

Age, Growth, and Reproduction of the Queen Triggerfish, *Balistes vetula*, from the
U.S. Virgin Islands

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Age, Growth, and Reproduction of the Queen Triggerfish, *Balistes vetula*, from the
U.S. Virgin Islands

by
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CONTRIBUTION OF AUTHORS

Dr. Richard Nemeth initiated contact with St. Thomas commercial fishers, helped develop thesis objectives and structure, and provided constructive feedback throughout every step of the project.

Dr. Virginia Shervette served as Principal Investigator and secured funding for this project. She also designed the sampling, provided training in sample collection and processing, assisted in processing over 33% of the triggerfish samples, oversaw dorsal spine and histology analysis (which included reading all spine and gonad sample slides as first reader), performed data analysis, and offered invaluable mentoring in conducting life history research.

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All authors contributed to sample and data collection.

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Chapter 1: Introduction

Beginning in the 1960s, commercial marine fisheries in the tropics around the world started expanding at an accelerated rate due to the advent of new gear and fishing technologies (Pauly 1979). The increases in commercial fisheries led to a subsequent increase in fishing pressure by artisanal and local level fishers in nearshore, coastal areas (Pauly 1979). Dependence on fish as a food source is usually higher in coastal than in inland areas and roughly 20% of the world's population derives at least 20% of its protein from fish, while some small islands depend almost exclusively on coastal fishers for their protein (WHO 2016). Local fishers concentrate fishing efforts nearshore and tend to catch smaller-sized individuals, which have subsequently become more desirable products than larger individuals because they fit on a dinner plate. This “plate-fish market” is common in the United States Virgin Islands (USVI) and other islands in the Caribbean and applies to several reef species, such as red hind *Epinephelus guttatus*, yellowtail snapper *Ocyurus chrysurus* and queen triggerfish *Balistes vetula*.

Queen triggerfish, *Balistes vetula*, is a reef fish species that occurs throughout the western Atlantic Ocean, ranging from Massachusetts (Carpenter 2002) to Brazil (Albuquerque et al. 2011). Adults of this species are found on coral reef habitats, sandy, and grassy areas (Carpenter 2002), and on artificial reefs (Randall 1962). They range in depth from 6-100 meters (Aiken 1975). This species is known to be diurnal and is often seen either solitary or in small groups (Randall 1968), with the exception of spawning aggregations. Adults feed opportunistically by foraging for a variety of invertebrates (and occasionally vertebrates) along the reef (Randall 1967, Menezes 1979, Reinthal et al. 1984, von Schiller and Garcia 2000). Queen triggerfish in the Caribbean feed on a variety of echinoderms, including *Diadema antillarum*, mollusks, crustaceans, polychaetes, and fishes (Randall 1967). This suggests that queen triggerfish are able to capture a diverse set of prey from a wide variety of habitats, enabling them to adapt to shifts in local food webs.

The queen triggerfish is currently considered a data-deficient species due to the lack of species-specific data, especially in the Caribbean (Bryan 2012). Stocks have only been assessed through means of indirect evidence such as analysis of collected specimens' mean size (Albuquerque et al. 2011) and annual catch reports from commercial fishers (Bryan 2012). The IUCN Red List currently lists the queen triggerfish status as “Near Threatened”, as it nearly

meets the 30% reduction threshold for the “Vulnerable” category (Liu et al. 2015). This is a change from the previous IUCN assessment in 1996 that placed this species in the “Vulnerable” category, which meant that a population reduction of at least 20% was expected within the following ten years (Roberts 1996). Based on the 2015 assessment, 20 years later, this suggests that a greater reduction was seen than what was expected after the 1996 assessment.

The queen triggerfish has slow growth, can reach large sizes, and is relatively long-lived (Albuquerque et al. 2011); however, information on the Caribbean populations is limited regarding peak spawning season, spawning season duration, and size- and age-at-maturity. Based on the limited information available, *B. vetula* may be a K-selected species, which are more vulnerable to fishing pressure than r-selected species (Fromentin and Fonteneau 2001). However, to better understand how fishing pressure could affect queen triggerfish populations, more information is needed about basic life history so that this species can be effectively managed as part of the Caribbean’s tropical fisheries. Specifically, age and growth rate are two of the most influential life history characteristics controlling the productivity of fish populations (Campana and Thorrold 2001).

