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Abstract Princess parrotfish *Scarus taeniopterus* is one of the top three parrotfish species landed in the Caribbean, and the top *Scarus* species targeted in commercial fishing efforts; however, a paucity of information exists concerning basic life history information for Caribbean parrotfish species. Prior to this work, no comprehensive life history information existed in the literature for princess parrotfish. This study provides the first comprehensive documentation of age, growth, size/age at sexual maturity, and size/age at transition for a Caribbean *Scarus* species. Sampling of 759 fish occurred in Puerto Rico and the US Virgin Islands from October 2015 to February 2020. Females ranged from 50 to 250 mm total length (TL) and 0 to 7 years of age, males ranged from 159 to 314 mm TL and 2 to 11 years, and transitional fish ranged from 140 to 292 mm TL and 2 to 6 years. Previously unknown von Bertalanffy parameters (L_∞ = 301 and $k = 0.316$) and length at median sexual maturity ($LM_{50} = 119$ mm TL), age at median sexual maturity ($AM_{50} = 1.5$ years), length at median sexual transition ($LS_{50} = 223$ mm TL), and age at median sexual transition ($AS_{50} = 4.2$ years) will enable stock assessments and informed management for this Caribbean parrotfish.

Keywords Caribbean · Scarinae · Labridae · Life history

Introduction

Parrotfishes provide many important ecological functions within coral reef ecosystems (Bruggemann et al. 1996; Bonaldo et al. 2006; Adam et al. 2015; Clements et al. 2017; Campbell et al. 2018) in addition to comprising a large portion of reef fish fisheries for locals in the Caribbean. As a dominant group of reef fishes in terms of biomass and abundance, scientists and conservationists have emphasized the importance of parrotfishes in maintaining healthy and resilient coral reefs due to their top-down role in the control of macroalgae and removal of dead coral skeletal material (Bruggemann et al. 1996; McAfee and Morgan 1996; Mumby 2006; Francini et al. 2010; Dromard et al. 2015). In the Caribbean, this support of "parrotfish" has morphed into broad campaigns such as "Pass on Parrotfish" meant to discourage consumption of parrotfish species and promoting a ban on all fishing of "parrotfish" (https://www.nature.org/en-us/about-us/where-we-work/caribbean/stories-in-caribbean/pass-on-parrotfish/). However, the overly broad application of campaigns like this, no matter how well-intentioned, can result in negative consequences.

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Campaigns and fisheries management programs that lump multiple species into a single group are erroneously treating a diversity of species with different life history attributes and differing levels of resiliency to potential fishing pressure as if they are a single species (DeMartini and Howard 2016; DeMartini et al. 2018). This multispecies group in the Caribbean encompasses seven species of parrotfishes that are currently targeted in fishing efforts (CFMC 1985; Causey et al. 2002; Matos-Caraballo et al. 2005; NOAA 2009; Jackson et al. 2014; SEDAR 2016) and three additional parrotfish species that are already widely recognized as imperiled and protected within many Caribbean jurisdictions through fishing prohibitions (Bozec et al. 2016). The main process to regulate fisheries is through formal stock assessments, which use standard processes to evaluate the current status of region-specific stocks of a species, and then based on the scientifically robust stock assessment results, management strategies are implemented and enforced (Ricker 1975; Gulland 1987; Pauly and Morgan 1987; Huynh et al. 2020). For management efforts to succeed, the majority of fishers must buy into the results and recognize the need for the regulatory actions in promoting the long-term sustainability of fisheries.

Parrotfish species across the Caribbean are referred to as data-deficient/data-poor species because of a lack of knowledge concerning the key life history parameters needed to assess parrotfish species stocks. The seven parrotfish species currently targeted in the Caribbean are as follows: princess parrotfish *Scarus taeniopterus*, queen parrotfish *Sc. vetula*, striped parrotfish *Sc. iseri*, stoplight parrotfish *Sparisoma viride*, redtail parrotfish *Sp. chrysopterum*, redband parrotfish *Sp. aurofrenatum*, and yellowtail parrotfish *Sp. rubripinne* (CFMC 1985; Jackson et al. 2014; SEDAR 2016). Differences among species and regions exist in the maximum reported sizes, reproductive strategies, growth rates, and ecological roles within coral reef ecosystems and to date, only stoplight parrotfish has been investigated in a few locations concerning age and growth (Van Rooij et al. 1995; van Rooij and Videler 1997; Choat et al. 2003). The need for population-specific information on age, growth, and reproduction for all of the fisheries-targeted Caribbean parrotfish species cannot be overstated (Paddack et al. 2009; SEDAR 2016).

A few scientific studies in the Caribbean have reported limited direct evidence that demonstrates impacts of fishing pressure on some Caribbean parrotfish species (Choat et al. 2003; Hawkins and Roberts 2004) and those studies did not evaluate all species across all Caribbean management regimes, but rather were limited spatially and temporally. Each Caribbean nation/territory/jurisdiction differs in its management of reef fish fisheries and the health of a jurisdiction's parrotfish species populations cannot be determined based on the findings in another jurisdiction. For fisheries management efforts to succeed, local fishers must be supportive, and a majority of fishers must be willing to comply with regulations. Campaigns and fisheries regulations that are not based on scientific evidence will not be followed by local fishers (Glenn et al. 2012; Pita et al. 2012). An additional consequence of such efforts is that fishers are less inclined to trust anyone they associate with fisheries management, including scientists that depend on the collaboration of local fishers to obtain the scientific data necessary for stock assessments (Glenn et al. 2012). Additionally, researchers working on obtaining and publishing their research on the life history parameters needed to conduct stock assessments may encounter biased reviewers and editors who have placed more emphasis on preconceived assumptions instead of rigorous scientific inquiry (Hilborn 2006) relating to parrotfishes, which further impedes filling in the critical data-gaps so that proper assessments can be done and management strategies implemented.

