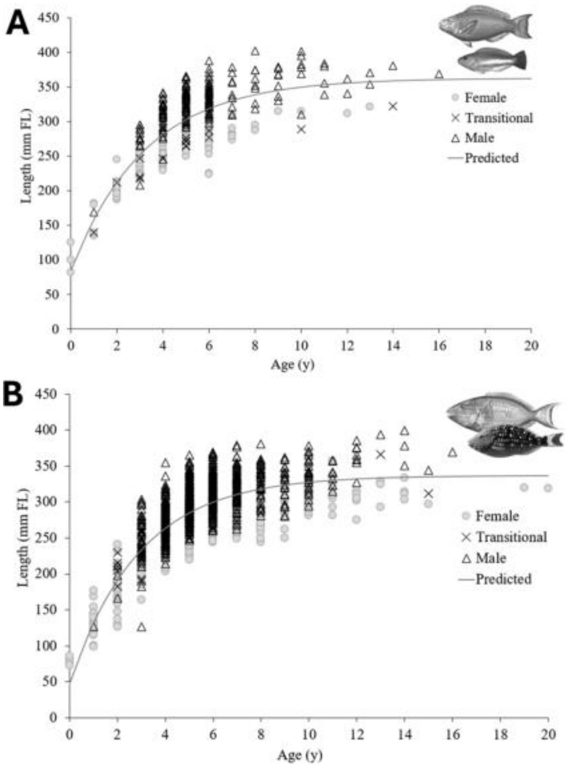

Fig. 3 Length-at-age and von Bertalanffy growth curves for U.S. Caribbean queen parrotfish (**A**) and stoplight parrotfish (**B**)

Queen parrotfish

Results from our study provide new insights concerning the biology of queen parrotfish. The main source of life history-related information about this species prior to our work is a study from San Blas, Panama, on samples collected over 50 years ago (Robertson and Warner 1978). In that study, a total of 151 queen parrotfish were speared from shallow water habitats (depths < 15 m) and processed for gonad histology. Of those samples, 19 were TP males (~200–320 mm SL; size ranges for the Panama study were estimated from length frequency graphs) and 132 were IP individuals (~100–260 mm SL). For the IP fish, 129 were female and three were male. The Panama study documented an overlap in the size ranges between TP and IP fish of ~60 mm (Robertson and Warner 1978); the current study showed a similar overlap in size ranges (63 mm). The maximum sizes of IP and TP fish from Panama and the U.S. Caribbean were somewhat smaller than maximum sizes reported from

Table 5 Results for von Bertalanffy growth functions for U.S. Caribbean queen parrotfish and stoplight parrotfish (95% confidence intervals)

Model	N	L_∞ (mm)	K	t_0
Scarus vetula				
FL mm t_0-fixed	387	347 (338–356)	0.42 (0.39–0.46)	−0.06*
FL mm	387	363 (350–377)	0.31 (0.26–0.36)	−0.87 (−1.30 to −0.54)
SL mm t_0-fixed	387	290 (282–298)	0.41 (0.38–0.45)	−0.06*
SL mm	387	301 (286–300)	0.32 (0.26–0.38)	−0.74 (−1.25 to −0.36)
Sparisoma viride				
FL mm t_0-fixed	1649	332 (328–335)	0.39 (0.35–0.41)	−0.06*
FL mm	1649	338 (328–335)	0.33 (0.31–0.36)	−0.52 (−0.72 to −0.35)
SL mm t_0-fixed	1649	287 (282–290)	0.38 (282–290)	−0.06*
SL mm	1649	297 (286–300)	0.33 (0.31–0.36)	−0.40 (−0.59 to −0.23)

Asterisk (*) denotes a fixed value of 0.6 was utilized

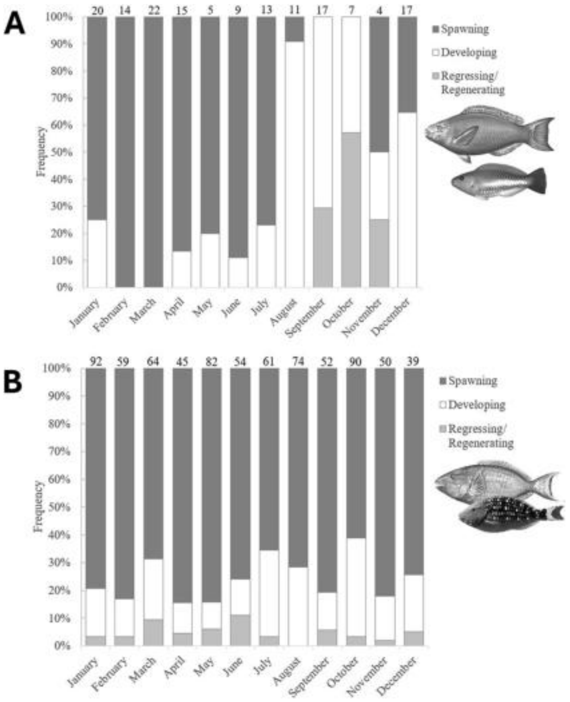

Fig. 4 Reproductive seasonality for females in the U.S. Caribbean. Monthly percentages of individuals in each reproductive phase are for queen parrotfish (**A**) and stoplight parrotfish (**B**). The number of samples analyzed for each month is provided above each bar

Table 6 Size and age at sexual maturity and sexual transition (95% prediction intervals)

Parameter	*Scarus vetula*		*Sparisoma viride*	
	n	Estimate	*n*	Estimate
Sexual maturity				
LM_{50}	163	192 (187–197)	768	153 (140–165)
AM_{50}	161	1.9 (1.0–2.0)	731	1.6 (1.4–1.9)
Transition				
LT_{50}	369	293 (288–297)	1637	279 (275–282)
AT_{50}	366	4.5 (3.9–5.0)	1558	4.5 (3.4–5.3)

a spawning aggregation in Bermuda (Rivera Hernández and Shervette 2024a): IP maximum length was 391 mm FL/325 mm SL and TP maximum length was 456 mm FL/399 mm SL. This trend in maximum sizes documented from the three regions indicates that maximum length for queen parrotfish may increase with increasing latitude; a similar trend has been observed for other reef-associated fishes (Robertson et al. 2005; Taylor et al. 2019; Shervette et al. 2021).