1.1 Size, Age, and Growth

Species-specific, fishery-dependent and –independent data are limited for queen triggerfish, which means most assessments are based on indirect methods such as length-based analysis. In order to carry out these length-based population analyses, data from the U.S. Caribbean Trip Interview Program (TIP) has been summarized by island and gear type. Between 1983 and 2011, lengths were recorded from 25,073 *B. vetula* collected by a variety of commercial gear types in Puerto Rico, St. Thomas, St. John, and St. Croix (Bryan 2012). The fork lengths were variable over time for the USVI, particularly in St. Thomas/St. John. Due to an incomplete data set, it is unclear if the variability is representative of each islands’ mean size through time or if it is due to incomplete time series. The annual mean length and length frequencies from St. Croix appear to be smaller than St. Thomas/St. John for most of the time series with the exception of 1983 (Figure 1). However, from 1985-1986 and 1993-1994, St. Croix queen triggerfish mean size was larger than queen triggerfish in Puerto Rico. We also see sharp declines and increases in size in the regional population in certain years, such as 1999-2000, followed by an increase a few years later in 2001-2003 (Figure 1). The reason for these

repeated declines and subsequent increases in mean size could be due to recruitment pulses, or an influx of new cohorts into the fished population, which could bring the mean size down. However, the exact reason for those peaks is unclear. This suggests that the length frequencies of queen triggerfish across the U.S. Caribbean have differed among the islands since the 1980s. It also shows that length-based population assessments are still limited due to the data gaps from multiple years in the USVI. Consistent, long-term data collection is required to understand a fishery's status and how it has changed through time.

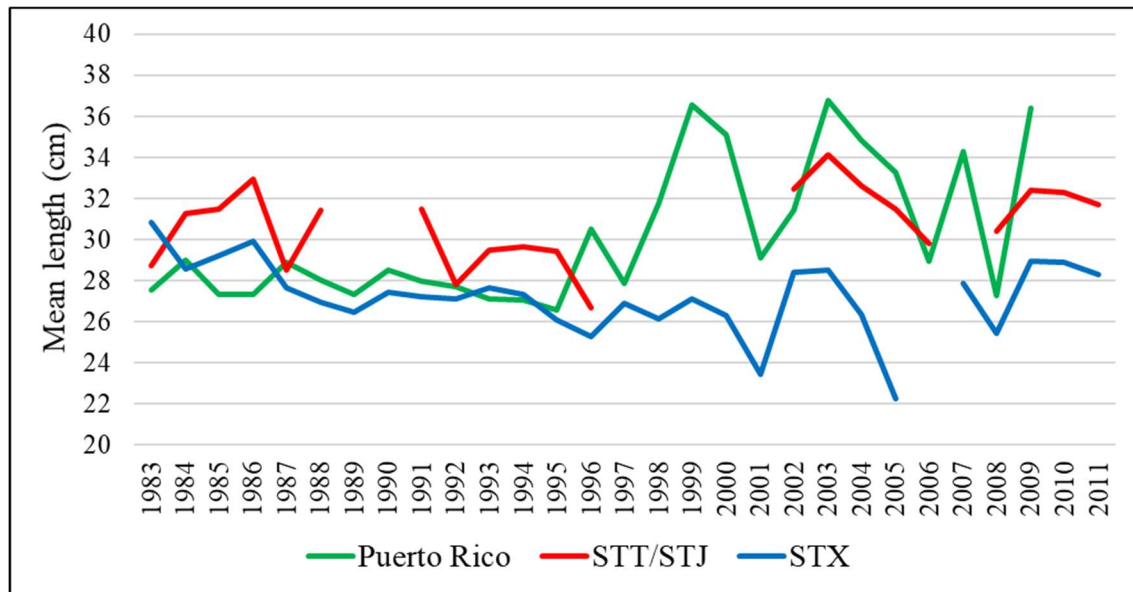


Figure 1. Mean length frequency data for Puerto Rico, St. Thomas/St. John, and St. Croix pot and trap fisheries from 1983-2011. Breaks in the lines represent data gaps in the time series for an island. Data was adapted from Bryan 2012.