Princess parrotfish is one of the most common parrotfish species across the Caribbean (Kramer 2003). In the US Caribbean, it occurs as juveniles and adults in association with reef flats in shallow areas up to the deeper reef slope (Tzadik and Appeldoorn 2013). Princess parrotfish is one of the top three parrotfish species landed in the US Caribbean, and the top *Scarus* species targeted in commercial fishing efforts (Kojis and Quinn 2004; Matos-Caraballo 2004; Kojis and Quinn 2006; Matos-Caraballo 2012, 2018). It is a fully dichromatic species and a protogynous hermaphrodite (Reinboth 1970). Most terminal color phase males establish a permanent territory that contains a harem of several females (Dubin 1981; Dubin and Baker 1982). Non-haremic groups of initial phase individuals wander through territories and groups of terminal and initial phase fish have been observed as part of large feeding groups (Dubin 1981). Spawning typically occurs in pairs during early morning hours and is often preceded by courting behaviors that last for around 20 min (Dubin 1981). Initial phase males may engage in alternative mating strategies (Robertson and Warner 1978). Much research has reported on diet, feeding behavior, and trophic ecology of princess parrotfish (Paddack et al. 2006; Cardoso et al. 2009; Burkepile and Hay 2011; Adam et al. 2015; Dromard et al. 2015; Adam et al. 2018). However, a dearth of understanding exists concerning basic life history information for this species. No investigations in the current literature have reported on population age structure, growth parameters, size/age at sexual maturity, and size/age at sexual transition despite the importance of princess parrotfish to Caribbean fisheries and its ecological role within coral reef ecosystems. A greater emphasis on exploring the age, growth, and maturity of data-deficient Caribbean fishes is critical for proper management (SEDAR 2011, 2016). Effective fisheries management requires a detailed understanding of the life history strategies of managed species (Chale-Matsau et al. 2001; King and McFarlane 2003). The overall goal of the current study was to fill in these critical data-gaps for princess parrotfish *Scarus taeniopterus*. The specific objectives were as follows: (1) to document the size and weight relationship, allowing convenient comparisons among measurement types; (2) to document size and age structure for princess parrotfish from US Caribbean waters; (3) to determine the growth rate for this species; and (4) to document the size and age at maturity and sexual transition.

Materials and methods

Study areas

The US Caribbean is located in the western part of the Caribbean archipelago and includes Puerto Rico (PR) and the US Virgin Islands (USVI; Fig. 1). Coral reef ecosystems cover approximately 3370 km^2 within three nautical miles of Puerto Rico and ~ 344 km^2 in the US Virgin Islands (Causey et al. 2002; Rohmann et al. 2005). Puerto Rico has a coastline of 1384 km and is bordered in the north, west, and south by deep ocean waters. The north coast of PR is characterized by a relatively narrow shelf (<1–3-km wide) and the coral reefs are dominated by macroalgae with low abundances of scleractinian corals. The exception to this is in the northeastern corner which contains a wider shelf (~5 km) with substantial scleractinian coral populations. The shelf platform of eastern PR extends to encompass the major islands of Culebra and Vieques and the waters are dominated by expansive fringing reef systems. The shelf off southern and western Puerto Rico ranges up to 26-km wide and supports extensive coral reef ecosystems. Across all Puerto Rican waters, four parrotfish species are commonly landed as part of the reef fish fisheries (in descending order percent contribution): stoplight parrotfish, redtail parrotfish, princess parrotfish, and queen parrotfish (Matos-Caraballo 2004; Matos-Caraballo 2018). The average annual

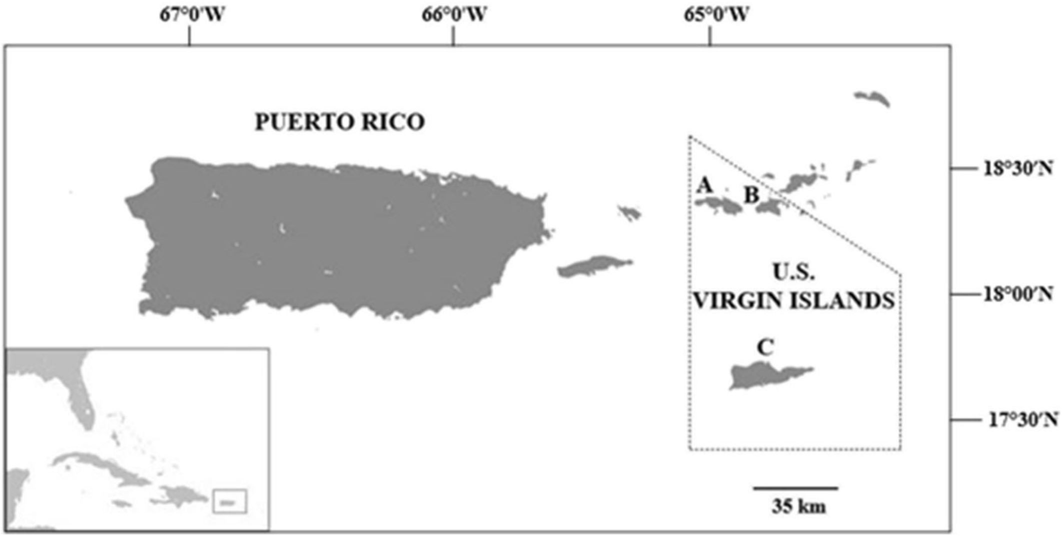


Fig. 1 Map of the US Caribbean, the study area for the current study. The US Caribbean consists of the Commonwealth of Puerto Rico and the US Virgin Islands (within the dotted box). The US Virgin Islands includes (A) St. Thomas, (B) St. John, and (C) St. Croix

landings of parrotfishes in PR for 2007–2011 were 25,809 lb. (Matos-Caraballo 2012). In PR, parrotfish species are fished with a variety of gears, including traps, spears, and nets.

