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Queen Triggerfish *Balistes vetula* Age-Based Population Demographics and Reproductive Biology for Waters of the North Caribbean

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Abstract: Queen triggerfish *Balistes vetula* is an important reef-associated species for commercial fisheries in the U.S. Caribbean. It exhibits a relatively unique reproductive strategy as a nesting benthic spawner, investing substantial energy in territorial defense, building and maintaining nests, and caring for fertilized eggs during the reproductive season. Prior to this study, no comprehensive life history information existed in the literature for queen triggerfish. This study provides the first comprehensive documentation of age, growth, size/age at sexual maturity, reproductive seasonality, and reproductive output for a *Balistes* species in the Caribbean. From 2013 to 2023, we collected 2190 fish samples from fisheries-dependent and -independent sources from the waters of Puerto Rico and the U.S. Virgin Islands. Fish ranged from 67 to 477 mm fork length (FL). We documented that queen triggerfish is sexually dimorphic with males attaining larger mean sizes-at-age compared to females and the species is characterized by a moderately young age at median sexual maturity (A_{50} = 3.3 y). The maximum age for our U.S. Caribbean samples was 23 y based on increment counts from otoliths. Spawning season encompassed the months of December to August in the region, and female spawning frequency ranged from an estimated 2 to 84 times per year; female spawning frequency increased with increasing size and age of fish. We documented that commercial fishers in the U.S. Caribbean mainly target "plate-size" individuals, defined in our study as 235–405 mm FL, which appears to act as a self-imposed slot size range limit and results in the fishery not removing individuals in the smallest and largest size groups at high rates. The percentage of immature fish from fisheries-dependent sources was close to 0 (0.8%). Commercial fishing for queen triggerfish in the region currently appears to be sustainable, but monitoring of the population should continue.

Keywords: life history; triggerfish age estimation; reproductive histology; tropical fisheries

Key Contribution: Queen triggerfish is a nesting benthic spawner, invests energy in brood care of fertilized eggs, and exhibits group-synchronous oogenesis and indeterminate fecundity, and females can spawn up to an estimated maximum of 84 times a year; these reproductive characteristics combined with a protracted spawning season of nine months in the U.S. Caribbean region suggests the evolution of a bet-hedging reproductive strategy that ensures at least some offspring will encounter favorable conditions for survival and growth in the early life stages.

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1. Introduction

Queen triggerfish *Balistes vetula* is a widely distributed member of the family Balistidae found in tropical and sub-tropical waters of the western Atlantic; the geographical range in which it occurs with some abundance extends from waters off the coasts of North Carolina [1,2], throughout the Caribbean Sea [3–6], and as far south as western Atlantic waters of southern Brazil [7,8]. A study on the genetic population structure of queen triggerfish from sites sampled throughout the Caribbean and south Florida documented a homogenous distribution of genetic variants, indicating high connectivity across the region with no isolation detected [9].

Queen triggerfish occurs at depths up to 275 m and is associated with reef, rubble, and adjacent sandy habitats [5]. Several studies from north Caribbean waters have documented habitat attributes for areas where queen triggerfish most commonly occur. Diver surveys in Saba Bank, BVI, documented adults associated with the whole spectrum of coral reef ecosystem strata, but most abundant in the outer reef flat zone characterized by hard bottom/pavement and submerged inner reef flat zone with low relief pavement and scattered rubble [10,11]. Two studies from west Puerto Rico noted adult queen triggerfish were associated with wall habitat of the continental slope at depths greater than 30 m [12,13]. On-going video survey research of deepwater Puerto Rico coral habitats has documented queen triggerfish in association with hard bottom reef areas up to a maximum depth of 115 m (K. Overly, NMFS, personal communication). Preliminary analysis of queen triggerfish mean size at depth recorded for fish from visual surveys conducted as part of the National Coral Reef Monitoring Program in waters of the U.S. Caribbean indicated a significant correlation between depth and size; mean size of queen triggerfish increased with increasing depth of observations (L. J. Grove/J. Blondeau, Reef Fish Ecology Unit, NOAA, unpublished data).

Queen triggerfish is a sexually dimorphic gonochorist characterized by a relatively medium size at sexual maturity [4]. It is a nesting benthic spawner that exhibits group-synchronous oogenesis and indeterminate fecundity [4] and may form spawning aggregations during at least some months of its spawning season in association with the full moon [4,14]. The annual spawning season for queen triggerfish, determined through histological analysis of female gonad samples, starts as early as December and extends to August in waters of the north Caribbean [4].

No published investigation exists on nesting strategies and associated spawning behaviors of queen triggerfish. Researchers in the north Caribbean investigating spawning aggregations of red hind *Epinephelus guttatus* around the full moon noted that queen triggerfish appear to occupy benthic nests at the same time (Figure 1). One of the red hind aggregation sites where queen triggerfish nests occurred is Lang Bank, St. Croix [15]. Bryan et al. (2019) investigated the spatial and temporal movement patterns of queen triggerfish via surgically implanting acoustic transmitters in 55 queen triggerfish caught in the Buck Island Reef National Monument (BIRNM), St. Croix, USVI, and reported that during the full moon periods of January to March, 12 individuals undertook repeated migrations to Lang Bank. In the same study, several other tagged fish larger than the size of 100% sexual maturity remained within the BIRNM during the same-season spawning periods, which may indicate a local resident nesting area for queen triggerfish [14].

Triggerfish species are mostly aged using the first dorsal spine, mainly due to the ease of obtaining the spines relative to extracting triggerfish otoliths, which are small, fragile, and take more effort to extract [16–21]. However, otoliths are considered to provide more accurate and precise age estimates when compared to alternative aging structures, like spines, scales, and fin rays, which can significantly underestimate the true age of a fish compared to otoliths [22–25]. Prior to our investigations on otolith-based age estimation in *Balistes* species, both gray triggerfish and queen triggerfish were thought to live relatively short lives with maximum spine-based age estimates of 15 y [17,26] and 14 y [7], respectively. Shervette and Rivera Hernández [6] utilized radiocarbon analysis of eye lens cores to validate the otolith-based age estimation for a *Balistes* triggerfish species and documented that queen triggerfish is a relatively long-living reef fish attaining a maximum age of 40 y. Otolith-based age estimation of gray triggerfish also extended longevity to a maximum age estimate of 20 y [2].

Figure 1. Queen triggerfish benthic nesting activity in waters of west PR. The image is from 21 Feb 2022 (five days after the full moon), by Verónica Seda, of a queen triggerfish tending to her nest in Abrir La Sierra. Note that the female appears to be flashing white blotches; similar coloration signals have been noted in other triggerfishes when a female is guarding her nest and tending to the eggs. Nests observed in this region were described as a pit about 25–50 cm deep in sandy depressions between the colonized substratum that could be between 1 and 3 m in diameter where one of the *B. vetula* would remain blowing head down near the substratum if egg masses were present (M. Scharer, HJR, personal communication).