Queen parrotfish from the U.S. Caribbean demonstrated the typical pattern in population length structure of female, sexually transitioning, and male fish for protogynous reef fishes (Warner 1975; Shapiro 1981a; Jones et al. 2021). Overall, females were significantly smaller than males and occurred at significantly greater proportions in the smaller length groups, but by 322 mm FL, all queen parrotfish from our study region were male or transitioning to male. Males were absent from the smallest length groups (the smallest male was a 169 mm FL IP fish), although 2% of all males were IP individuals and 2% of all IP fish were male. Robertson and Warner (1978) noted that 2% of IP queen parrotfish examined from Panama were also male. Similar trends in length structure were documented for other *Scarus* species; princess parrotfish *Sc. taeniopterus* females in the

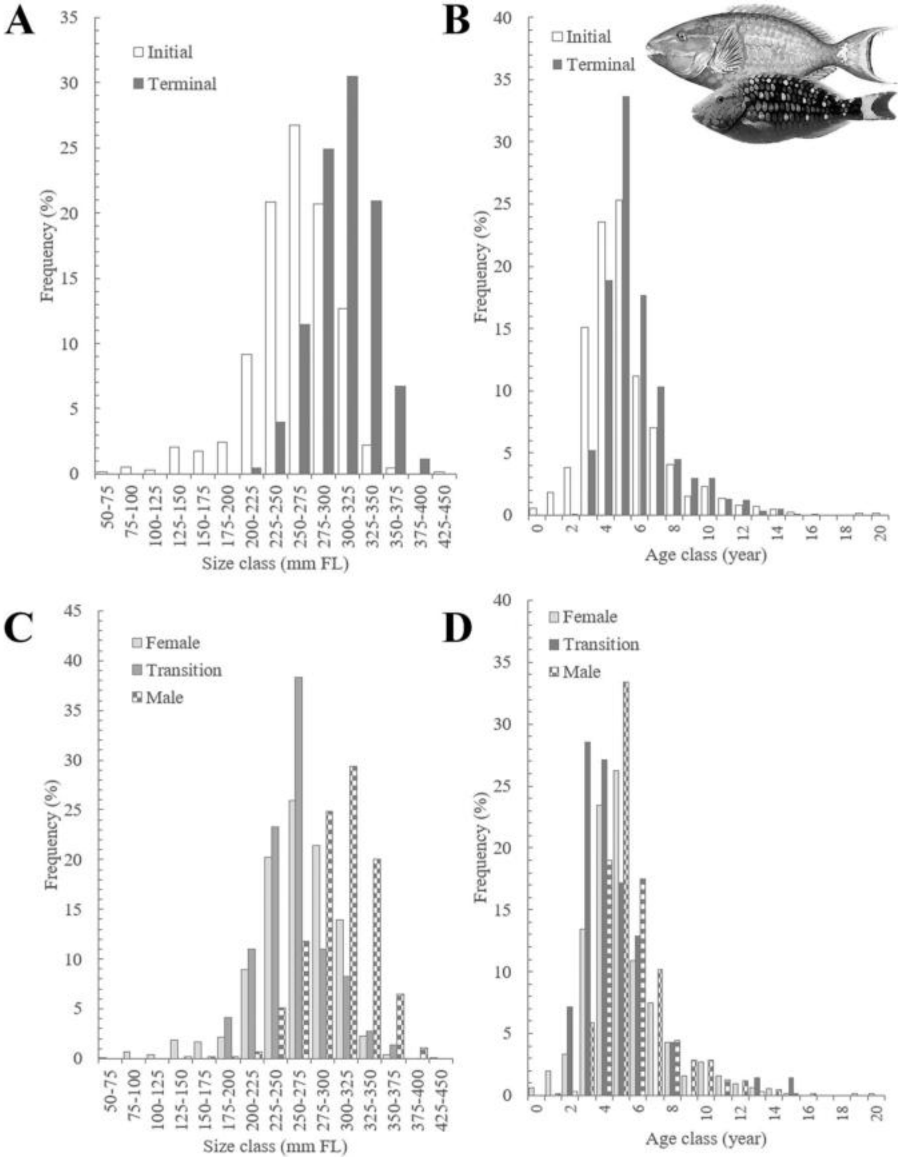

Fig. 5 Length frequency (**A**, **C**) and age frequency (**B**, **D**) comparisons for U.S. Caribbean stoplight parrotfish initial color phase versus terminal color phase (**A**, **B**) and female, sexually transitioning ("Transition"), and male fish (**C**, **D**)

U.S. Caribbean were limited to a maximum length of 250 mm TL and males attained a maximum length of 314 mm TL (Jones et al. 2021). Not all parrotfish species exhibit this sex-specific length pattern. For example, stoplight parrotfish females and males from the current study overlapped in length across a broader length range and the largest individual stoplight parrotfish collected was female.

The largest queen parrotfish sampled in the current study was 402 mm FL. Four other Atlantic parrotfish species reach similar maximum lengths: gray parrotfish *Sparisma axillare* has a maximum reported length of 430 mm TL (Robertson and Van Tassell 2019); redtail parrotfish *Sparisoma chrysopterum* has a maximum length in the U.S. Caribbean of 394 mm FL (Stevens et al. 2019); yellowtail parrotfish *Sparisoma rubripenne* has a maximum reported length of 395 mm FL in the U.S. Caribbean (Stevens et al. 2019); and stoplight parrotfish has a maximum length of 433 mm FL (current study). Other parrotfish species in this region that contribute to fisheries attain somewhat smaller maximum lengths: striped parrotfish *Scarus iseri* grows to 270 mm TL (Robertson and

Van Tassell 2019). Princess parrotfish reaches a maximum length of 314 mm TL in the U.S. Caribbean (Jones et al. 2021), and redband parrotfish *Sparisoma aurofrenatum* grows up to 280 mm TL (Robertson and Van Tassell 2019).