USVI is divided into two management platforms: St. Thomas (STT) and St. John (STJ) in the north and St. Croix (STX) in the south. STT/STJ are situated on a relatively large insular shelf platform that contains a fishable area of 147 km^2 at depths less than 25 m and 1303 km^2 at depths of 25–65 m (Kadison et al. 2017). STT/STJ commercial fishers that obtain parrotfish species mainly employ fish and lobster traps at depths greater than 20 m, fishing further from shore, along the expansive shelf waters containing a diversity of coral reef habitat (Kojis and Quinn 2004, 2006). The two main parrotfish species caught in the trap fishery are stoplight and redtail. On rare occasions, queen parrotfish, princess parrotfish, yellowtail parrotfish, and redband parrotfish are also landed. For the years of 1998–2008, annual parrotfish landings ranged from 20,000 to 58,000 lb. STX, located 60 km south, is separated from STT/STJ by the deep waters of Anegada Pass and resides on a much narrower shelf platform that contains 261 km^2 of fishable waters at depths less than 25 m and only 36 km^2 at depths greater than 25 m (Kadison et al. 2017). STX commercial fishers mainly utilize spearfishing to target parrotfish species and four species dominate the catch: stoplight, redtail, redband, and princess (Kojis and Quinn 2006; Kojis et al. 2017). Yellowtail parrotfish and queen parrotfish are also caught on occasion and striped parrotfish is rarely caught. Annual landings of parrotfish ranged from 200,000 to 430,000 lb. for 1998–2008.

Collection and initial processing

Princess parrotfish samples were collected from the waters of Puerto Rico and two of the main islands in USVI (STX and STT; Fig. 1). Sampling of princess parrotfish occurred from October 2015 through February 2020. Fish samples were obtained from a combination of fishery-dependent and fishery-independent collections with a variety of gear types (in descending order of number of fish collected: spear, trammel-net, traps; Table 1). All fish were kept on ice until processing. Initial processing included weighing each fish (± 1 g) and measuring (± 1 mm) for standard length (SL), fork length (FL), and total length (TL). The complete gonads were removed, weighed (± 0.01 g), and fixed in 11% formalin-buffered seawater or PAGA (Polyethylene glycol, acetic Acid, Glycerol, and ethyl Alcohol) for histological evaluation (Zanini et al. 2012). The sagittal otoliths were removed by cutting through the dorsal portion of the head, removed, cleaned, dried, and placed in plastic vials for later age determination.

Age, growth, and transition

One sagittal otolith from each fish sample was embedded in a resin epoxy and allowed to harden for at least 24 h, then sectioned transversely through the nucleus to a thickness of ~0.3 mm using a low-speed saw equipped with a diamond blade (GSMFC 2003). At least 2 sections were obtained for each otolith and mounted on glass slides using a clear mounting medium. Ages for all otoliths were determined based on the number of increments counted using a stereoscope with transmitted light at a magnification of ×20–40. Each of the increments consisted of a set of one translucent band and one opaque band and was counted from the core to the margin along the sulcus. A second reader evaluated a random subset of 50% of the otoliths. In cases of disagreement, the two readers evaluated the otolith sections together and reached a consensus increment count.

Table 1 Sampling summary of princess parrotfish across the islands of Puerto Rico (PR), St. Thomas (STT), and St. Croix (STX)

	Puerto Rico	St. Thomas	St. Croix	All islands
Total fish sampled	54	32	673	759
Fishery-independent	28	32	303	363
Initial phase	23	27	264	314
Female	17	22	159	198
Transitional	6	2	84	92
Male	-	2	21	23
Unknown	-	1	-	1
Terminal phase (all-male)	5	5	39	200
Fishery-dependent	26	-	370	396
Initial phase	2	-	44	46
Female	2	-	30	32
Transitional	-	-	12	12
Male	-	-	2	2
Unknown	-	-	-	0
Terminal phase (all-male)	24	-	326	350

Increment counts were assessed without knowledge of fish size or time of year that the sample was collected. For each otolith, readers noted if the last opaque zone occurred on the otolith section edge or if a translucent zone had begun forming after the opaque zone in order to evaluate if opaque zones were deposited annually. For this analysis, the proportion of otoliths with opaque zones on the edge was plotted by month. The lack of multimodal distribution (i.e., lack of multiple peaks in a single calendar year) was seen as confirmation of annual increment deposition (Smylie et al. 2016; Kelly-Stormer et al. 2017).

Accurate, long-term, species-specific harvest data are limited for Caribbean fisheries (Appeldoorn et al. 1992; SEDAR 2009). To ensure optimal use of the limited data that are presented, it is beneficial to convert from one type of measurement to another (such as from standard length to total length). In the field or at port sampling, logistical concerns may allow only one type of size measure to be taken. The ability to calculate one length from another could facilitate the comparison of field data to published literature. Conversions also encourage the sharing of data among managers and researchers who previously used different measure types. Regression equations can be used for the conversions, but they must be based on large sample sizes and show high R^2 in order to yield accurate results. Length-weight relationships and comparisons among standard, fork, and total lengths were investigated with regression equations. Length relationships were determined through linear regressions. The length-weight regression had the form of

$$W = a\mathrm{TL}^b$$

where W was total body weight in grams, TL was total length in mm, and "a" and "b" were the intercept and slope parameters, respectively.

The size-at-age data obtained from the otolith analyses were used to generate an overall growth curve for princess parrotfish samples. Lifetime growth parameters were estimated by fitting size-at-age data to the von Bertalanffy growth function 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 mean asymptotic length (TL mm), K is the growth coefficient, and t_0 is the age at which fish have a theoretical length of zero. Growth parameters were estimated for size-at-age data combined across the three islands and not separately for each island due to the differences mentioned above in the primary gear used by fishers among islands. Additionally, combining samples caught by multiple gear types is an acceptable way to reduce gear biases of population estimates (Wilson et al. 2015; Allman et al. 2018; Shervette et al. 2021).

Size and age at median sexual maturity and at median sexual transition were calculated with logistic regression. Maturity (mature/not mature) and sex (male/not male) were treated as binomial response variables. No transitional fish were included in the logistic regression for sexual transition. Logistic regressions were conducted using the *logit* function transformation and the generalized linear model procedure in R (Ogle 2013).