Growth and population information on *B. vetula* is also lacking. Out of 12 studies that examined *B. vetula* lengths, only two estimated and reported the age of individual queen triggerfish. The maximum age reported for this species is 14 years (Albuquerque et al. 2011) while another study reported a maximum age of 7 years (Manooch and Drennon 1986). The maximum reported length for *B. vetula* is 572 mm fork length and was observed in the USVI (Randall 1968). The average growth rate for the USVI, determined from a study of 23 tagged and recaptured fish, was 4.4 mm per month and ranged up to 6.8 mm per month (Randall 1962). In addition to tag and recapture studies, growth rates are determined by age and length data from a representative sample of a population or fishery, encompassing all ages and size classes.

However, fish growth rates differ from location to location, due to environmental conditions (Pauly 1979) as well as differences in sampling of each study (Allman et al. 2017).

1.2 Reproduction

Balistes vetula is a gonochoristic species, having two distinct sexes, and individuals reproduce via external fertilization (Aiken 1975). The spawning behavior of queen triggerfish and other *Balistes* species is relatively unique for a large-bodied reef fish. Triggerfish species produce large numbers of small demersal eggs followed by a short period of biparental care (Lobel & Johannes 1980, Gladstone 1994). In the USVI, spawning behaviors of queen triggerfish have been observed in St. Croix (Jonathan Brown, personal communication). These observations occurred in January and February of 2014 and 2015 at depths of 40-50 m. Queen triggerfish created nests that were small depressions composed of a mixture of rubble and sand, where the female laid beads of eggs within the depression resembling the size and shape of a doughnut. Female queen triggerfish were observed hovering over the nest and undulating their ventral and anal fins after depositing the eggs, while males were swimming in the water column from 24-36 m, appearing to patrol or guard several nests (Jonathan Brown, personal communication). Males fertilized the eggs once laid and chased away other individuals within their territory of nests (Jonathan Brown, personal communication). These spawning behaviors are similar to what has been described for other triggerfish species. The yellowmargin triggerfish *Psuedobalistes flavimarginatus* in the Pacific also exhibit a lek-like spawning system of male established territories with multiple females and biparental egg care (Gladstone 1994). Gray triggerfish *Balistes capriscus* also exhibit very similar spawning behaviors in the Atlantic, including male territory establishment, demersal nest building, female nest inspection, and biparental care (Simmons 2008). Biparental care is normally associated with monogamous mating systems (Gladstone 1994); however, triggerfish species seem to be exceptions as their mating systems are polygamous. While many of these reproductive behaviors appear similar across species within the family Balistidae, no published literature specifically on the spawning of queen triggerfish exists.

One previous study has reported on aspects of reproduction in queen triggerfish (Aiken 1975). That study compared macroscopic gonadal “stage” to length data but did not verify gonad condition through histology. Aiken (1975) found that females were ripe in all months except

April and June and the peak of spawning was January-February and August-October. Most of the samples were small maturing individuals but males attained a larger maximum size than females. No published study exists to-date that combines age, growth, and reproductive biology of queen triggerfish.

1.3 USVI Fishery

Traditionally, *B. vetula* are less targeted by fisheries off the southeastern US, but are more abundant in Caribbean fisheries (Manooch and Drennon 1987). Tropical fisheries of the Caribbean region are considered small-scale, artisanal operations that target a variety of reef fishes (Garrison et al. 1998, Kojis and Quinn 2006, Ramdeen et al. 2015). Artisanal, multi-species fisheries are often multi-gear fisheries, to achieve the desired mix of species (Munro and Smith 1984). Trap fishing is one of the oldest fishing methods and is widely used in the Caribbean, representing a large part of fishing effort and landings (Stevenson and Stuart 1980, Munro 1983, Gobert 1998, Garrison et al. 2004, Hawkins et al. 2007). Other common fishing techniques in the Caribbean region include linefishing, the second most practiced method of reef fish exploitation, and spearfishing, which has become an important economic activity (Munro 1983).