Population age structure among queen parrotfish female, transitioning, and male fish suggests that most individuals start out as female since only females occurred in the age-0 group; the youngest transitioning fish collected were in the 1-year age group. The maximum age attained by females was 14 years in the U.S. Caribbean, while the maximum age attained by males in this region was 16 years. The oldest queen parrotfish documented from throughout its geographic range was a 21-year-old TP male collected in Bermuda (Rivera Hernández and Shervette 2024c). Transitioning fish in the current study ranged in age from 1 to 14 years. These trends in ages combined with the sex-specific trends in maximum length for queen parrotfish indicate that for the population in the U.S. Caribbean, individuals start out life as female and if they live long enough, transition to male. A similar pattern in population age structure was also observed for princess parrotfish (Jones et al. 2021). Some species of parrotfishes in the *Scarus* genus exhibit different patterns in sex related population age structure. For example, female bluepatch parrotfish *Sc. forsteni*, palenose parrotfish *Sc. psittacus*, and yellowband parrotfish *Sc. schlegeli* attained older maximum ages than males (Taylor and Choat 2014).

The current study is the first to report on age and growth for queen parrotfish. The growth coefficient (K = 0.42) computed for samples from the U.S. Caribbean fell within the range of K reported for other *Scarus* species. The growth coefficient documented for palenose parrotfish populations from several regions in the Pacific ranged from 0.35 to 0.91 (Choat et al. 1996; Taylor and Choat 2014; DeMartini et al. 2018). Pacific populations of yellowband parrotfish have growth coefficients ranging from 0.22 to 1.03 (Choat et al. 1996; Taylor and Choat 2014). Princess parrotfish from the U.S. Caribbean had a growth coefficient of 0.32 (Jones et al. 2021). Overall, parrotfishes in the genus *Scarus* display a wide range in estimates of K and for at least some of these species, growth may be responsive to a combination of anthropogenic and environmental factors (Taylor and Choat 2014).

Maximum reported ages vary widely for Atlantic *Scarus* parrotfish species. Striped parrotfish attain an estimated maximum age of 10 years (Rivera Hernández and Shervette 2024c), followed closely by princess parrotfish with a maximum age of 11 years (Jones et al. 2021) and Zelinda's parrotfish *Sc. zelindae* with a maximum age of 12 years (Comeros-Raynal et al. 2012). Blue parrotfish *Sc. coeruleus* and rainbow parrotfish *Sc. guacamaia* both attain maximum ages of 16 years (Comeros-Raynal et al. 2012). Greenbeak parrotfish *Sc. trispinosus* live to a maximum reported age of 22 years (Freitas et al. 2019). The oldest age documented for any Atlantic parrotfish species is 31 years from a midnight parrotfish *Sc. Coelestinus* (Jones et al. 2021). We documented a maximum age of 16 years for queen parrotfish from the U.S. Caribbean which was less than the maximum age of 21 years reported for queen parrotfish from Bermuda (Rivera Hernández and Shervette 2024c).

The spawning season of U.S. Caribbean queen parrotfish lasted from November through August, nearly year-round. Other parrotfish species in our study region also exhibit year-round spawning including princess parrotfish (Jones 2020), stoplight parrotfish (current study), and redtail parrotfish (Figuerola et al. 1998). Near year-round spawning combined with utilizing multiple mating strategies may contribute to high reproductive output for queen parrotfish in the U.S. Caribbean.

Queen parrotfish had a length at median sexual maturity (LM_{50}) of 192 mm FL and an age at median sexual maturity (AM_{50}) of 1.9 years. The LM_{50} occurred at approximately 55% of the asymptotic length (L_∞) estimated for the U.S. Caribbean population. Length and age at sexual maturity can vary among regions within a single parrotfish species. For example, LM_{50} estimates for palenose parrotfish *Sc. psittacus* from Hawaiian collections were 139 mm FL versus 103 mm FL for fish from Guam (Taylor and Choat 2014; DeMartini and Howard 2016); Redlip parrotfish *Sc. rubroviolaceus* from Guam had an estimated LM_{50} of 350 mm FL and from Hawaii had an estimated LM_{50} of 271 mm FL (Taylor and Choat 2014; DeMartini and Howard 2016). Queen parrotfish length and age at sexual maturity may also vary by region emphasizing the importance of documenting region-specific maturity patterns for parrotfishes.

Queen parrotfish in the U.S. Caribbean had a median length at sexual transition (LT_{50}) and median age at sexual transition (AT_{50}) of 293 mm FL and 4.5 years. The LT_{50} occurred at approximately 84% of the asymptotic length growth parameter estimate and AT_{50} was 28% of the maximum age documented for the U.S. Caribbean. Although no other study has reported on size and age at sexual transition for queen parrotfish previously, LT_{50} has been estimated for two other *Scarus* species in the Greater Caribbean (Molloy et al. 2011; Jones et al. 2021). Princess parrotfish from the U.S. Caribbean had an LT_{50} of 223 mm TL which was 71% of the maximum length of (314 mm TL) reported from the study. Molloy et al. (2011) estimated LT_{50} for striped parrotfish *Sc. iseri* from several sites across the Caribbean, based on the assumption that all IP fish observed during visual surveys were female and all TP fish were male; LT_{50} ranged from a low of 128 mm TL for a site where maximum size of fish observed was 170 mm TL (at 76% of the maximum length observed) to 241 mm TL (at 74% of the maximum length of 330 mm TL observed at the site). Princess parrotfish from the U.S. Caribbean had an estimated AT_{50} of 4.2 years which occurred at 38% of the maximum age documented for the species in the study (Jones et al. 2021). The process of sexual transition appears to be partly under social control for many protogynous reef fish species and can result in regional differences in estimates of length and age at sex change (Shapiro 1981b; Nemtzov 1985; Munoz and Warner 2003; McBride and Johnson 2007; Molloy et al. 2011). Future investigation examining the size and age at sexual transition for queen parrotfish from other regions in the Caribbean will provide further insights related to the timing of sex change in this species.