Sex and maturity determination

Gonads initially fixed in PAGA solution were transferred to 11% formalin seawater-buffered solution upon return to the lab. All gonads remained in formalin for a minimum of 7 days then were transferred to 70% isopropyl alcohol. Standard histological procedures for gonad preparation were followed (Kelly-Stormer et al. 2017; Rivera Hernández et al. 2019). Gonads were dehydrated and vacuum-infiltrated with paraffin wax in an overnight tissue processor then embedded in paraffin blocks. At least three transverse sections (7-μm thick) of the medial or posterior segments of each gonad were cut using a rotary microtome, then sections were affixed to glass slides, stained, and counter-stained with Gill hematoxylin and eosin-y then cover-slipped.

Gonad slides were microscopically evaluated by two independent readers at ×40–400 magnification. Readers conducted their evaluations without knowledge of the specimens' dates of capture, lengths, or ages to prevent bias. In cases of disagreement, the readers interpreted the slides together to reach consensus. Sex was determined by the presence of oogenesis or spermatogenesis in the tissue (Sadovy and Shapiro 1987; Brown-Peterson et al. 2011). Tissues that showed only oogenesis or predominant oogenesis with concomitant spermatogenic activity were considered female, and tissues that showed only spermatogenesis or predominant spermatogenesis with some residual atretic oocytes were considered male. Transitioning individuals were narrowly defined by tissues containing pre-vitellogenic or atretic vitellogenic oocytes with intrusion of spermatogenic tissue (McBride and Johnson 2007). Maturity in females was determined by the appearance of cortical alveolar and/or vitellogenic oocytes, which signify the start of the "developing" phase (Brown-Peterson et al. 2011). We did not observe the existence of primary males in our samples so no immature males were observed.

Differences in size and age compositions between females, transitioning, and males were determined though separate pairwise Kolmogorov-Smirnov (K-S) tests, with the basic null hypothesis that age or size did not vary with sex. Bonferroni corrections were applied to adjust the *p*-values of pairwise comparisons. Any *p*-value <0.05 was considered significant.

Results

From October 2015 to February 2020, a total of 759 princess parrotfish were collected from the US Caribbean study area (Table 1, Fig. 1). Fifty-four fish samples were collected from Puerto Rico, 32 from St. Thomas, and 673 from St. Croix. Across all islands, 360 fish were in the initial color phase and 399 were in the terminal color phase. Of the 758 fish that were successfully evaluated for gonad histology, 230 were female, 424 were male, and 104 were transitioning (Table 1). Of the 759 fish processed for this study, 52% were fisheries-dependent (FD) samples (Table 1).

Linear regression analyses indicated that standard length (SL), fork length (FL), and total length (TL) were significantly correlated with each other. The R^2 values for these regressions were from 0.97 for FL–SL ($n = 362$), 0.98 for FL–TL ($n = 410$), and 0.99 for SL–TL; ($n = 667$; Table 2). Length was also significantly correlated with weight ($R^2 = 0.98$; $n = 751$; Table 2 and Fig. 2).

Total length across all islands ranged from 50 to 314 mm with a mean of 233 mm ± 36.9 SD (Table 3). Initial phase fish ranged in size from 50 to 292 mm TL with a mean of 208 mm ± 35.2 SD, and terminal phase fish had a size range of 197–314 mm with a mean of 255 mm ± 21.2 SD. Total lengths ranged from 50 to 250 mm in females with a mean of 199 mm ± 36.3 SD; from 159 to 314 mm in males with a mean of 253 mm ± 22.0 SD; and from 140 to 292 mm in transitional fish with a mean of 223 mm ± 27.4 SD (Table 3 and Fig. 3). Separate pairwise Kolmogorov-Smirnov tests with Bonferroni-corrected *p*-values confirmed that distributions of total lengths were significantly different between males and females ($D = 0.73426$, $p < 0.001$), females and transitioning fish ($D = 0.36606$, $p < 0.001$), and males and transitioning fish ($D = 0.56297$, $p < 0.001$).

Table 2 Regression equations for length-weight relationships and for standard, fork, and total lengths in princess parrotfish. The length-weight equation is the form $W = a\mathrm{TL}^b$. *W* weight in grams, *TL* total length in mm, *FL* fork length in mm, *SL* standard length in mm, *S.E.* standard error. $p < 0.001$ for all regressions

Category	Regression equation	Adjusted R^2
Female	$W=(2.57\times10^{-5})\mathrm{TL}^{2.94}$	0.99
Male	$W=(4.57\times10^{-5})\mathrm{TL}^{2.84}$	0.92
Transitional	$W=(5.62\times10^{-6})\mathrm{TL}^{3.24}$	0.97
Initial phase	$W=(1.70\times10^{-5})\mathrm{TL}^{3.02}$	0.98
Terminal phase	$W=(5.37\times10^{-5})\mathrm{TL}^{2.82}$	0.91
All	$W=(1.98\times10^{-5})\mathrm{TL}^{3.00}$	0.98
	FL=0.96TL+5.70	0.98
	SL=0.81TL+1.20	0.99
	FL=1.16SL+9.68	0.97

Of the 759 total princess parrotfish collected, 754 were aged by counting increments on sectioned otoliths. Results from the marginal increment analysis indicated that opaque zones formed in the late fall and early winter months (October–January) and that increment deposition was annual (Fig. 4). Ages for fish across all islands ranged from 0 to 11 years with a mean of 5 years ±1.0 SD (Table 3). Initial phase fish showed an age range from 0 to 7 years with a mean of 4 years ±1.0 SD, and