The USVI reef fish fisheries are an example of a small-scale, multi-gear, multi-species enterprise. Caribbean fishers operate from small open vessels, between 4-6m in length, use relatively inexpensive gear, and sell their catches directly to consumers or local markets (Munro and Smith 1984, Ramdeen et al. 2015). As of 2017, St. Thomas/St. John had 119 registered fishers while St. Croix had 141 registered commercial fishers (Kojis et al. 2017). However, not all registered fishers actively fish (Kojis and Quinn 2011). Each island in the territory has a long history of fishing (Kojis and Quinn 2006). Historically, trap fishing was the primary gear of the USVI, but as economic conditions and technology improved, fishers expanded their fishing ranges and diversified into gear types such as spearfishing on SCUBA, netting, and line fishing (Kojis and Quinn 2006). While traps are still the principle fishing gear in St. Thomas/St. John, they have become less important in St. Croix. This is due to two reasons: (1) even though economic conditions and technology improved, the proximity of the shelf edge to the coast of St. Croix led to an increase in linefishing for deeper water pelagic species and snapper species, instead of increasing the number of traps and (2) the shallow, insular shelf made deployed traps

susceptible to hurricane damage. When Hurricane Hugo hit in 1989, many fishers chose not to replace lost or damaged traps and switched to other gears such as line fishing, netting, and spearfishing on SCUBA (Kojis and Quinn 2006). Trap fishers still operate in St. Croix, although not as many as historically (Bryan 2015). For these reasons, St. Croix's fisheries have more gear types while St. Thomas/St. John primarily use lobster and fish traps to catch multiple reef fish species.

In the USVI queen triggerfish, nicknamed Ol'wife, comprise a considerable portion of reef fish landings taken primarily by traps (Bryan 2015). Parrotfish (23%), snappers (14%), triggerfish (10%), groupers (9%), surgeonfish (8%), and grunts (8%) are the most common commercial fisheries species, with lobsters (8%) also comprising an important part (Ramdeen et al. 2015). Triggerfish landings category has traditionally included filefish and triggerfish, making it difficult to tease apart landings of individual species before 2011 (McCarthy 2012). In 1985, *B. vetula* made up about 22% by weight of the total trap catch and approximately 10-15% of the total landing (Manooch and Drennon 1987). McCarthy (2012) reported triggerfish annual landings from 2000-2011 in St. Thomas/St. John were approximately 31,750-45,360 kg/year and in St. Croix approximately 9,980-17,237 kg/year.

In order to protect fish species from the effects of overfishing, the U.S. Fishery Management Councils must set annual catch limits (ACLs), as well as size, gear, and seasonality restrictions. These management decisions are based on an estimate of overfishing limits, which themselves stem from estimates of maximum sustainable yield (MSY). However, a severe lack of data exists regarding the basic life history of queen triggerfish in the U.S. Caribbean. Without a solid understanding of life history, including regional differences in growth and reproduction, MSY cannot be accurately estimated based on catch and effort reported by the local fisheries. Fish population stock assessments rely heavily on scientifically-derived estimates of age-at-sexual maturity, size-at-sexual maturity, and spawning stock biomass (Vitale et al. 2009). Since queen triggerfish is a popular, targeted food fish in the USVI, research is needed to fill in data gaps so that fisheries resource managers can better determine the status and manage the resource.

To address the critical data gaps identified for queen triggerfish in the USVI, the current study utilized direct techniques of assessing age, growth, and reproduction of queen triggerfish in the U.S. Virgin Islands of St. Thomas and St. Croix. Our objectives were to determine the age

and size structure, growth, sex ratio, size- and age-at-maturity, and spawning seasonality of *B. vetula* from fisheries-dependent samples. We also compared these life history traits between St. Thomas and St. Croix in order to understand differences in populations between the two island shelves. This information was collected in an effort to provide important life history information to fisheries managers so that they can assess the queen triggerfish stocks and develop island specific management strategies.

Chapter 2: Methods

2.1 Study Location

The United States Virgin Islands (USVI) is located in the northeastern Caribbean between the Caribbean Sea and the North Atlantic Ocean, approximately 64 km east of Puerto Rico. The territory consists of three main islands: St. Croix, St. Thomas, and St. John with a total estimated human population of 103,574 (CIA 2016). St. Croix is the largest of the three islands, with an area of approximately 220 km² (Stoffle et al. 2009), and a flatter terrain than the second largest island St. Thomas, which is 80 km² and more mountainous (Platenberg and Boulon 2006). St. Thomas and St. John are located on the Puerto Rican shelf approximately 64 km north of St. Croix, which is a separate geographic feature on a small, insular platform. The islands resemble table tops, due to their positions atop platforms. Just offshore, these platforms drop steeply down to around 20 m, and then slope gradually to around 100 m on the Atlantic side and 40 m on the Caribbean side. Caribbean waters of the U.S. are characterized by islands separated by deep water. Depth of water between the northern USVI (St. Thomas/St. John) and St. Croix is nearly 5 km (Figure 2). The extreme depths of the waters separating the northern islands from St. Croix likely act as barriers for the dispersal of post-larval reef fish (CFMC 1985). The shallow shelf extending off St. Croix is relatively small and drops off to deeper water typically less than 5 km from shore, whereas off St. Thomas/St. John the shelf is wide and extends about 11-13 km from the coast (Kojis and Quinn 2006).