In the waters of the Atlantic and Caribbean, queen triggerfish is considered a data-deficient/data-poor species due to a lack of information on population demographics. In the U.S. Caribbean, no current information was available on queen triggerfish population age structure and growth rates, despite its importance as one of the top commercially landed reef fish species in all U.S. Caribbean management platforms (Figure 2): Puerto Rico (PR), St. Thomas/St. John (STT/J), and St. Croix (STX) [4,27,28]. To fill in critical life history information gaps for queen triggerfish, the main goal of this study was to document the age, growth, and reproductive biology of this species in U.S. Caribbean waters utilizing a combination of fishery-dependent (FD) and fishery-independent (FI) samples. Specific objectives included (1) describing length and age structure for males and females across the three U.S. Caribbean management platforms; (2) calculating growth overall and separately for females and males; (3) evaluating gear selectivity by examining differences in gear-specific mean size and mean age; (4) providing updated information on size at sexual maturity, spawning interval, spawning seasonality; and (5) reporting on age at sexual maturity.

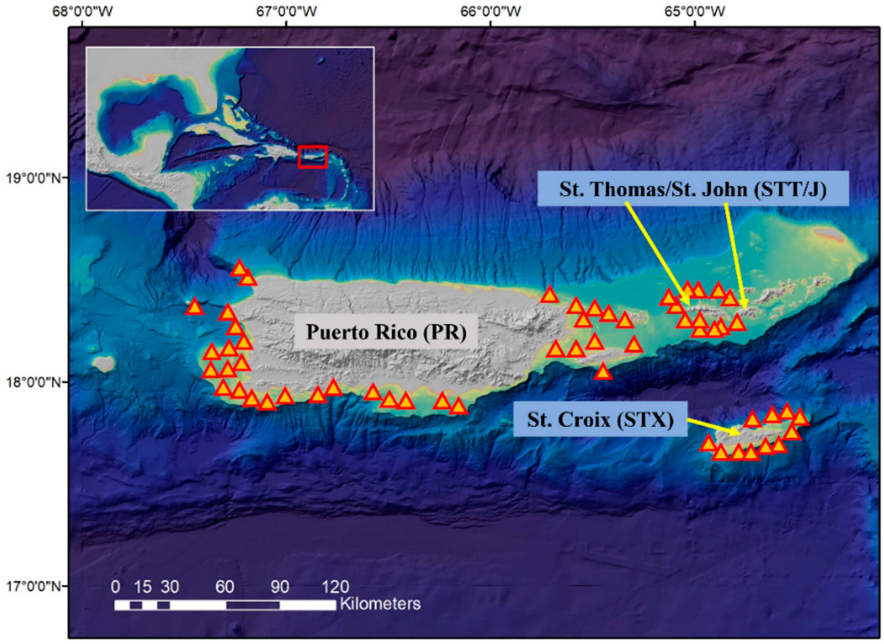

Figure 2. Map of the U.S. Caribbean sampling region. Triangles represent general locations where samples were collected.

2. Methods

2.1. Study Region and Management

The U.S. Caribbean is located in the western portion of the Caribbean archipelago (Figure 2) and includes the territories of Puerto Rico (PR) and the U.S. Virgin Islands (USVI). It is divided into three fisheries management island platforms that reflect ecological, cultural (e.g., traditional fishing practices), and market preference distinctions specific to each platform area [29]. The largest island management platform is PR in the west. The waters of PR are characterized by extensive coral reef ecosystems that extend across approximately 3370 km^2 within 3 nautical miles of the main island of PR and its associated smaller islands. In terms of average annual landings (reported in pounds [lb]), queen triggerfish ranks in the top five commercially targeted reef-associated fishes [27]. Queen triggerfish is caught commercially in PR mainly via trap (41% of catch) and spearfishing (47% of catch) [30]. Annual reported landings of queen triggerfish for PR from 2012 to 2019 ranged from 40,000 to 72,000 lb [30].

The USVI is composed of two fisheries management platforms: STT/J in the north and STX in the south. STT/J occurs on a large shelf platform containing a fishable area of 1500 km^2 and consists of a complex network of reef ecosystems [31]. Queen triggerfish is mainly caught commercially in STT/J by traps (98% of catch), is the top reef fish landed (in terms of total mass of catch), and is primarily fished in shelf waters at depths > 25 m [32]. Reported annual commercial landings of queen triggerfish in STT/J ranged from 33,000 to 56,000 lb for 2011–2019 [30].

The management platform of STX is located approximately 60 km south of STT/J, separated from the northern platform by the deep waters of the Anegada Pass. STX sits on a narrow platform surrounded by approximately 300 km^2 of shelf waters containing a network of coral reefs and associated ecosystems. Over 85% of the fishable area is at depths < 25 m [31]. Commercial fishers in STX target queen triggerfish mainly using hook-and-line gear, traps, and spearfishing [30]. Queen triggerfish ranks in the top five reef fish species landed in terms of total mass [33]. Reported annual commercial landings for this species in STX ranged from 3000 to 26,000 lb for 2011–2019 [30].

2.2. Field Collection and Processing

Fish samples were collected through (1) fisheries-dependent (FD) sampling via the purchase of fish from local fishers (2013–2023); (2) the fisheries-independent (FI) Southeast Area Monitoring and Assessment Program-Caribbean (SEAMAP-C); and (3) opportunistic FI sampling via collaboration with local fishers (2014–2023). Fishery-dependent samples were obtained directly from fishers and divided into two FD sample types: FD random were collected by randomly selecting all triggerfish from one side of a cooler containing the day's catch or by purchasing all queen triggerfish landed by a fisher on the day of sampling; FD nonrandom were collected by haphazardly selecting a subsample of queen triggerfish from a fisher at market which meant that the catch may have been combined from multiple trips and an unknown portion of fish may have been sold prior to our sampling. Fishery-independent SEAMAP-C samples were caught as part of the reef fish annual hook-and-line surveys conducted from 2014 to 2020. Small juvenile queen triggerfish were collected using a dipnet. 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 that they encountered, 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 by fishers for sale to locals were represented in the data. All fish were kept on ice 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 [4]. Queen triggerfish otoliths were extracted and stored according to the protocol described in Rivera Hernandez and Shervette [34].