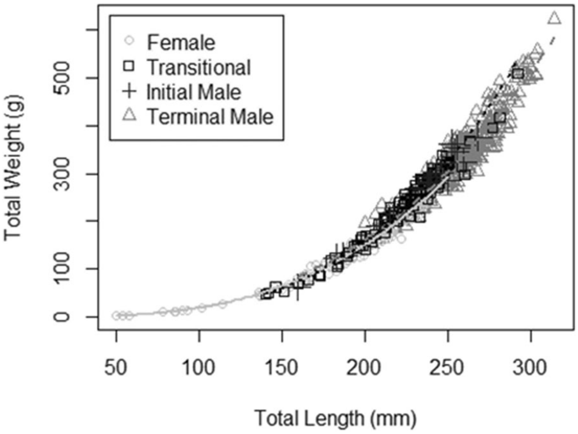


Fig. 2 Length-weight relationship in princess parrotfish with data points representing female, initial male, terminal male, and transitioning individuals. The lines represent the fitted length-weight relationship for female (solid), initial and terminal males together (dashed), and transitioning (dotted) fish

terminal phase fish showed an age range from 3 to 11 years with a mean of 6 years ±1.4 SD. Ages ranged from 0 to 7 years in females with a mean of 4 years ±1.0 SD; from 2 to 11 years in males with a mean of 6 years ±1.4 SD; and from 2 to 6 years in transitional fish with a mean of 4 years ±1.0 (Table 3 and Fig. 3). Separate pairwise Kolmogorov-Smirnov tests with Bonferroni-corrected *p*-values confirmed that distributions of age were significantly different between males and females ($D = 0.65875$, $p < 0.001$, $n = 601$) and between males and transitional fish ($D = 0.53769$, $p < 0.001$, $n = 523$) but were not significantly different between females and transitional fish ($D = 0.12106$, $p = 0.31$, $n = 304$).

Total length and age data fit to a von Bertalanffy growth curve showed a mean asymptotic length (L_∞) of 301 mm TL and a growth coefficient (K) of 0.32 (Fig. 5). The age at which the fish had a theoretical length of zero (t_0) was −0.18 (Table 4).

The total length at median maturity (LM_{50}; total length at which 50% of the fish were mature) was 119 mm with a 95% confidence interval of 113 to 120 mm (Table 5). The age at median sexual maturity (AM_{50}), or the age at which 50% of the fish were mature, was 1.5 years with a 95% confidence interval of 1.48 to 1.51 years (Table 5). The total length at median sexual transition (LS_{50}; total length at which 50% of the fish were male) was 223 mm with a 95% confidence interval of 220 to 225 mm (Table 5). The age at median sexual transition (AS_{50}), or the age at which 50% of the fish were male, was 4.2 years with a 95% confidence interval of 4.0 to 4.3 years (Table 5). In addition to providing size or age at median maturity or transition, the logistic regression equations can provide the probability that a fish will be mature or male at a specified size or age (Table 5).

Table 3 Summary of total length and age in all princess parrotfish

Category	Mean size (TL mm); range (*n*)	Mean age (y); range (*n*)
Initial phase	208; 50–292 (*n*=360)	3.8; 0–7 (*n*=359)
Female	199; 50–250 (*n*=230)	3.7; 0–7 (*n*=229)
Transitional	223; 140–292 (*n*=104)	4.1; 2–6 (n=104)
Male	235; 159–268 (*n*=25)	4.1; 2–6 (*n*=25)
Terminal phase (all male)	255; 197–314 (*n*=399)	5.8; 3–11 (*n*=396)
Overall	233; 50–314 (*n*=759)	4.9; 0–11 (*n*=754)

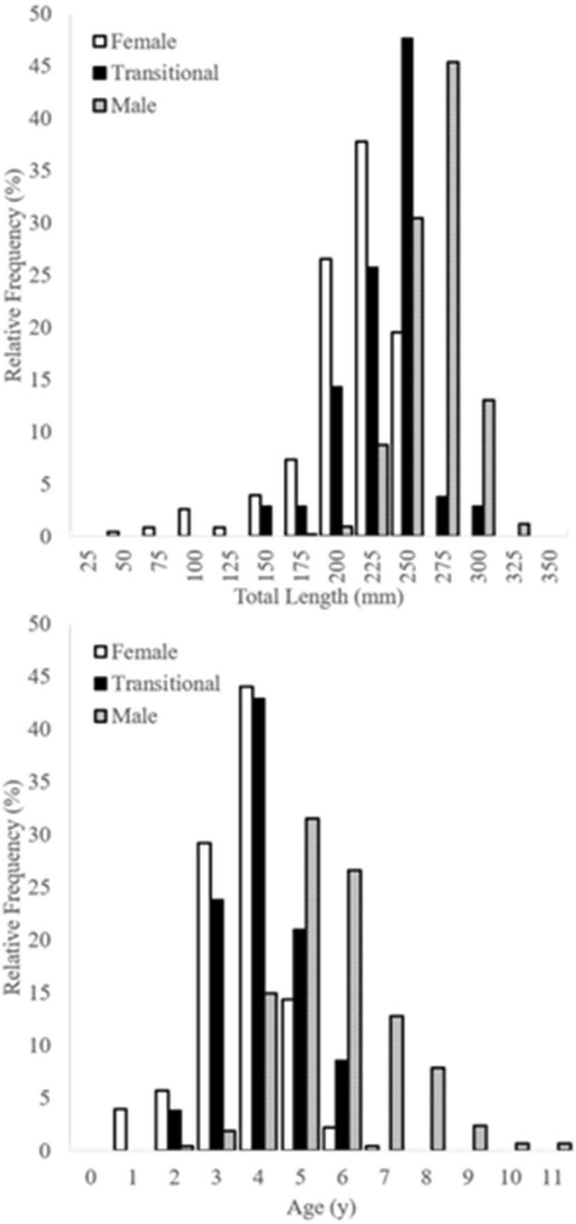
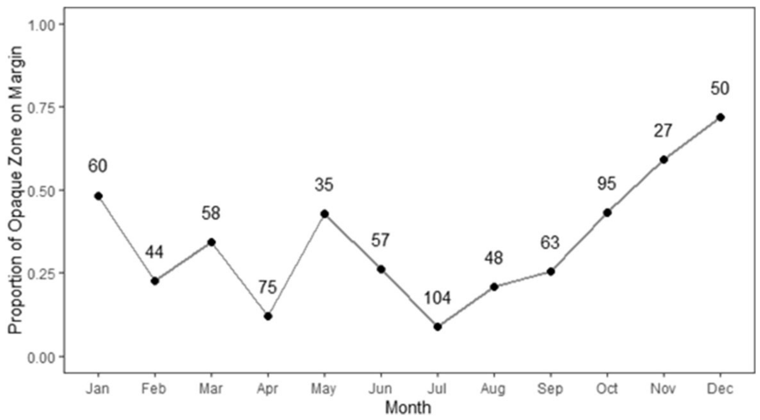