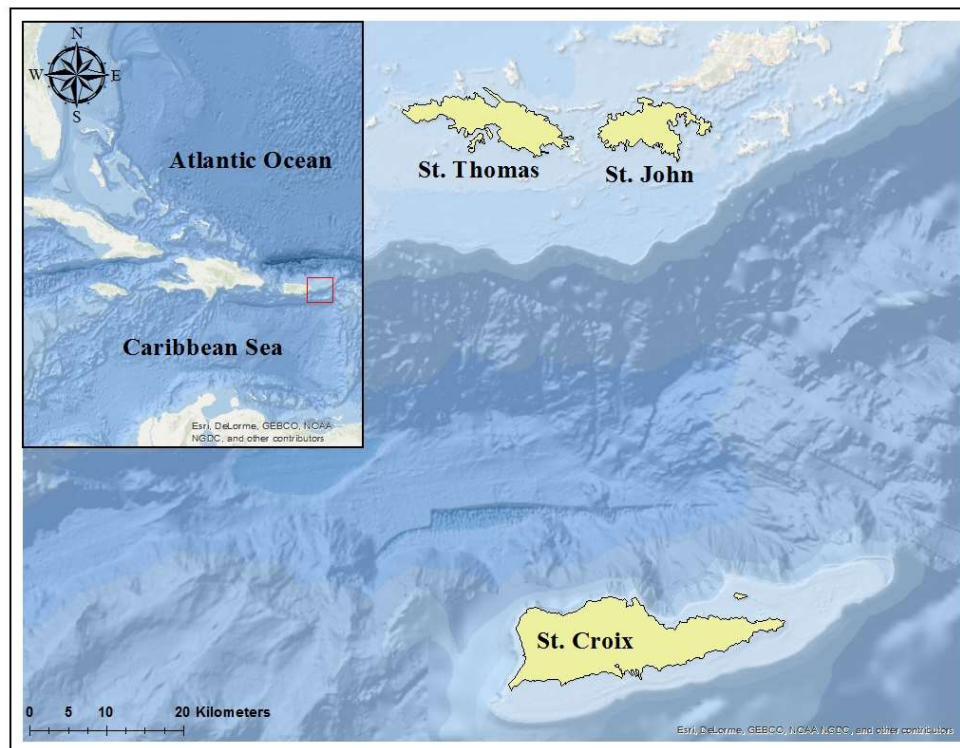


Figure 2. Map of the Caribbean, showing the location of the three U.S. Virgin Islands. Contour lines defining shelf edges represent 100 m depths.

In St. Thomas, fishers set their traps in depths between 20 and 40 m. Sets were pulled one to two times a week. Trap openings ranged from 25.4-38.1 cm in order to target plate size reef fishes. In St. Croix, spear fishers did three or four dives a day in depths ranging from 3 to 20 m. Fishing areas in the Virgin Islands are mapped into 4.02 km by 4.02 km quadrants that specify zones where fishers report their catches.

2.2 Sample Collection and Processing

Monthly fisheries-dependent queen triggerfish samples were purchased from St. Thomas and St. Croix fishers between October 2015 and August 2017 to be processed for analyses of age and reproduction. During week-long sampling events in February, July, November 2016, and May 2017, all queen triggerfish (or a randomly selected portion of the catch) from each fisher were purchased directly from the boat as the fishers returned from fishing. In other months, whenever a fisher had more than 10 queen triggerfish in the catch, we would randomly select 20 to 30 individuals that spanned the range of sizes in the available catch. If a fisher had 10 or fewer individuals, all triggerfish from the catch were purchased.