2.3. Population Demographics

Length and weight measurements were used for exploring trends related to population demographics. Regression analyses were used to establish length–length and length–weight relationships using combined fish length and weight data from FD and FI samples. A two-factor ANOVA was used to test for significant differences in the mean length (FL) by sample source (FI versus FD) and sex (female versus male). Separate Kolmogorov–Smirnov (K-S) tests were used to determine if significant differences occurred in length frequency distributions between males and females, between FD and FI samples, and between FD trap and spear samples. Fishers from throughout the region have noted on several occasions that members of the local communities preferentially purchase "plate-size" fish for most reef fish species and compose most of their market [28,35]. However, restaurants will sometimes purchase larger fish (greater than the typical plate size) at a reduced price per pound, so occasionally larger fish are kept and sold to a restaurant. Therefore, to quantify the general length range of "plate-size fish" targeted by U.S. Caribbean fishers we used FD random samples to separately compute the 2.5 and 97.5 percentiles for length distributions of fish brought to market that were caught with traps and via spearfishing.

2.4. Age Estimation and Growth

Sagittal otoliths were read whole for age estimation, as described in Rivera Hernandez and Shervette [6]. This age estimation method was recently validated for north Caribbean queen triggerfish via bomb radiocarbon [6]. Sagittal otoliths from each fish were read by a primary reader (VRS) with no knowledge of fish size, date of collection, or sex. A subset of otoliths was read independently and blind by a secondary reader (JMRH). Percent agreement and Average Percent Error (APE) were computed to evaluate between-reader precision, as reported in Shervette and Rivera Hernandez [6], along with a detailed accounting of the otolith-based age estimation method validation results. A birthdate of 1 February was used to compute fractional ages from otolith opaque zone counts, as described in Shervette and Rivera Hernández [6]. A two-factor ANOVA was used to test for significant differences in mean age by sample source (FI versus FD) and sex (female versus male). Separate pairwise K-S tests were used to compare age frequency distributions between sexes, between sample sources (FD versus FI), and between FD traps of caught and speared fish. To quantify the general age range of "plate-size fish" targeted by U.S. Caribbean fishers, we used FD random samples to compute the 2.5 and 97.5 percentiles for age distributions of fish brought to market that were caught with traps and via spearfishing.

For size-at-age data, using fractional ages, separate von Bertalanffy growth functions (VBGFs) were fit to estimated ages using the least squares method with the solver function in Microsoft Excel [36] for the following groups: all samples combined, males, and females and previously reported in Shervette and Rivera Hernandez [6]. Since that publication, additional samples were collected and aged (2022–2023), so VBGF results were updated to include those.

2.5. Reproductive Biology

Gonads were removed from each queen triggerfish sample; either the whole gonad or the posterior portion of each gonad was fixed in 11% seawater-buffered formalin, Davidson's fixative, or polyethylene glycol–ethyl alcohol–glycerol–acetic acid (PAGA) fixative for up to two weeks and then transferred to 70% isopropanol. Gonad samples were processed using standard histological procedures for triggerfish species [4,19]. The 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. Stained sections were viewed using a compound microscope to determine sex and reproductive phase, assessed according to the histological criteria described in Rivera Hernandez et al. [4]. 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 phase assignment. If no consensus was reached, then that specimen was eliminated from the analyses.

Rivera Hernández et al. [4] described the methods used in the current study to document aspects of queen triggerfish reproductive biology for PR and STX using samples collected from the two management platforms for 2013–2018. Rivera Hernández et al. [4] specifically compared results for sex-specific size structure, size at sexual maturity, spawning seasonality, and spawning interval/frequency between PR (n = 581) and STX (n = 567). The current study analyzed additional queen triggerfish samples collected from 2019 to 2023 for PR (total PR n = 711) and STX (total STX n = 734) plus unpublished data for STT/J samples collected from 2015 to 2023 (STT/J total n = 745). In addition, age estimates from these combined collections enabled the computation of age at sexual maturity. Therefore, the current study used information on size, sex, reproductive phase, and age for all queen triggerfish samples collection throughout the U.S. Caribbean from 2013 to 2023 (n = 2190 overall; n = 2044 with gonad histology information).

The proportion of spawning-capable females relative to the total number of mature females in developing, regressing, and regenerating reproductive phases for each month was plotted to document the overall spawning season and peak spawning period for the U.S. Caribbean region. Spawning fraction, the proportion of actively spawning females relative to the total number of mature females, was calculated. The spawning interval was calculated using the early postovulatory follicle method [4]. To estimate the spawning interval (number of days between spawning events) for mature female queen triggerfish overall, by length class and by age class, the following equation was used: spawning interval = 1/spawning fraction. Spawning frequency was computed to estimate the number of times females could spawn within a year by dividing 267 days (the number of days within the spawning season of U.S. Caribbean queen triggerfish females spawning frequency [4].

Size (L_{50}) and age (A_{50}) at median sexual maturity of males, females, and all individuals combined from the U.S. Caribbean were calculated using separate logistic regressions.

Additional size and age at maturity values were also computed for sizes and ages at which 90% (L_{90} and A_{90}) and 95% (L_{95} and A_{95}) of individuals were sexually mature. For logistic regression analyses, maturity was treated as a binomial response variable. Logistic regressions were conducted using the logit function transformation and the generalized linear model procedure in R. Lastly, to obtain a general understanding of the proportion of the queen triggerfish commercial catch in the U.S. Caribbean that are sexually immature fish, we used FD random samples to compute the percentage of individuals that were immature overall and separately for fish caught with traps and spears.

3. Results

3.1. Population Demographics and Growth

A total of 2190 queen triggerfish samples ranging in size from 67 to 473 mm FL (mean FL = 313 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). Queen triggerfish males ranged in size from 67 to 473 mm FL (mean FL = 323 mm) and females ranged in size from 83 to 466 mm FL (mean FL = 300 mm; Table 1). Males were significantly larger than females (Table 3). Length frequency distributions were significantly different between females and males with a larger proportion of females in the smaller length classes (Table 4; Figure 3). Queen triggerfish sampled from FD sources ranged in length from 204 to 458 mm FL (mean FL = 319 mm) and from FI sources ranged from 67 to 473 mm FL (mean FL = 280 mm; Table 1).