Fig. 3 Size (top) and age (bottom) frequency distributions for princess parrotfish females, transitional, and males

Discussion

The current study is the first to publish critical comprehensive information on life history parameters (age structure, growth, size/age at maturity, and transition) for a Caribbean parrotfish species. Parrotfishes throughout the Caribbean have been investigated extensively for their important roles in coral reef ecosystems as algal grazers, bioeroders, and as trophic links between

Fig. 4 Marginal increment analysis for princess parrotfish. Opaque zones of otoliths formed in the late fall and early winter months (October–January). Numbers above each dot indicate the monthly sample size with otolith margin information



primary producers and consumers. Efforts to protect parrotfish species populations are well-intentioned; however, without documenting key life history parameters, fisheries managers cannot conduct scientifically rigorous stock assessments to determine the impacts of fishing pressure and to justify establishing regulatory tools to ensure the long-term sustainability of these species.

Many studies have noted the difficulty in age estimation for parrotfish species (Choat et al. 2002; Freitas et al. 2014). As with most tropical fish species that do not encounter dramatic seasonal differences in their environment, otolith increments are poorly defined and hard to visualize (Green et al. 2009). Despite the challenges, increments are visible when otoliths are sectioned, thus allowing otolith-based age determination to occur in parrotfishes and other tropical species (Green et al. 2009; Freitas et al. 2019). So far, studies that have evaluated the temporal periodicity of sagittal otolith increment formation in parrotfish species documented that increments form on an annual cycle (Choat et al. 1996; Freitas et al. 2019). The current study, using marginal increment analysis, also confirmed the annual deposition of increments, as only one primary peak in the frequency of opaque zones on the margin occurred (October–January).

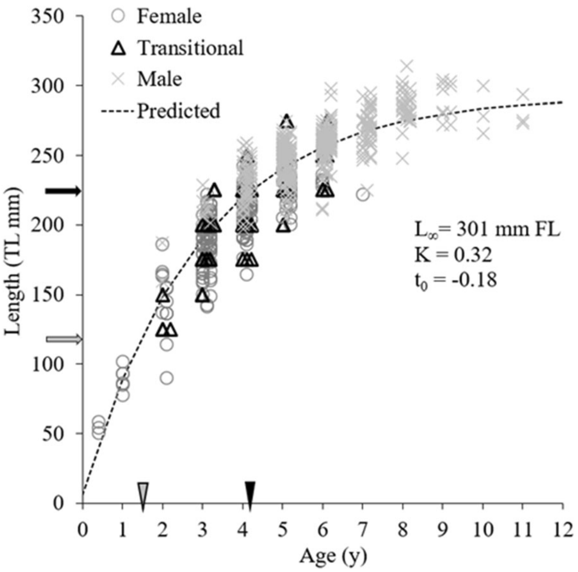


Fig. 5 Size-at-age with fitted von Bertalanffy growth curve for princess parrotfish. Median age at sexual maturity (AM_{50}) and sexual transition (AS_{50}) are indicated with the gray and black inverted triangles, respectively. Median size at sexual maturity (LM_{50}) and sexual transition (LS_{50}) are indicated by the gray and black arrows, respectively

Most studies reporting on the sex and color phase ratios of parrotfish species populations have documented more females than males and more initial phase individuals than terminal phase (Robertson and Warner 1978). However, the female to male ratio of our samples was 1:1.8 and the initial to terminal color phase ratio was 1:1.1. The higher proportion of males and terminal phase samples was probably due to utilizing a large number of fishery-dependent samples (~52%), and the biases associated with that. One of the main fishery methods for catching *Scarus* parrotfish species in the US Caribbean is spearfishing (SEDAR 2009; Pavlowich and Kapuscinski 2017) which enables fishers to selectively target larger fish for their efforts. Through fishery-independent sampling, we were able to target initial phase samples (including more females) across the range of sizes in which they occurred at sampling sites. In order to assess the overall ratio of female to male and initial to terminal individuals that occur in US Caribbean populations, a randomized sampling design would be essential.

Table 4 Population parameters for princess parrotfish from the US Caribbean

	n	L_∞ (TL mm)	K	$t_{\circ}$	Size range transitional	LM_{50}/AM_{50}	LS_{50}/AS_{50}
TL	759	301 (294 to 308)	0.32 (0.29 to 0.35)	−0.18 (−0.05 to −0.39)	140–292	119/1.5	223/4.2
FL	-	295	-	-	140–286	119	220
SL	-	245	-	-	115–233	78	182

Princess parrotfish from the US Caribbean exhibited a clear pattern in the population length/size structure of females, transitional, and males typical of protogynous hermaphroditic fishes (Warner 1975; Shapiro 1981). Females were significantly smaller than males, dominating the smaller sizes, but by 250 mm TL all fish were male or transitioning to male. Males were absent from the smaller size groups (smallest male = 140 mm TL), although 6% of all males were initial color phase individuals and 7% of all initial phase fish were male. Similar trends have been reported for some parrotfish species in the Pacific; *Scarus forsteni* females from a population in Guam were limited to a maximum size of 298 mm FL while males obtained a maximum size of 339 mm FL (Taylor and Choat 2014). Not all parrotfish species exhibit this pattern of size; stoplight parrotfish female and male sizes overlap across a broad size range and the largest individual collected from a US Caribbean population was female (Wagner 2019).