Stoplight parrotfish

The main sources of stoplight parrotfish life history information prior to our study that reported on color phase and size include a summary of fish collected in San Blas, Panama (Robertson and Warner 1978), underwater observations from Bonnaire (van Rooij et al. 1995b; van Rooij et al. 1996a; van Rooij et al. 1996b), an age-based demographics study from the Florida Keys (Paddack et al. 2009), and a reproductive biology study from Turks and Caicos (Koltes 1993). In the Panama study, a total of 268 stoplight parrotfish were speared in shallow water (≤ 15-m depth) habitat and processed for gonad histology (Robertson and Warner 1978). Of those samples, 34 were TP males (100–330 mm SL), six were males in the process of transitioning from IP to TP coloration (130–200 mm SL), and 228 were IP individuals (80–280 mm SL). For the IP fish, 225 were female and 23 were male. The Panama study documented an overlap in the size ranges between TP and IP fish of ~180 mm. In Bonnaire, visual surveys of fish were conducted at multiple sites that ranged in depth from 1 to 26 m (van Rooij et al. 1995b; van Rooij et al. 1996a; van Rooij et al. 1996b). TP fish ranged from 210 to 399 mm FL and the maximum size reported for IP fish was 314 mm FL resulting in an overlap in length between the color phases of 104 mm. In the Florida Keys, stoplight parrotfish were sampled in habitats at depths < 15 m (Paddack et al. 2009); the maximum size of IP fish was 350 mm FL and TP fish ranged in size from 182 mm FL (converted from SL) to 420 mm FL with an overlap in length of 168 mm. In Turks and Caicos, fish were speared in reef habitats at depths < 15 m (Koltes 1993). A total of 220 fish were collected; IP fish ranged from 100 to 367 mm SL and TP fish ranged from 179 to 370 mm SL with an overlap in lengths of 188 mm. In the current study, IP fish ranged from 73 to 433 mm FL and TP fish ranged from 210 to 399 mm FL with an overlap in length between the color phases of 223 mm. Stoplight parrotfish appear to exhibit regional differences in maximum lengths attained within color phases and variability in the overlap of color phase length ranges. Interestingly, the current study collected fish from the widest range of depths with the maximum depth of collection > 40 m. It is possible that larger IP fish occur in the other study regions at deeper sites that were not sampled. Collins and McBride (2011) reported on depth related trends in length distributions for another protogynous Labridae species, hogfish *Lachnolaimus maximus*, that also has males that defend territories containing multiple females. Significantly larger females and males occurred in deeper waters (≥ 30 m).

Stoplight parrotfish from the U.S. Caribbean exhibited the typical pattern in population length structure among sexes for protogynous species when considering the general length trends. A significantly greater proportion of females occurred in the smaller length groups, but a few females attained relatively large sizes with the largest fish sampled being a female. This specific pattern is notably different than what we observed for queen parrotfish in which all individuals were transitioning to male or male by a certain length. Some populations of parrotfish species from the Pacific have females that attain similar maximum sizes as males, including bicolor parrotfish *Cetoscarus bicolour* in Pohnpei (Taylor and Choat 2014) and redlip parrotfish *Sc. rubriviolaceus* in Hawaii (DeMartini et al. 2018).

The largest stoplight parrotfish collected in the current study was 433 mm FL (376 mm SL). Slightly smaller maximum lengths were observed from Bonnaire (400 mm FL) (van Rooij et al. 1995b; van Rooij et al. 1996a), from Florida (420 mm FL) (Paddack et al. 2009), and from Turks and Caicos (370 mm SL, which converts to 427 mm FL) (Koltes 1993). The largest stoplight parrotfish reported from a peer-reviewed demographics study was from Bahamas (379 mm SL which converts to 437 mm FL) (Choat et al. 2003). Recent visual surveys of stoplight parrotfish in the U.S. Caribbean reported a maximum observed length of 420 mm FL (Grove et al. 2024).

Stoplight parrotfish age structure of females, sexually transitioning fish, and males indicated that most individuals start out as females since only females occurred in the age-0 group; the youngest transitioning fish and males aged in our study were in the age-1 group. In contrast to sex-specific age patterns observed for typical protogynous fishes, stoplight parrotfish females can attain older ages compared to males. The oldest male we documented in the current study was 16 years while several females we aged were older than that (the maximum age documented for a female in the current study was 20 years). This seems to indicate that not all stoplight parrotfish females transition to males. Paddack et al. (2009) also noted that female stoplight parrotfish from Florida samples attained older ages than males.

The current study is the first to report on age and growth for stoplight parrotfish that included a large sample size ($n = 1714$) collected from a wide range of depths (the maximum depth sampled was > 40 m). Two previous studies reported on growth parameter estimates for stoplight parrotfish utilizing length-at-age data derived from otolith-based age estimates. Choat et al. (2003) aged fish from four regions of the Caribbean, but only obtained samples via spearfishing in habitats at depths ≤ 15 m. Regional locations sampled included the Bahamas ($n = 108$), Venezuela ($n = 118$), Panama ($n = 82$), and Barbados ($n = 109$). Growth coefficients (K) and L_∞ were computed by region using fixed t_0 values of −0.05 and −0.06 (Choat et al. 2003); K ranged from 0.45 to 0.82 and L_∞ ranged from 264 mm SL (converted to 309 mm FL) to 357 mm SL (converted to 412 mm FL). A study from Florida Keys computed K and L_∞ (t_0 fixed at −0.06) using length-at-age results from 176 fish collected using spearfishing from depths < 15 m; $K = 0.84$ and $L_\infty = 269$ mm SL (converted to 315 mm FL) (Paddack et al. 2009). In the U.S. Caribbean, we obtained length-at-age data from a much larger number of samples compared to the other two studies; we sampled fish using a more diverse assortment of gears (castnet, traps, and spears); and we obtained stoplight parrotfish from habitats across a broader range of depths. In our study, when t_0 was fixed at −0.06, $K = 0.38$ and $L_\infty = 287$ mm SL (332 mm FL). Direct comparisons of VBGF parameter estimates among these studies are inappropriate due to the obvious differences in study designs/sample collections. However, the current study represents the most comprehensive assessment for growth parameter estimates for stoplight parrotfish from a specific region. Several studies have noted that growth in some parrotfish species is plastic and can vary within and among regions due to differences in environmental quality, fishing pressure, and other factors (Gust 2004; Paddack et al. 2009; Taylor and Choat 2014).