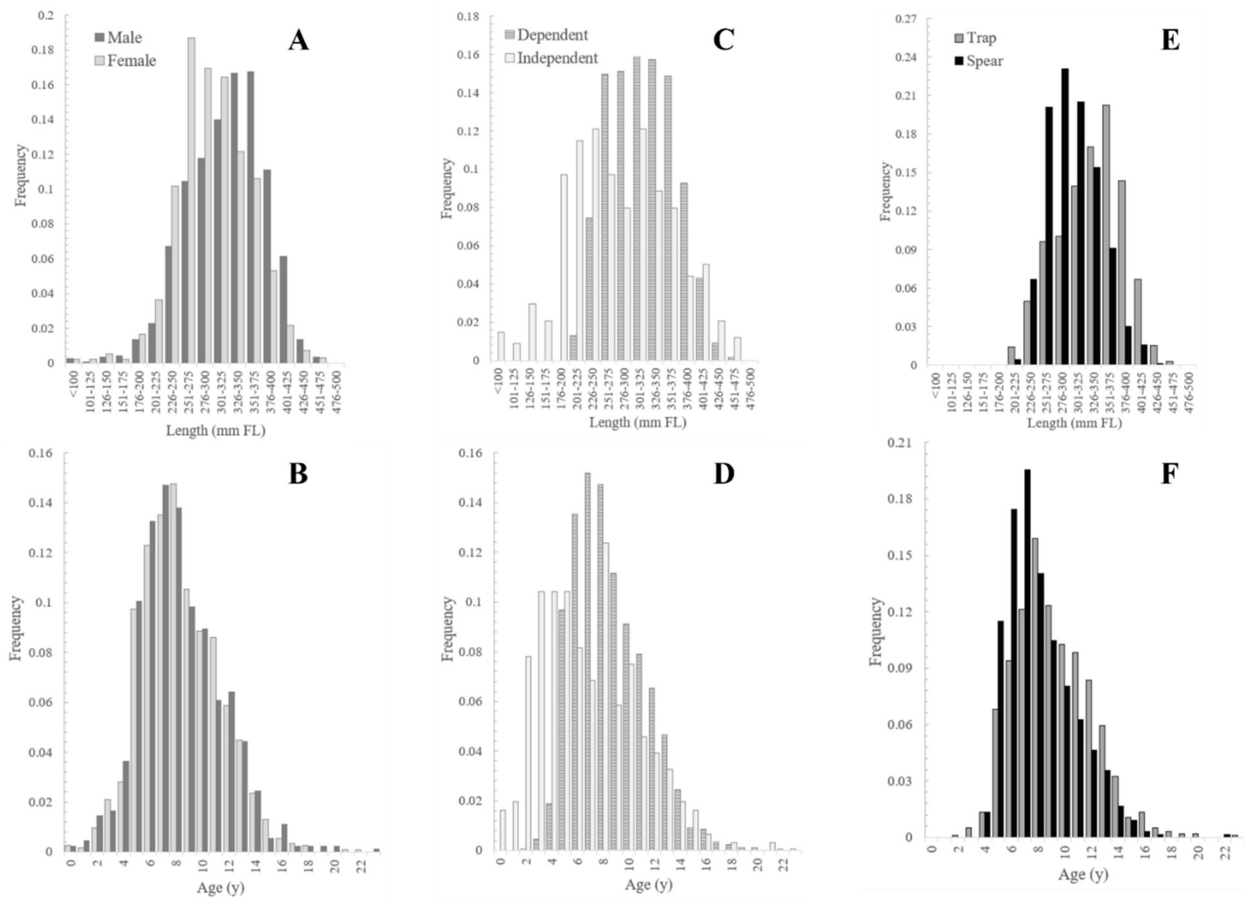

Figure 3. Length frequency (**A**,**C**,**E**) comparisons and age frequency (**B**,**D**,**F**) for U.S. Caribbean queen triggerfish males versus females (**A**,**B**), fisheries-dependent versus fisheries-independent samples (**C**,**D**), and trap- versus spear-caught fish samples (**E**,**F**). “Frequency” is reported in terms of proportions.

Table 1. Summary of queen triggerfish samples caught by sex, gear type, source, and island management platform.

	Size			Age		
Category	**n**	**Mean FL mm**	**Range**	**n**	**Mean Age y**	**Range**
Overall	2190	313	67–473	2068	8.3	0–23
Male	1188	323	67–473	1137	8.4	0–22
Female	962	300	83–466	904	8.2	0–23
Unknown	40	315	129–430	27	8.5	2–16
Source						
FD	1851	319	204–458	1764	8.6	2–23
FI	342	280	67–473	304	6.8	0–21
Trap	1040	334	150–473	1007	9.1	2–23
Spear	893	295	67–433	851	7.8	0–22
Hook	129	333	190–410	84	8.5	3–15
Net	130	254	83–434	126	5.9	0–18
Island						
Puerto Rico	711	296	67–434	662	7.9	0–20
St. Thomas/John	745	341	150–473	706	9.3	2–23
St. Croix	734	300	190–414	700	7.7	2–22

Table 2. U.S. Caribbean queen triggerfish length–length and length–weight conversion relationships derived from regression analyses.

Variables				
x	**y**	**n**	**Equation**	**R^2**
SL	FL	1735	$y = 1.103x + 10.393$	0.9866
SL	TL	1727	$y = 1.2325x + 10.093$	0.9860
SL	Wt	1457	$y = 0.0001x^{2.7291}$	0.9232
FL	SL	1735	$y = 0.8619x - 6.4446$	0.9866
FL	TL	1811	$y = 1.0752x - 0.9754$	0.9963
FL	Wt	1457	$y = 0.00004x^{2.8599}$	0.9511
TL	SL	1727	$y = 0.8x - 5.2792$	0.9860
TL	FL	1811	$y = 0.9266x + 1.7728$	0.9963
TL	Wt	1452	$y = 0.00004x^{2.8197}$	0.9389

Table 3. ANOVA analyses results for mean length and mean age between sexes and between fisheries source.

Source	**df**	**Sum of Squares**	**Mean Square**	***F***	***p***
Length (FL mm)					
Sex	1	141,631	141,631	46.67	<0.001
Source	1	423,404	423,404	139.52	<0.001
Sex × Source	1	767	767	0.25	0.615
Error	2146	6,512,623	3035		
Age (y)					
Sex	1	21	21	2.42	0.120
Source	1	779	779	87.92	<0.001
Sex × Source	1	26	26	2.97	0.850
Error	2040	8834	9		

Table 4. Results of the Kolmogorov–Smirnov tests.

Comparison	N	D	*p*
Length (FL mm)			
Female versus male	962 + 1188	5.03	<0.001
FD versus FI	1851 + 339	5.50	<0.001
FD Trap versus spear	989 + 702	6.77	<0.001
Age (y)			
Female versus male	905 + 1139	0.79	0.554
FD versus FI	1764 + 307	4.95	<0.001
FD Trap versus spear	956 + 670	3.87	<0.001

FD fish were significantly larger than FI fish (Table 3). Length frequency distributions were significantly different between FD and FI samples (Table 4; Figure 3); a greater proportion of FD fish were sampled from the bigger length classes. Length frequency comparison between FD fish caught with traps versus spearfishing indicated that a significantly greater proportion of fish caught via spearfishing occurred in the smaller length classes (Table 4; Figure 3).