The largest princess parrotfish collected in our study was 314 mm TL which is close to the maximum reported size of 300 mm TL for this species (Robertson and Van Tassell 2019). Two other Caribbean parrotfish species reach similar maximum lengths: *Scarus iseri* has a maximum reported length of 270 mm TL, and *Sparisoma aurofrenatum* has a maximum length of 280 mm TL (Robertson and Van Tassell 2019). The other major parrotfishes in the Caribbean that contribute to fisheries attain much larger maximum sizes; *Scarus vetula* grows to 500 mm TL, *Sparisoma viride* has a maximum size of 640 mm TL, *Sparisoma chrysopterum* reaches a maximum of 460 mm TL, and *Sparisoma rubripinne* grows up to 480 mm TL (Robertson and Van Tassell 2019).

Princess parrotfish age structure among female, transitional, and male fish support the idea that at least for this Caribbean population, individuals start out as female, since only females occurred in the age-0 and age-1 classes; the youngest male collected was 2 years. The maximum age attained by females was 7 years, while males had a maximum age of 11 years. Transitional fish ranged in age from 2 to 6 years. This combined with the difference between males and females in maximum size indicates that princess parrotfish in the US Caribbean appear to start out life as female and if they live long enough will eventually transition to male. In contrast, stoplight parrotfish *Sparisoma viride* does not seem to exhibit this pattern; females had a similar maximum age as males in the US Caribbean (Wagner 2019) and appeared to live longer than males in Florida (Paddack et al. 2009). Parrotfishes in the genus *Scarus* and beyond from the Pacific exhibit a diversity of differing patterns in sex-related population age structure. In Guam and Pohnpei, females of the species *Scarus forsteni*, *Scarus*

Table 5 Logistic regression equations for probability mature or probability male at size and age. The probability equation provides the probability (p) that a fish of size or age x will be mature or male based on its logistic regression equation

Parameter	Slope	Intercept	Probability equation
Length (mm TL) at maturity	1.08	−128.02	$p = \frac{e^{-128.02+1.08x}}{1+e^{-128.02+1.08x}}$
Age (y) at maturity	40.03	−59.85	$p = \frac{e^{-59.85+40.03x}}{1+e^{-59.85+40.03x}}$
Length (mm TL) at transition	0.10	−21.14	$p = \frac{e^{-21.14+0.10x}}{1+e^{-21.14+0.10x}}$
Age (y) at transition	1.65	−6.90	$p = \frac{e^{-6.90+1.65x}}{1+e^{-6.90+1.65x}}$

psittacus, and *Scarus schlegeli* reach older maximum ages compared to males, while *Cetoscarus bicolor* females attained a maximum age of 8 years versus males in the population living to 12 years (Taylor and Choat 2014).

The current study is the first to report age and growth of princess parrotfish. The growth coefficient ($K = 0.316$) for this species fell within the lower portion of the range of K reported for parrotfish populations from the Pacific. *Chlorusus perspicillatus* in Hawai'i had a growth coefficient of 0.23 (DeMartini et al. 2018). *Chlorusus microrhinos* from Guam (Taylor and Choat 2014) and *Scarus niger* from Australia (Choat et al. 1996) had growth coefficients of 0.34 and 0.37, respectively. For parrotfishes in the Pacific, growth varies tremendously within species by region; Hawai'i and Guam populations of *Chlorusus spilurus* had growth coefficients of 0.40 and 0.93, respectively (Taylor and Choat 2014; DeMartini et al. 2018). *Scarus psittacus* populations from Hawai'i, Guam, and Australia had corresponding growth coefficients of 0.49, 0.91, and 0.35 (Choat et al. 1996; Taylor and Choat 2014; DeMartini et al. 2018). *Scarus schlegeli* from Australia had a growth coefficient of 0.22 (Choat et al. 1996) compared to 1.03 reported for the Guam population (Taylor and Choat 2014). Additional research has demonstrated that growth can even vary within a region for a parrotfish species (Gust et al. 2002). Overall, parrotfishes display a high degree of plasticity in growth and for some species, this characteristic may be highly responsive to anthropogenic or environmental factors (Taylor and Choat 2014). The lower growth coefficient documented for princess parrotfish in the current study may reflect an inherent difference in growth rate but could also relate to differences in fishing pressure, environment, and calculations of the von Bertalanffy function.

The maximum reported ages for *Scarus* species investigated across the globe ranges from 6 to 31 years. The maximum reported age was 6 years for populations of *Scarus psittacus* from Hawai'i and Guam (Taylor and Choat 2014; DeMartini et al. 2018) and a population of *Scarus ghobban* from Pohnpei (Taylor and Choat 2014). In Guam, *Scarus schlegeli*, *Scarus forsteni*, and *Scarus altipinnus* had maximum reported ages of 8, 12, and 14 years, respectively (Taylor and Choat 2014). We documented a maximum age of 11 years for princess parrotfish. Several species of *Scarus* attain even older maximum ages: the oldest from the Pacific, *Scarus frenatus* from Australia had a maximum reported age of 20 years (Choat et al. 1996) and *Scarus rubroviolaceus* in Hawai'i reached a maximum age of 19 years (DeMartini et al. 2018). A paucity of information exists on maximum ages for Caribbean *Scarus* species; however, the oldest individual from this genus that we have aged to-date was a midnight parrotfish *Scarus coelestinus* from Bermuda waters with an estimated age of 31 years (Fig. 6).

Princess parrotfish had a length at median sexual maturity (LM_{50}) of 119 mm TL and an age at median sexual maturity (AM_{50}) of 1.4 years. The LM_{50} occurred at approximately 53% of the mean total length of all princess parrotfish (233 mm) and the AS_{50} occurred at approximately 28% of the mean age of all princess parrotfish (5 years; Table 5). *Scarus psittacus* in Guam and Hawaii had similar LM_{50} values and also reached median sexual maturity around 1–2 years of age (Taylor and Choat 2014; DeMartini and Howard 2016; DeMartini et al. 2018). The striped parrotfish *Scarus iseri*, which is often mistaken for princess parrotfish, had mature females as small as 40 mm SL (Robertson and Warner 1978). *Sparisoma viride* in the US Caribbean has a LM_{50} of 169 mm FL (Wagner 2019).