Stoplight parrotfish in the U.S. Caribbean spawned throughout the year. A similar observation of year-round spawning was reported for this species in Bonnaire (van Rooij et al. 1995a; van Rooij et al. 1996b). The reproductive output for stoplight parrotfish is high; females in Bonnaire were observed to release ~10,000 eggs during each daily spawning event (van Rooij et al. 1996b). Adult female stoplight parrotfish in Bonnaire spawned at least once daily, and some females were observed to spawn two or more times in a day (van Rooij et al. 1996b). Daily spawning combined with a year-round spawning season indicate that female stoplight parrotfish invest a large amount of energy in reproduction. This high energy investment in spawning output could mean less investment of energy towards somatic growth and lead to a decoupling of size and age. van Rooij et al. (1995b) investigated stoplight parrotfish growth plasticity among different life phases and social categories using mark-recapture and repeated stereographic measurements of free-swimming fish. That study found that growth was fastest in TP males living in groups compared to IP females and territorial TP males that spawned daily, year-round. The authors suggested that TP group males "traded growth against current reproduction and thereby enhance their chances to acquire the status of a territorial male with higher reproductive success" in the future (van Rooij et al. 1995b).

In the current study, stoplight parrotfish had a length at median sexual maturity of 153 mm FL and an age at median maturity of 1.6 years. The LM_{50} occurred at approximately 45% of L_∞ and at 35% of the maximum length recorded for the region. A study from Panama noted that female stoplight parrotfish were sexually mature at approximately 160 mm FL (converted from SL), but the study did not report a value for LM_{50} (Robertson and Warner 1978). Visual survey work from Bonnaire noted that the smallest IP fish observed to spawn occurred in the 150–160-mm FL size group (van Rooij et al. 1995a; van Rooij et al. 1996b). No other studies in the peer-reviewed literature reported on age at sexual maturity for stoplight parrotfish; however, it is not unusual for reef fishes to attain sexual maturity within the first few years of life (McBride and Johnson 2007; Collins and McBride 2015; DeMartini et al. 2018; DiMaggio 2023; Rivera Hernández and Shervette 2024b). Age at sexual maturity is considered a critical life history trait that impacts a population resiliency to fishing exploitation and species that sexually mature late in life are more susceptible to over exploitation (Jennings et al. 1999; Reynolds et al. 2005). Therefore, a relatively young age at sexual maturity in parrotfish species may correlate with potentially higher resiliency to fishing pressure, but additional factors to consider in evaluating this include vulnerability to capture, depth and habitat distribution, and overall regional abundance (Taylor and Choat 2014).

U.S. Caribbean stoplight parrotfish had a median size and age at sexual transition of 279 mm FL and 4.5 years. For some protogynous fish species, the size and age at sexual transition are plastic and mediated by a combination of social and environmental factors (Warner 1975; Shapiro 1981b; Nemtzov 1985; Munoz and Warner 2003; McBride and Johnson 2007). Molloy et al. (2011) examined variability of LT_{50} for stoplight parrotfish across multiple sites throughout the western Atlantic based on the assumption that all IP fish were female and all TP fish were male. LT_{50} ranged from 173 mm FL, at a site where maximum length observed for the species was 200 mm FL, to 305 mm FL at a site where a maximum length of 470 mm FL was recorded. The percentage of LT_{50} out of the maximum length recorded for a specific site ranged from 65 to 91% (Molloy et al. 2011). The LT_{50} for stoplight parrotfish in the U.S. Caribbean was 64% of the maximum length observed in the region. The variability in length at sexual transition reported from throughout the western Atlantic and the observation from the current study that not all females transition to males further illustrate that the timing of sex change in stoplight parrotfish is plastic.

Conclusions

Life history traits, including maximum size/age attained, length/age at sexual maturity and transition, and spawning strategy, can be useful predictors in evaluating the vulnerability of protogynous fish species to fishing pressure (Alonzo and Mangel 2005). Strong predictors of vulnerability to overexploitation of a fisheries species include as follows: short or limited spawning season and a strong reliance on formation of predictable spawning aggregations as the main mode of spawning (Johannes et al. 1999; Sadovy and Colin 2011); large size and late age at sexual maturity (Taylor and Choat 2014); fixed size/age or narrow size/age ranges at sexual transition (Alonzo and Mangel 2005); slow growth and high habitat specificity (Roberts and Hawkins 1999); and the removal of immature individuals through fisheries exploitation (Froese 2004). Overall, queen parrotfish and stoplight parrotfish in the U.S. Caribbean do not appear to exhibit any of these strong predictors of vulnerability to overexploitation. In the current study, both parrotfish species were characterized by near year-round or year-round spawning. Although both species were observed to pair spawn during summer spawning aggregations in Bermuda, in the Caribbean, queen parrotfish and stoplight parrotfish mainly reproduce through TP males maintaining permanent territories containing multiple females with which the male spawns and territorial males utilizing temporary territories to attract females for pair spawning at deeper reef sites (Clavijo 1983; van Rooij et al. 1996b). Both species in the U.S. Caribbean sexually mature at relatively small sizes within the first few years of life. Queen parrotfish females transition to males by a maximum size and age, but the size and age ranges in which transitioning fish occurred were broad (140–327 mm FL and 1–14 years). Stoplight parrotfish females did not all transition to males since the largest and oldest fish sampled were females. Also, the size and age ranges in which transitioning stoplight parrotfish individuals occurred were broad (183–366 mm FL and 2–15 years). Based on VBGF parameter estimates of K for U.S. Caribbean samples, both species exhibited moderately rapid growth. Queen parrotfish and stoplight parrotfish occurred across a wide range of habitat depths and are known to forage across a diversity of reef habitat types. Lastly, 0% of FD queen parrotfish and stoplight parrotfish samples processed for life history were sexually immature. The lack of immature fish sampled from the fisheries may relate to U.S. Caribbean management efforts currently in place that limit the minimum mesh size for traps (which ensures that smaller fish can escape from the traps), the ban on using gillnets to target parrotfish species, and the market driven targeting of "plate-size" fish by commercial spearfishers. In addition, the USVI 2001 moratorium on issuance of new commercial fishing licenses for reef-associated fisheries limits overall fishing activity in the region. The life history parameter estimates obtained through the current study can be used to conduct stock assessments for the region so that fisheries managers can better understand the current stock statuses and use the results to further guide management efforts for U.S. Caribbean queen parrotfish and stoplight parrotfish in ensuring the long-term sustainability of commercial fishing for these species.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics Fish samples obtained by authors of this study and reported on here were collected and handled in accordance within the guidelines of the U.S. Government Principles for the Utilization and Care of Vertebrate Animals Used in Testing, Research and Training (https://olaw.nih.gov/sites/default/files/PHSPolicyLabAnimals.pdf). This research was conducted under USCA IACUC protocol #053012-BIO-04.