FD random samples included a total of 973 queen triggerfish caught with traps (n = 442) and spears (n = 531). For FD random fish caught with traps, the inner 95 percentile range was 232–415 mm FL, and for fish caught via spearfishing, it was 241–379 mm FL (Table 5). The overall inner 95th percentile range for the length of all FD random samples combined was 235–405 mm FL, hereafter referenced as the size range of plate-size fish.

Table 5. Summary of queen triggerfish FD random samples and the 2.5th and 97.5% percentiles (95th percentile range) related to FL and age for defining characteristics of "plate-size" fish targeted by local fishers by traps and spearfishing.

	Length (mm FL)		Age (y)	
Gear	**n**	**95th Percentile Range**	**n**	**95th Percentile Range**
Trap	442	232–415	435	4–15
Spear	531	241–379	507	5–14
Overall	973	235–405	942	5–14

A total of 2068 samples were aged using the validated otolith age estimation method. Queen triggerfish ages ranged from 0 to 23 y with a mean overall age of 8.4 y (Table 1). Mean age did not differ significantly between males and females but differed between FD and FI samples; FD samples had significantly older ages compared to FI samples (Table 3). The age frequency comparison indicated that a significantly larger proportion of FD fish occurred in older age groups compared to FI fish samples (Table 4; Figure 3). The age frequency comparison between trap fish and spear fish indicated that a significantly greater proportion of fish caught via spearfishing occurred in younger age groups (Table 4; Figure 3).

The overall age range for FD random samples for the 2.5–97.5 percentiles was 5–14 y (Table 5). For FD random fish caught with traps, the age range was 4–15 y, and for fish caught with spears, the range was 5–14 y.

The von Bertalanffy growth equation for all U.S. Caribbean length-at-age data was $FL_t = 427 \times (1 - e^{-0.15[t - 0.585]})$. Males attained a larger asymptotic length than females; K was 0.15 for both sexes and overall (Table 6; Figure 4).

Table 6. Results for von Bertalanffy growth functions for U.S. Caribbean queen triggerfish (95% confidence intervals). Parameter estimates were obtained for all samples combined and separately for males and females.

Group	N	L_∞ (mm)	K	t_0	R^2
All	2068	427 (419–434)	0.15 (0.14–0.16)	−0.585	0.69
Male	1139	439 (429–448)	0.15 (0.14–0.16)	−0.585	0.72
Female	905	407 (397–418)	0.16 (0.15–0.17)	−0.585	0.70

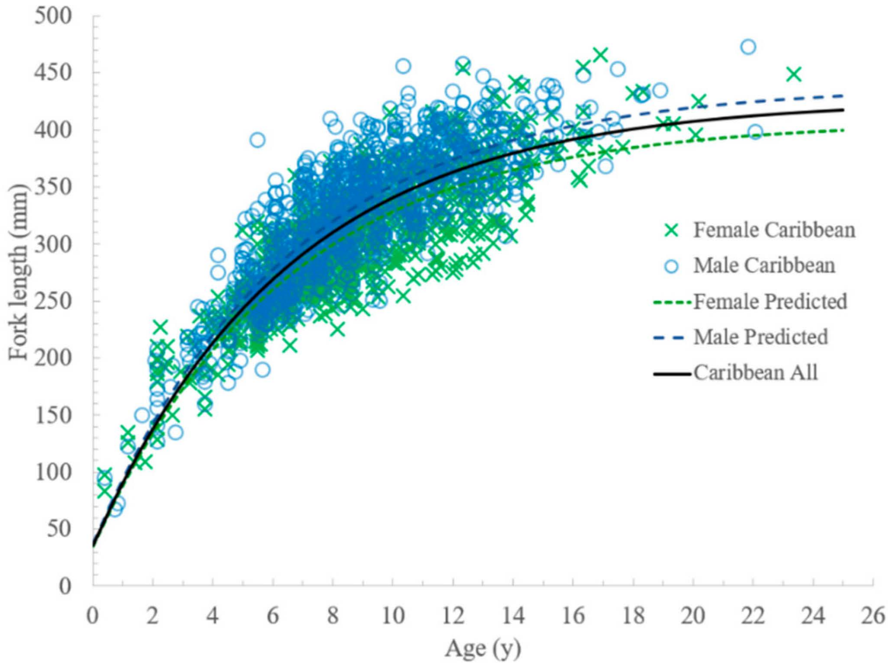

Figure 4. Length-at-age and von Bertalanffy growth curves for U.S. Caribbean queen triggerfish.

3.2. Reproductive Biology

Sex and reproductive phase were assigned to 2044 individuals. Actively spawning females occurred from December to August in low proportions relative to the total number of mature female samples each month; peak spawning for females was from December to February (Figure 5). Male queen triggerfish that were in the spawning-capable phase occurred in all months of the year at relatively high proportions compared to all mature males sampled (Figure 5).

As aggregating nesting benthic spawners, queen triggerfish females exhibited group-synchronous oogenesis and indeterminate fecundity over the spawning season that started as early as the week after the full moon in December and extended until August. The overall spawning fraction was 0.5 (Table 7). The overall spawning interval, defined as the number of days between spawning events in a female, was 19 d, indicating that a female spawns around 13 times over the estimated ~270-day spawning season (Table 7). When examining trends in spawning fraction, interval, and frequency by length, spawning frequency increased with increasing length class. Females in the smallest FL class had an estimated spawning frequency of two times over the spawning season, while females in the largest FL class had an estimated spawning frequency of 69 times over the spawning season (Table 7). Similar increases in spawning frequency occurred when examined by age classes. This means that larger/older females can spawn 6–7 times each month during the December–August spawning season and younger/smaller females spawn less frequently.