US Caribbean princess parrotfish had a similar LS_{50} as *Scarus psittacus* in Hawaii ($LS_{50} = 226$ mm FL; DeMartini and Howard 2016) and Guam ($LS_{50} = 193$ mm FL; Taylor and Choat 2014) and as *Scarus schegeli* in Guam ($LS_{50} = 220$ mm FL; Taylor and Choat 2014). *Scarus psittacus* in Hawaii reached median sexual transition at approximately the same age as princess parrotfish ($AS_{50} = 2$–4 years; DeMartini et al. 2018). In contrast, larger *Scarus* species including *Scarus rubroviolaceus* in Hawaii and Guam did not reach median sexual maturity until 473 mm FL and 329 mm FL, respectively (Taylor and Choat 2014; DeMartini and Howard 2016; DeMartini et al. 2018).

Princess parrotfish had a length at median sexual transition (LS_{50}) of 224 mm TL and an age at median sexual transition (AS_{50}) of 4 years (Table 5). The LS_{50} occurred at approximately 96% of the mean total length of all sampled princess parrotfish (233 mm) and the AS_{50} occurred at approximately 84% of the mean age in all princess parrotfish (5.0 years). In some contexts, such as providing input data for stock assessment models, it is helpful to describe size and age at transition in a single number like the LS_{50} or AS_{50}. However, it is important to note that the process of sexual transition is

Fig. 6 Midnight parrotfish *Scarus coelestinus* otolith section. Researchers from Bermuda conducting a reef fish aggregations study donated sagittal otoliths from parrotfish samples they collected. This is the otolith section from a midnight parrotfish that was 656 mm FL/728 mm TL collected in 2016 with an estimated age of 31 years

observed across a range of values. For example, transitioning princess parrotfish ranged from 140 to 292 mm TL and from 2 to 6 years in age. The sexual transition process is primarily under social control (Muñoz and Warner 2003; McBride and Johnson 2007) with likely influence from hormones (Cardwell and Liley 1991a, b) and may lead to fluctuating sizes and ages at transition. In some species of parrotfishes, terminal male parrotfish form polygynous mating systems and invest energy in guarding a small number of females from other males attempting to enter its territory (Winn and Bardach 1957; Barlow 1975); Dubin (1981) observed that in the Caribbean, most terminal phase princess parrotfish established an exclusive, permanent territory ranging in size from 120 to 500 m^2 that contained a harem of 3–5 females. Reproductive success may increase more quickly with size in large, dominant, female-guarding males than in females, so females that transition to males may increase their lifetime reproductive potential (Ghiselin 1969; Muñoz and Warner 2003). After the terminal male is removed from a polygynous mating system, a female initiates transition and may demonstrate the gonadal features, color phase, and behavior of a terminal male within as few as 20 days (Muñoz and Warner 2003). Females may also transition to initial phase males. In the US Caribbean princess parrotfish population, over 7% of the initial phase individuals were male. Because initial phase males resemble females in size and color, these males may avoid confrontation with terminal males and "steal" a spawn with a female (Barlow 1975).

Life history traits such as length/age at sexual maturity and transition and maximum length/age are useful predictors of parrotfish species vulnerability to fishing pressure. A study from the western Pacific characterized growth, timing of sexual maturation, and timing of sexual transition for local populations of 12 parrotfish species in Guam and Pohnpei. The parrotfishes exhibited a diverse range of variability in maximum body size, growth rate, age classes, size/age at reproductive maturity, and size/age at transition (Taylor and Choat 2014). A quantitative analysis of these life history characteristics separated the species into three main groups: (1) "small-bodied" parrotfishes characterized by relatively small maximum sizes and asymptotic sizes, small sizes at medium sexual maturity, and young median ages at sexual maturity; (2) "large-bodied" parrotfishes characterized by relatively large maximum sizes and asymptotic sizes, large median sizes at sexual maturity, and older median ages at sexual maturity; and (3) intermediate parrotfishes that exhibited a mix of characteristics which did not coincide with the patterns of the first two groups. Species in the "large-bodied" group potentially would respond more negatively to intense fishing pressure, while "small-bodied" species would be more resilient (Hawkins and Roberts 2004; Taylor and Choat 2014; DeMartini and Howard 2016; DeMartini et al. 2018; Pavlowich et al. 2018). Similar to the Pacific species *Scarus forsteni*, *Scarus ghobban*, and *Scarus rubroviolaceus*, princess parrotfish from the US Caribbean had a mixture of life history attributes (slow growth combined with small size at sexual maturity, young age at sexual maturity) that place it in the intermediate parrotfish group (Taylor and Choat 2014; DeMartini et al. 2018). The response of species in this intermediate group to intense fishing pressure may depend on additional factors, such as vulnerability to capture and region-specific distribution patterns across depth and habitat (Taylor and Choat 2014). Pavlowich et al. (2018) concluded that focused fishing pressure on terminal males, which we documented for princess parrotfish caught mainly by spearfishing, may ensure robust populations of initial phase fish, providing a robust amount of spawning stock biomass. However, even though decreases in size or age at maturity and transition may not be immediately problematic or evident for a parrotfish population, these parameters serve as important indicators of fishing pressure impacts and should be documented and monitored for changing trends (Pavlowich et al. 2018).

Conclusions

The current study provided some of the first age and growth data available for princess parrotfish and some of the first published values for *Scarus* species in the US Caribbean. The study had a large sample size of 759 fish with generally strong representation from each month. The size and age class structures of princess parrotfish were representative of a protogynous hermaphrodite. Relationships among length measures and between length and weight were strong and are useful for reliable conversions. Princess parrotfish in the US Caribbean had a lower growth coefficient than some Pacific *Scarus* species; however, they were not the slowest growing of all *Scarus* species. *Scarus taeniopterus* in the US Caribbean had a moderate maximum age compared to Pacific parrotfish species. Vital age and growth data for a data-deficient *Scarus* parrotfish species are now available to Caribbean researchers and fisheries managers, providing life history parameters for stock assessments and biological information for management decisions.

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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 statement 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.

Conflict of interest The authors declare no competing interests.

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