Competing interests The authors declare no competing interests.

References

Alonzo SH, Mangel M (2005) Sex-change rules, stock dynamics, and the performance of spawning-per-recruit measures in protogynous stocks. Fish Bull 103:229–245

Beamish RJ, Fournier DA (1981) A method for comparing the precision of a set of age determinations. Can J Fish Aquat Sci 38(8):982–983. https://doi.org/10.1139/f81-132

Bruggemann JH, Kuyper MWM, Breeman AM (1994) Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). Mar Ecol Prog Ser 112(1/2):51–66. https://doi.org/10.3354/meps12600

Bruggemann JH, van Kessel AM, van Rooij JM, Breeman AM (1996) Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: implications of fish size, feeding mode and habitat use. Mar Ecol Prog Ser 134(1–3):59–71. https://doi.org/10.3354/meps134059

Causey B, Delaney J, Diaz E, Dodge RE, Garcia JR, Higgins J, Jaap W, Matos CA, Schmahl GP, Rogers C, Miller MW, Turgeon DD (2002) Status of coral reefs in the US Caribbean and Gulf of Mexico: Florida, Texas, Puerto Rico, US Virgin Islands and Navassa

CFMC (1985) Fisheries management plan, final environmental impact statement, and draft regulatory impact review for the shallow-water reeffish fishery of Puerto Rico and the U.S. Virgin Islands. Caribbean Fisheries Management Council and NOAA NMFS

CFMC (2019a) Comprehensive fishery management plan for the Puerto Rico exclusive economic zone. Caribbean Fisheries Management Council, San Juan, PR

CFMC (2019b) Comprehensive fishery management plan for the St. Croix exclusive economic zone Caribbean Fisheries Management Counci, San Juan, PR

CFMC (2019c) Comprehensive fishery management plan for the St. Thomas/St. John exclusive economic zone. Caribbean Fisheries Management Council, San Juan, PR

Choat J, Axe L, Lou D (1996) Growth and longevity in fishes of the family Scaridae. Mar Ecol Prog Ser 145:33–41. https://doi.org/10.3354/meps145033

Choat JH, Robertson Ackerman JL, Posada JM (2003) An age-based demographic analysis of the Caribbean stoplight parrotfish *Sparisoma viride*. Mar Ecol Prog Ser 246:265–277. https://doi.org/10.3354/meps246265

Clavijo IE (1983) Pair spawning and formation of a lek-like mating system in the parrotfish *Scarus vetula*. Copeia 1983(1):253–256. https://doi.org/10.2307/1444725

Collins A, McBride R (2015) Variations in reproductive potential between nearshore and offshore spawning contingents of hogfish in the eastern Gulf of Mexico. Fish Manage Ecol 22(2):113–124. https://doi.org/10.1111/fme.12102

Collins AB, McBride RS (2011) Demographics by depth: spatially explicit life-history dynamics of a protogynous reef fish. Fish Bull 109(2):232–243

Comeros-Raynal MT et al (2012) The likelihood of extinction of iconic and dominant herbivores and detritivores of coral reefs: the parrotfishes and surgeonfishes. Plos One 7(7):e39825. https://doi.org/10.1371/journal.pone.0039825

DeMartini E, Howard K (2016) Comparisons of body sizes at sexual maturity and at sex change in the parrotfishes of Hawaii: input needed for management regulations and stock assessments. J Fish Biol 88(2):523–541. https://doi.org/10.1111/jfb.12831

DeMartini EE, Andrews AH, Howard KG, Taylor BM, Lou D-C, Donovan MK (2018) Comparative growth, age at maturity and sex change, and longevity of Hawaiian parrotfishes, with bomb radiocarbon validation. Can J Fish Aquat Sci 75(4):580–589. https://doi.org/10.1139/cjfas-2016-0523

DiMaggio L (2023) Documenting age, growth, and reproductive biology for a data deficient fisheries species, lane snapper *Lutjanus synagris* in the U.S. Caribbean. University of Charleston, Charleston, SC

Dromard CR, Bouchon-Navaro Y, Harmelin-Vivien M, Bouchon C (2015) Diversity of trophic niches among herbivorous fishes on a Caribbean reef (Guadeloupe, Lesser Antilles), evidenced by stable isotope and gut content analyses. J Sea Res 95:124–131. https://doi.org/10.1016/j.seares.2014.07.014

Figuerola M, Matos-Caraballo D, Torres W (1998) Maturation and reproductive seasonality of four reef fish species in Puerto Rico. Proc Gulf Caribb Fish Inst 50:938–968