For each fish sample, we measured standard length (SL), fork length (FL), and total length (taken from the upper lobe unless damaged; TL) to the nearest mm and total weight to the nearest g. The first dorsal spine was removed, cleaned of excess tissue, and then stored dry until further processing. Gonads were removed and weighed whole to the nearest 0.01 g, and then a selected portion was preserved for later histological processing in order to determine sex and reproductive phase.

To determine whether the population size structure differed between males and females and between islands, we used separate Kolmogorov-Smirnov (K-S) tests to evaluate the following null hypotheses: 1) overall size frequency distributions did not differ between males and females; 2) size frequency distributions did not differ between males and females from St. Thomas; 3) size frequency distributions did not differ between males and females from St. Croix; 4) size frequency distributions of males did not differ between St. Thomas and St. Croix; and 5) size frequency distributions of females did not differ between St. Thomas and St. Croix. To determine if mean size significantly differed between sexes and islands, we used a two-factor ANOVA with size (FL) as the dependent factor and with island and sex as the independent factors.

Statistical analyses were conducted in Excel using XLSTAT, SPSS, and in RStudio. Results were considered significant at p-values less than 0.05. When assumptions for statistical test were not met, the data were log transformed. All maps were made in ArcMap version 10.4.1.

2.3 Age and Growth

Ages for queen triggerfish samples collected from St. Thomas were estimated using the first dorsal spine. This is currently the accepted structure for estimating age in queen triggerfish (Manooch and Drennon 1987, Albuquerque et al. 2011) Dorsal spines were processed following the methods from Kelly-Stormer et al. (2017). A low speed wafering saw with a diamond edged-blade was used to cut 2-3 transverse sections (0.3-0.5 mm thick) immediately distal to the condyle groove. Spine sections were mounted on glass slides with a clear mounting medium and viewed under a dissecting microscope at 10-20x magnification using transmitted light. Increment counts were determined by identifying and enumerating the pattern of faster-growing (opaque) and slower-growing (translucent) zones in the spine sections. For this study, increment counts

were considered age estimates. However, direct age validation of the first dorsal spine has not been done for this species. At least one reader estimated age for each fish sample by counting the number of translucent zones in a spine section with no knowledge of fish size or date of capture. A second reader independently estimated age for 28% of the samples. Spine sections for which reader disagreement occurred were reevaluated simultaneously by both readers, and a consensus count was recorded as the final age estimate in whole years (y).

Triggerfish dorsal spines can be difficult to read and other studies have reported low between-reader precision for age estimates from dorsal spine sections (Kelly-Stormer et al. 2017, Burton et al. 2015). Therefore, we assessed reader precision using the same methods so that precision estimates could be compared among studies. Between-reader precision was estimated by calculating percent agreement between readers for perfect agreement and for agreement within +/- 1 yr. We also computed average percent error (APE) for age estimates between readers (Beamish and Fournier 1981).

Together, a translucent, or slow-growing, zone and an opaque, or fast-growing, zone constitute one year of growth. The final zone on the spine section margins, or edge of the spine, was evaluated as either being a translucent zone or an opaque zone (Figure 3). Using age-3 through age-6 fish collected from St. Thomas, we estimated the timing of increment formation by examining the monthly proportion of spines with translucent zones at the spine edge, similar to other triggerfish age studies (Burton et al. 2015, Kelly-Stormer et al. 2017) This allowed for a reasonable approximation of increment periodicity, if not a full validation.