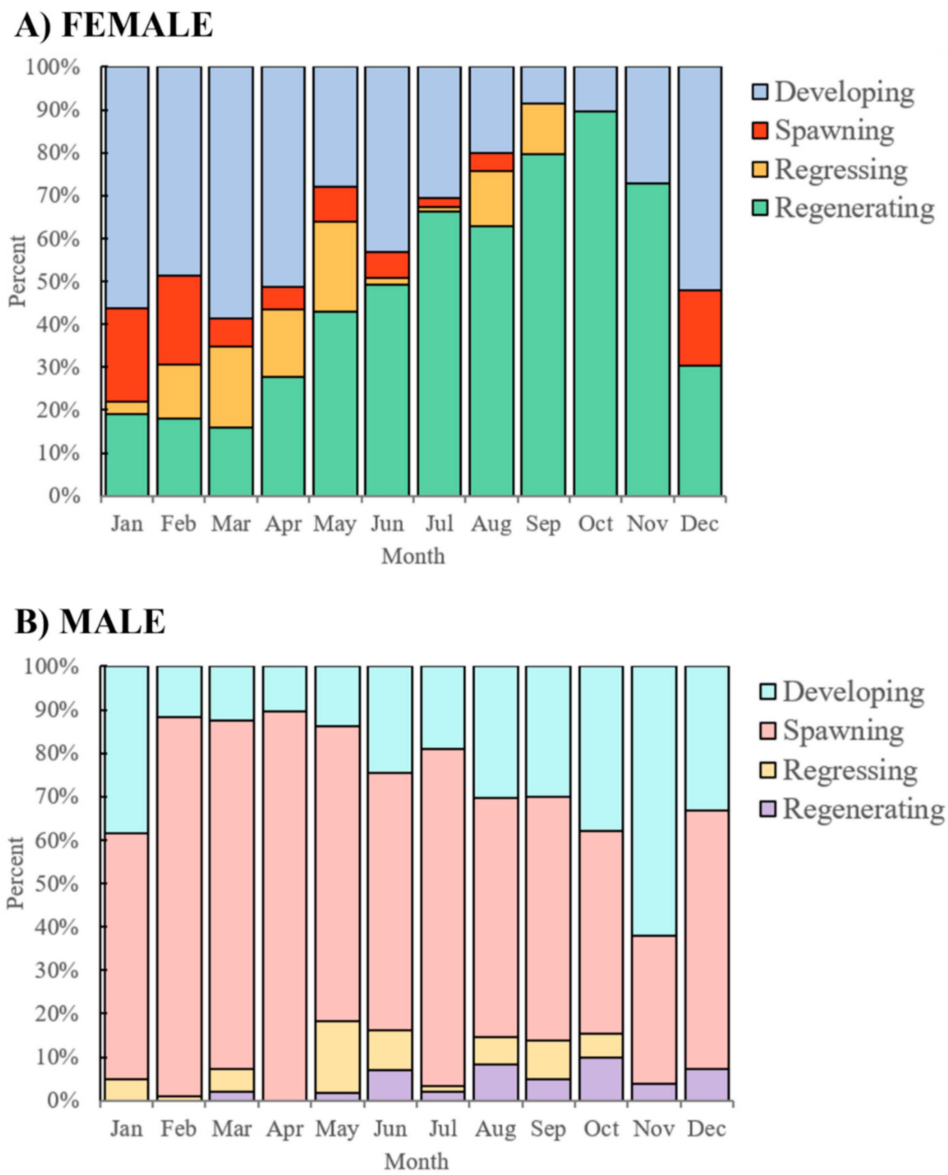

Figure 5. Reproductive seasonality for queen triggerfish females (**A**) and males (**B**) in the U.S. Caribbean. Monthly percentages of individuals in each reproductive phase are presented.

Table 7. Female queen triggerfish estimates for spawning fraction, spawning interval, and spawning frequency summarized overall, by size classes, and by age classes.

	Number of Mature Females	Spawning Fraction	Spawning Interval	Spawning Frequency
Overall	830	0.05	19 d	13/y
FL class (mm)				
≤300	427	0.01	142 d	2/y
301–350	275	0.05	20 d	14/y
351–400	153	0.11	9 d	30/y
401+	31	0.26	4 d	69/y
Age class (y)				
≤5	87	0.01	87 d	3/y
6–10	544	0.04	25 d	11/y
11–15	180	0.08	13 d	21/y
16+	19	0.32	3 d	84/y

The smallest mature male was 122 mm FL, and the largest immature male was 242 mm FL; the L_{50} of males was 206 mm FL (Table 8). The smallest mature female was 196 mm FL, and the largest immature female was 257 mm FL. The L_{50} of females was 227 mm FL (Table 8). The combined L_{50} was 212 mm FL (Table 8). The youngest mature male was 1 y, and the oldest immature male was 5 y; the A_{50} of males was 2.7 y (Table 8). The youngest mature female was 2 y, and the oldest immature female was 6 y; the A_{50} of females was 4.1 y (Table 8). The combined A_{50} was 3.3 y (Table 8). Using queen triggerfish FD random samples, we determined that overall, the percentage of immature fish landed by commercial trap- and spear-fishing efforts was extremely low (<1%; Table 9).

Table 8. Size and age at sexual maturity (95% prediction intervals).

Parameter	All	Male	Female
Size (FL mm)	N = 2148	N = 1187	N = 961
L_{50}	211 (208–217)	193 (177–203)	225 (220–230)
L_{90}	241 (236–244)	222 (214–229)	247 (243–251)
L_{95}	251 (246–255)	232 (222–240)	254 (251–259)
Age (y)	N = 2042	N = 1138	N = 904
A_{50}	3.3 (3.1–3.6)	2.7 (3.8–4.4)	4.1 (3.8–4.4)
A_{90}	4.9 (4.7–5.1)	3.9 (5.2–5.7)	5.5 (5.2–5.7)
A_{95}	5.5 (5.2–5.7)	4.3 (5.7–6.2)	6.0 (5.7–6.2)

Table 9. Summary of queen triggerfish samples from FD random collections that were determined through gonad histology as immature and mature. Maturity information is indicated by gear type and for all samples combined.

Gear	Number (#) of Fish with Maturity Information	#Immature/ #Mature	Percent Immature
Trap	438	3/435	0.7%
Spear	526	4/522	0.8%
Overall	964	7/957	0.7%

4. Discussion

This is the first peer-reviewed study to provide comprehensive life history information (age, growth, and reproductive biology) for queen triggerfish. We documented that queen triggerfish is sexually dimorphic with adult males attaining larger sizes-at-age than females. Queen triggerfish is characterized by a moderately young age at sexual maturity. We also showed that gear-related differences existed in size and age at capture, which further emphasizes the importance of combining gear-specific catches across a broad range of depths for reef fishes when seeking to document a comprehensive understanding of population life history trends for a region.

4.1. Population Demographics and Growth

The mean length of male queen triggerfish was significantly larger than females in the U.S. Caribbean region. Similar findings were documented for queen triggerfish and gray triggerfish in southeastern U.S. Atlantic (SEUS) waters [2,19] and for gray triggerfish in the Gulf of Mexico (GOM) [37]. Male and female queen triggerfish also exhibited different rates of growth in the U.S. Caribbean [6], with males attaining a larger size at age, a larger asymptotic length (L_{∞}), and a larger maximum length compared to females. Shervette and Rivera Hernández [2] reported similar trends for gray triggerfish in SEUS waters.