Francini RB, Ferreira CM, Coni EO, De Moura RL, Kaufman L (2010) Foraging activity of roving herbivorous reef fish (Acanthuridae and Scaridae) in eastern Brazil: influence of resource availability and interference competition. J Mar Biol Assoc UK 90(3):481–492. https://doi.org/10.1017/S0025315409991147

Freitas MO, Previero M, Leite JR, Francini-Filho RB, Minte-Vera CV, Moura RL (2019) Age, growth, reproduction and management of Southwestern Atlantic's largest and endangered herbivorous reef fish, *Scarus trispinosus* Valenciennes, 1840. PeerJ 7:e7459. https://doi.org/10.7717/peerj.7459

Froese R (2004) Keep it simple: three indicators to deal with overfishing. Fish Fish 5(1):86–91. https://doi.org/10.1111/j.1467-2979.2004.00144.x

Grove LJ, Blondeau J, Ault JS (2024) Fishery-independent reef fish visual survey population density and length composition for stoplight parrotfish in the St. Croix. SEDAR84-WP-14. SEDAR, North Charleston, SC

Gust N (2004) Variation in the population biology of protogynous coral reef fishes over tens of kilometres. Can J Fish Aquat Sci 61(2):205–218. https://doi.org/10.1139/f03-160

Jackson J, Donovan M, Cramer K, Debrot A (2014) Part I: overview and synthesis for the wider Caribbean region status and trends of Caribbean coral reefs: 1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland

Jennings S, Reynolds JD, Polunin NV (1999) Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. Conserv Biol 13(6):1466–1475. https://doi.org/10.1046/j.1523-1739.1999.98324.x

Johannes R, Squire L, Graham T, Sadovy Y, Renguul H (1999) Spawning aggregations of groupers (Serranidae) in Palau. Marine Conservation Research Series Publ#1. Nat Conserv Res 1:1–144

Jones DD (2020) Addressing life history information gaps in a data-deficient Caribbean reef fish, the princess parrotfish *Scarus taeniopterus*. MS thesis, College of Charleston, Charleston, SC

Jones DD, Rivera Hernández JM, Shervette VR (2021) Princess parrotfish *Scarus taeniopterus* age, growth, maturity, and transition. Environ Biol Fish 104(5):581–595. https://doi.org/10.1007/s10641-021-01097-5

Kadison E, Brandt M, Nemeth R, Martens J, Blondeau J, Smith T (2017) Abundance of commercially important reef fish indicates different levels of over-exploitation across shelves of the U.S. Virgin Islands. Plos One 12(7):e0180063. https://doi.org/10.1371/journal.pone.0180063

Koltes KH (1993) Aspects of the reproductive biology and social structure of the stoplight parrotfish *Sparisoma viride*, at Grand Turk, Turks and Caicos Islands, BWI. B Mar Sci 52(2):792–805

Luckhurst BE (2011) Observations at a multispecies parrotfish (Scaridae) spawning aggregation site at Bermuda with notes on the predation behavior of black grouper (*Mycteroperca bonaci*). Gulf and Caribbean Research 23(1):55–60. https://doi.org/10.18785/gcr.2301.06

Manning JC, McCoy SJ (2023) Preferential consumption of benthic cyanobacterial mats by Caribbean parrotfishes. Coral Reefs 42(5):967–975. https://doi.org/10.1007/s00338-023-02404-5

Matos-Caraballo D (2018) Puerto Rico/NMFS Cooperative Fisheries Statistics Program April 2012 – March 2018 NA07NMF4340039. DRNA Fisheries Research Laboratory, San Juan, PR

McAfee ST, Morgan SG (1996) Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. Mar Biol 125(3):427–437. https://doi.org/10.1007/BF00353255

McBride R, Johnson M (2007) Sexual development and reproductive seasonality of hogfish (Labridae: *Lachnolaimus maximus*), an hermaphroditic reef fish. J Fish Biol 71(5):1270–1292. https://doi.org/10.1111/j.1095-8649.2007.01580.x

Molloy PP, Paddack MJ, Reynolds JD, Gage MJ, Côté IM (2011) Relative size-at-sex-change in parrotfishes across the Caribbean: is there variance in a supposed life-history invariant? Evol Ecol 25:429–446. https://doi.org/10.1007/s10682-010-9404-3

Mumby PJ (2006) The impact of exploiting grazers (scaridae) on the dynamics of Caribbean coral reefs. Ecol Appl 16(2):747–769. https://doi.org/10.1890/1051-0761(2006)016[0747:TIOEGS]2.0.CO;2

Munoz RC, Warner RR (2003) A new version of the size-advantage hypothesis for sex change: incorporating sperm competition and size-fecundity skew. Am Nat 161(5):749–761. https://doi.org/10.1086/374345

Nemeth RS, Quandt A (2005) Differences in fish assemblage structure following the establishment of the Marine Conservation District, St. Thomas, US Virgin Islands. Proc Gulf Caribb Fish Inst 56:367–381

Nemtzov SC (1985) Social control of sex change in the Red Sea razorfish *Xyrichtys pentadactylus* (Teleostei, Labridae). Environ Biol Fish 14:199–211. https://doi.org/10.1007/BF00000827

NOAA (2009) Coral reef habitat assessment for U.S. Marine Protected Areas: Commonwealth of Puerto Rico. NOAA NOS Management and Budget Office

Olge DH (2016) Introductory fisheries analyses with R. Chapman and Hall/CRC, New York

Paddack MJ, Sponaugle S, Cowen RK (2009) Small-scale demographic variation in the stoplight parrotfish *Sparisoma viride*. J Fish Biol 75(10):2509–2526. https://doi.org/10.1111/j.1095-8649.2009.02451.x

Reynolds JD, Dulvy NK, Goodwin NB, Hutchings JA (2005) Biology of extinction risk in marine fishes. Proc R Soc Lond Ser B, Biol Sci 272(1579):2337–2344. https://doi.org/10.1098/rspb.2005.3281