These differences in length and growth between sexes in triggerfishes may relate to their sex-specific roles within their reproductive strategy as a territorial benthic nesting species [2,38]. Compared to other reef-associated fisheries species, triggerfish exhibit unique spawning behaviors [39] in that they are moderately large-bodied species with relatively high batch fecundity [39–41] but are benthic nesters and invest energy in defending spawning territories, nest defense, and caring for their broods of fertilized eggs until larvae hatch [39,41–43]. In situ observational studies that investigated the mating behavior of triggerfishes noted that territorial males defending spawning grounds were larger than females nesting within a male's territory [39,41,42]. Larger males, compared to smaller males, may succeed at a higher rate in defending territories from predators and conspecifics, which may also enhance success in attracting and mating with more females [39,44]. During nesting periods, females appear to invest a large amount of energy in nest preparation and maintenance, defending nests from potential egg predators, and in brood care of fertilized eggs [38,39,41,42,45]. The massive energy investment by female triggerfish into spawning and nesting efforts for multiple broods in a spawning season could mean that less energy goes towards somatic growth; this may partially explain why females are typically smaller than males [2,41,42].

The maximum size of queen triggerfish obtained for age estimation from the U.S. Caribbean in the current study was 473 mm FL using a combination of fishing methods/gears, including spearfishing, traps, and nets. The maximum size of queen triggerfish reported from port sampling efforts throughout the U.S. Caribbean from 2003 to 2020 for which both length and weight were recorded (so that length type of FL could be confirmed, and the accuracy of FL evaluated) was 480 mm FL [NOAA Trip Interview Program (TIP, NOAA Southeast Fisheries Science Center), unpublished data]. The maximum queen triggerfish FL size bin with observations noted from underwater visual surveys in the U.S. Caribbean was 491–500 mm FL [46]. However, queen triggerfish greater than 500 mm FL occurred during commercial port sampling efforts from waters of a higher latitude region; Shervette and Rivera Hernández [2] obtained queen triggerfish as large as 585 mm FL from offshore North Carolina. The maximum age documented for queen triggerfish from the U.S. Caribbean was 23 y (in the current study), while a maximum age of approximately 40 y was obtained for the species from the higher latitude region of North Carolina [2]. Several studies have documented latitudinal gradients related to maximum size and age obtained by fishes [47–50]. In fishes, the life span obtained by a species often increases with latitude because metabolism slows at lower temperatures [48,51]. For example, Shervette et al. [21] noted that gray triggerfish exhibit an increase in maximum size with increasing latitude. Taylor et al. [50] documented a significant and strong relationship between sea surface temperature (as it decreased with increasing latitude) and the maximum age for populations of a unicornfish species, whereby warmer waters at a lower latitude yielded shorter-lived populations. Robertson et al. [49] reported that the body size, growth rate, and life span of ocean surgeonfish populations were inversely related to water temperature. Trends in regional patterns of maximum size and age attained by queen triggerfish appear to also correlate with latitude.

Queen triggerfish in the youngest age classes and smallest size classes were observed infrequently in the current study. Post-larval pelagic habitat remains undocumented for queen triggerfish throughout its range. Only one published study has reported indirect evidence of small (<60 mm FL) queen triggerfish potentially utilizing pelagic habitat based on the occurrence of a few small individuals found in the stomach of a pelagic predator [52]. Little is currently known about habitat associations and needs for post-hatch and small juveniles of queen triggerfish. In spite of a lack of direct scientific documentation, many sources assume queen triggerfish individuals in these smallest life stages are pelagic and may associate with brown algae of the genus *Sargassum* [4,9,52], which form dynamic, floating systems in the western Atlantic that support myriad species of marine invertebrates and vertebrates [53–55]. The assumed association of queen triggerfish post-larvae and small juveniles with sargassum habitat is because several studies from the temperate waters of the western Atlantic documented high abundances of juvenile gray triggerfish *Balistes capriscus* associated with sargassum mats [56–58]. However, no extensive reports exist in the peer-reviewed literature on fishes associated with sargassum in tropical waters in the Caribbean. Future efforts to investigate the habitat use of sargassum by post-larvae and juveniles of fisheries species in the U.S. Caribbean could provide a better understanding of recruitment trends for a variety of species, possibly including queen triggerfish.

A lack of information in the published literature also exists concerning the benthic habitat of post-settlement queen triggerfish juveniles (50+ mm FL). The one study to note detailed benthic habitat characteristics for post-settlement juveniles was spatially limited to the coast of Panama [52] where juveniles occurred in shallow back reef areas (1–3 m depths) characterized by a mosaic of sand, sparse seagrass, scattered rock/rubble, and coral pavement interspersed with crevices that triggerfish used for refuge. During sampling efforts in the current study, we observed small triggerfish (50–80 mm FL) in the shallow (<5 m) nearshore waters of St. Croix (Figure 6) associated with similar habitats as described for Panama. We also observed and collected a few small queen triggerfish (60–80 mm FL) in PR from shallow seagrass edge sites and rock/rubble pavement areas interspersed with benthic macroalgae. These sites were at shallow depths not typically frequented by commercial fishers, and small fish at these sites were mainly caught via gear not typically utilized in commercial fishing.

Figure 6. Image of a small (65 mm FL) queen triggerfish from St. Croix observed in a nearshore, shallow water habitat characterized by a mosaic of sand, sparse seagrass, scattered rock/rubble, and pavement with an assortment of crevices. Photo by V Shervette.

4.2. Reproductive Biology

Queen triggerfish is a gonochoristic, reef-associated species. The females' reproductive strategy includes batch spawning, group synchronous oocyte development, and indeterminate fecundity [4]. The combination of these three female reproductive characteristics enables the release of eggs over an extended spawning season, increasing the survival probability of offspring [59]. Results from our study indicated that females could spawn up to 84 times within their protracted annual nine-month spawning season, and the spawning frequency of females increased with size and age (Table 7). It is common that in multi-batch, indeterminate spawners, larger and older female fish produce more batches over a longer period of time [60–63] and spawn more frequently than smaller, younger females [60,64].

The attributes of group synchronous oocyte development, batch spawning, and indeterminate fecundity combined with benthic nesting behaviors in triggerfishes may enable a high reproductive output for many triggerfish species, including queen triggerfish. In addition to queen triggerfish, reproductive histological assessments have been reported for gray triggerfish [19,65], black triggerfish *Melichthys niger* [66], and red-toothed triggerfish *Odonus niger* [67], with all three species also exhibiting group synchronous oocyte development, indeterminate fecundity, and batch spawning. All triggerfish species for which spawning behavior has been reported in the scientific literature are benthic nesters, and females can spawn multiple batches of eggs within a spawning season [4,19,41,42,66,67]. In general, maternal care of offspring is rare among coral reef fishes with external fertilization [68,69] but is common in triggerfishes during the benthic nesting period, in which females care for their brood of fertilized eggs by guarding them against potential egg predators and caring for them via blowing on them and fanning them until just before the eggs hatch and larvae swim up to a planktonic life phase [38,39,41–43]. Kuwamura [41] observed spawning activities of Picasso triggerfish *Rhinecanthus aculeatus* and noted that the spawning season lasted from July to September, and within that spawning season, spawning occurred during the periods of 1–2 days before the full and new moons to 4–6 days after. Within each ~one-week spawning period, females within a harem spawned 0–3 times [41]. The spawning interval of females that spawned more than once in a spawning period ranged from 1 to 6 days. Group synchronous oocyte development, indeterminate fecundity, and batch spawning enable female triggerfish to lay multiple batches within a spawning period and throughout their spawning season. Maternal care of fertilized eggs until hatching ensures that a high proportion of larvae within each batch successfully hatch and move on in search of ideal conditions for survival and growth.