Rivera Hernández JM, Peña Alvarado N, Correa Vélez K, Nemeth R, Appeldoorn R, Shervette V (2019) Queen triggerfish reproductive biology in US Caribbean waters. Trans Am 148(1):134–147. https://doi.org/10.1002/tafs.10124

Rivera Hernández JM, Shervette VR (2024a) Puzzling parrotfishes: radiocarbon age validation and updated longevity estimates for western Atlantic species in support of sustainable fisheries management. Plos One 19(5):e0302854. https://doi.org/10.1371/journal.pone.0302854

Rivera Hernández JM, Shervette VR (2024b) Queen triggerfish *Balistes vetula* age-based population demographics and reproductive biology for waters of the North Caribbean. Fishes 9(5):162. https://doi.org/10.3390/fishes9050162

Rivera Hernández JM, Shervette VR (2024c) Radiocarbon age validation for Caribbean parrotfishes. SEDAR84-WP-01. SEDAR, North Charleston, SC

Rivera Hernández JM, Shervette VR (2024d) Report on the status of U.S. Caribbean stoplight parrotfish *Sparisoma viride* age, growth, and reproductive biology for the SEDAR84 Stock Assessment SEDAR84-AP-01 SEDAR, North Charleston, SC

Roberts CM, Hawkins JP (1999) Extinction risk in the sea. Trends Ecol Evol 14(6):241–246. https://doi.org/10.1016/S0169-5347(98)01584-5

Robertson DR, Ackerman J, Choat JH, Posada JM, Pitt J (2005) Ocean surgeonfish *Acanthurus bahianus*. I. The geography of demography. Mar Ecol Prog Ser 295:229–244. https://doi.org/10.3354/meps295229

Robertson DR, Van Tassell J (2019) Fishes: Greater Caribbean Online information system. In: Smithsonian Tropical Research Institute, Balboa, Panama. https://biogeodb.stri.si.edu/caribbean/en/pages

Robertson DR, Warner RR (1978) Sexual patterns in the labroid fishes of the Western Caribbean, II, the parrotfishes (Scaridae). Smithsonian Contributions to Zoology No. 255. https://doi.org/10.5479/si.00810282.255

Sadovy Y, Colin PL (2011) Reef fish spawning aggregations: biology, research and management, vol 35. Springer, Netherlands

Sadovy Y, Shapiro DY (1987) Criteria for the diagnosis of hermaphroditism in fishes. Copeia 1:136–156. https://doi.org/10.2307/1446046

SEDAR (2016) SEDAR 46 Stock Assessment Report Caribbean Data-Limited Species. North Charleston, SC

Shapiro DY (1981a) Behavioural changes of protogynous sex reversal in a coral reef fish in the laboratory. Anim Behav 29(4):1185–1198. https://doi.org/10.1016/S0003-3472(81)80070-X

Shapiro DY (1981b) Size, maturation and the social control of sex reversal in the coral reef fish *Anthais squamipinnis*. J Zool 193(1):105–128. https://doi.org/10.1111/j.1469-7998.1981.tb01494.x

Shervette VR, Rivera Hernández JM (2022) Illuminating otoliths: new insights for life history of Balistes triggerfishes. J Fish Biology 101(6):1557–1568. https://doi.org/10.1111/jfb.15233

Shervette VR, Rivera Hernández JM, Drake D, Peña-Alvarado N, Santiago Soler W, Magras J (2020) Caribbean Hogfish: documenting critical life history information for a data-poor species in collaboration with U.S. Caribbean fishers. NOAA CRP Final Report. Aiken, SC

Shervette VR, Rivera Hernandez JM, Nunoo FKE (2021) Age and growth of grey triggerfish *Balistes capriscus* from trans-Atlantic populations. J Fish Biol 98(4):1120–1136. https://doi.org/10.1111/jfb.14644

Stevens MH, Smith SG, Ault JS (2019) Life history demographic parameter synthesis for exploited Florida and Caribbean coral reef fishes. Fish Fish 20(6):1196–1217. https://doi.org/10.1111/faf.12405

Taylor B, Choat J (2014) Comparative demography of commercially important parrotfish species from Micronesia. J Fish Biol 84(2):383–402. https://doi.org/10.1111/jfb.12294

Taylor BM et al (2019) Demographic plasticity facilitates ecological and economic resilience in a commercially important reef fish. J Anim Ecol 88(12):1888–1900. https://doi.org/10.1111/1365-2656.13095

van Rooij JM, Bruggemann JH, Videler JJ, Breeman AM (1995a) Ontogenic, social, spatial and seasonal variations in condition of the reef herbivore *Sparisoma viride*. Mar Biol 123(2):269–275. https://doi.org/10.1007/BF00353618

van Rooij JM, Bruggemann JH, Videler JJ, Breeman AM (1995b) Plastic growth of the herbivorous reef fish *Sparisoma viride*: field evidence for a trade-off between growth and reproduction. Mar Ecol Prog Ser 122(1–3):93–105. https://doi.org/10.3354/meps122093

van Rooij JM, Kok JP, Videler JJ (1996a) Local variability in population structure and density of the protogynous reef herbivore *Sparisoma viride*. Environ Biol Fish 47(1):65–80. https://doi.org/10.1007/BF00002380

van Rooij JM, Kroon FJ, Videler JJ (1996b) The social and mating system of the herbivorous reef fish *Sparisoma viride*: one-male versus multi-male groups. Environ Biol Fish 47(4):353–378. https://doi.org/10.1007/BF00005050

van Rooij JM, Videler JJ (1997) Mortality estimates from repeated visual censuses of a parrotfish (*Sparisoma viride*) population: demographic implications. Mar Biol 128(3):385–396. https://doi.org/10.1007/BF00005050

Warner RR (1975) The reproductive biology of the protogynous hermaphrodite *Pimelometopon pulchrum* (Pices: Labridae). Fish Bull 73(2):262

Zajovits SN (2021) Caribbean yellowtail snapper *Ocyurus chrysurus*: filling in critical gaps in life history and novel ageing validation utilizing Δ14C. MS thesis, University of South Carolina, Columbia, SC