Reproductive timing in many fish species strongly correlates to cyclic, reoccurring conditions that favor offspring survival [70]. This seems to be the case for gray triggerfish, a closely related congener of queen triggerfish, which co-occurs throughout much of the queen triggerfish geographic range [2]. In the waters of the western Atlantic, sargassum accumulates into massive mats described as predominant surface features in the continental shelf waters of the northern GOM from May to September [71] and in the waters of the SEUS from April to November [72], which overlaps with gray triggerfish spawning seasons in the two regions [19,65]. Pelagic sargassum underpins a diverse ecosystem [53–55] in which epiphytic cyanobacteria contribute to overall productivity [73], and a succession of bacteria, hydroids, and bryozoans colonize [74,75], which serve as food sources for a diverse assortment of invertebrates. The physical and organismal complexity of sargassum systems provide a structurally diverse pelagic habitat that serves as a refuge and food source for the juvenile pelagic stages of many reef-associated fish [56,58,76–78], including Caribbean, GOM, and SEUS gray triggerfish [56,58,79]. Further evidence of sargassum systems serving as important nursery habitats for post-larval and juvenile gray triggerfish has been provided from diet studies on these life stages. Rooker et al. [80] reported that juvenile gray triggerfish rely on sargassum and associated invertebrate fauna for nutrients. Ballard and Rakocinski [81] noted that gray triggerfish individuals 9–75 mm SL consumed sargassum epifauna, zooplankton, organic material, and copepods. Stachowiak [82] examined the stomach contents of gray triggerfish ranging in size from 14 to 112 mm SL and concluded that the species may have an obligate association with sargassum as juveniles.

Queen triggerfish adults co-occur in SEUS waters and parts of the northern GOM; however, post-larval and juvenile queen triggerfish have not been observed in association with sargassum in either region. This could be an artifact of low adult abundances of queen triggerfish in the SEUS and GOM regions, which occur at the northern edge of the species' geographic range. The reproductive season of queen triggerfish that occur in these northern regions is currently unknown, so it is unclear if queen triggerfish spawn during the time period that juveniles could use the sargassum habitat. In the U.S. Caribbean, the protracted queen triggerfish spawning season could be a result of less predictable cyclic conditions for larval and juvenile life stages. The 9-month spawning season may indicate the evolution of a bet-hedging strategy that ensures at least some offspring will encounter favorable conditions for survival and growth in the early life stages [62,83].

4.3. Observations Related to Fisheries Management

A localized decline in the abundance of queen triggerfish was recently reported for the Bahamas and Turks and Caicos [84], while abundance has increased throughout the waters of the U.S. Caribbean [46] despite queen triggerfish ranking as one of the top 10 fisheries species in the region. Certain characteristics of the U.S. Caribbean fishery for queen triggerfish may partially explain this discrepancy in abundance trends between the two regions. Commercial fishers in the U.S. Caribbean mostly target plate-size fish, defined in the current study as 235–405 mm FL (Table 5), which acts as a self-imposed slot size range limit and indicates that this fishery is not removing individuals in the smallest and largest size groups at a high rate. The process of overfishing occurs when a fishery stock is depleted faster than it can replenish itself and is characterized in part by a diminishment of the ability of a fish stock to reproduce [85,86]. Froese [85] noted that the assessment of potential overfishing related to this includes (1) evaluating the percentage of mature individuals in the catch with an ultimate target of ensuring that 100% of individuals landed have spawned at least once and (2) evaluating the proportion of the catch that is "mega-spawners" with the goal of minimizing the number of mega-spawners landed. The percentage of immature queen triggerfish from the FD random samples in the current study was close to 0 (0.8%; Table 9), indicating that the vast majority of queen triggerfish landed in the commercial fishery were sexually mature. Queen triggerfish in the largest size group (401+ mm FL) and oldest age group (16+ y) that spawned annually with the greatest frequency (Table 7) were mostly absent from the FD random samples in our study, indicating that the targeting of plate-size fish may exclude a large proportion of mega-spawning females. Further evidence of a lack of overfishing for the U.S. Caribbean queen triggerfish stock comes from underwater visual surveys from the region. Grove et al. (2022) [46] documented annual increases in the mean density of queen triggerfish in the waters of the three management platforms from 2013 to 2019 (the most recent year observations were reported).

Commercial fishing of queen triggerfish in the U.S. Caribbean currently appears to be sustainable, but monitoring queen triggerfish population health in the region should continue. The impacts of increasing water temperature trends in the region and stony coral disease have resulted in major coral die-offs [87], which, in turn, could impact the habitat and prey resources of fisheries species, including queen triggerfish. Therefore, continued monitoring of queen triggerfish in the region will also aid in detecting potential impacts of environmental changes on the queen triggerfish population in the U.S. Caribbean.

5. Conclusions

Queen triggerfish is an important reef-associated species for commercial fisheries in the U.S. Caribbean. This study provides the first comprehensive documentation of age, growth, size/age at sexual maturity, reproductive seasonality, and reproductive output for a *Balistes* species in the Caribbean. Our work confirmed that queen triggerfish is a sexually dimorphic gonochoristic species, and we documented that it is characterized by a moderately young age at sexual maturity. Trends in regional patterns of maximum size and age attained by queen triggerfish appear to correlate with latitude; fish in the U.S. Caribbean attained a smaller maximum size and younger maximum age compared to fish from the higher latitude waters of North Carolina. Queen triggerfish is a nesting benthic spawner, invests energy in brood care of fertilized eggs, and exhibits group-synchronous oogenesis and indeterminate fecundity. We estimated that female queen triggerfish can spawn up to 84 times a year. These reproductive characteristics combined with a protracted spawning season of nine months in the U.S. Caribbean region suggest the evolution of a bet-hedging reproductive strategy that ensures at least some offspring will encounter favorable conditions for survival and growth in the early life stages. We documented that commercial fishers in the U.S. Caribbean mainly target "plate-size" individuals, which appears to act as a self-imposed slot length range limit and results in the fishery not removing individuals in the smallest and largest size groups at high rates. The percentage of immature fish from fisheries-dependent sources was close to 0 (0.8%). Commercial fishing for queen triggerfish in the region currently appears to be sustainable, but monitoring of the population should continue.

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