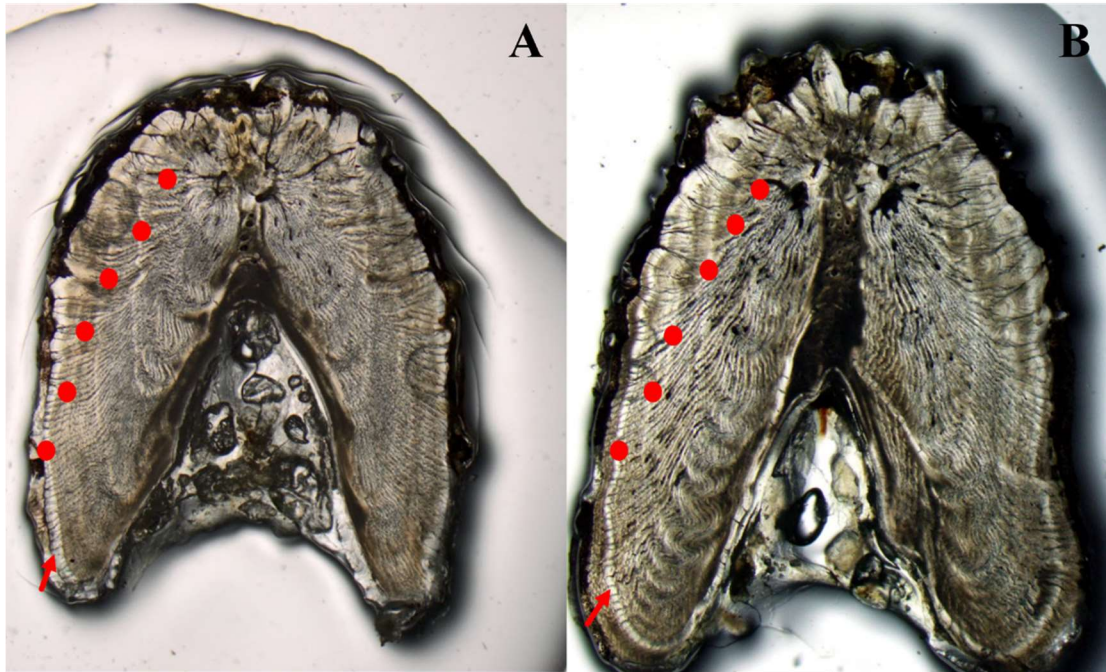


Figure 3. Two examples of age-6 queen triggerfish fish dorsal spine sections. Each increment is shown by the red dots and the red arrows represent the final translucent zone, which is either along the edge (A) or inside the edge (B) of the spine.

The age frequency distributions between males and females for St. Thomas was compared using a K-S test to test the null hypothesis that age structure did not differ between the sexes. A Student's t-test was also used to determine if mean age significantly differed between males and females.

To evaluate growth, the observed individual lengths at age were fitted to the von Bertalanffy growth equations as follows: $L_t = L_\infty (1 - e^{-k(t-t_0)})$; where L_t is the length (mm FL) at age t , L_∞ is the asymptotic length, k is the growth rate, and t_0 is a theoretical age at which the length is presumed equal to 0 (von Bertalanffy 1938). This model was applied to males and females separately. For comparison with other studies that did not determine the sex of the queen triggerfish samples (Manooch and Drennon 1987) or combined data across sexes to calculate the growth model (Albuquerque et al. 2011), we calculated an overall growth model for the combined sex data. In order to establish more biologically realistic growth models that include size at age-0, we set $L_0 = 49$ mm, which was the minimum size at age-0 queen triggerfish reported from a post-settlement recruitment event (Robertson 1988). Lastly, an analysis of residual sums of squares was used to determine if a significant difference existed between the growth models for males and females.

2.4 Reproduction

Gonads were removed from each fish. A section of the posterior portion of each gonad (when possible, the whole gonad) was preserved in 11% seawater formalin for 1-2 weeks and then transferred to a 50% solution of isopropanol. Gonad samples were processed using standard histological procedures (Harris and McGovern 1997, Harris et al. 2007). The gonad tissue samples were vacuum infiltrated and then blocked in paraffin wax. The tissue blocks were then sectioned three times (each ~7 μ m thick) using a rotary microtome. Each set of gonad tissue sections was mounted on a glass slide, stained with double-strength Gill hematoxylin, counter-stained with eosin-y, then cover-slipped.

Stained gonad sections were viewed under a compound microscope to determine the individual's sex and its reproductive phase, which was assessed according to a modified version of the histological criteria established for a similar triggerfish species (Table 1). Reproductive phase for each gonad samples was determined independently by two readers; samples for which reader disagreement occurred were re-evaluated simultaneously by the readers and a consensus phase was recorded.

Table 1. Histological criteria for assessing queen triggerfish reproductive phase, modified from Kelly-Stormer et al. (2017).

Reproductive Phase	Male	Female
Immature	Small transverse section compared to regenerating male; little or no spermatocyte development.	Primary growth oocytes only; no evidence of atresia. In comparison with regenerating female, most primary growth oocytes <60 μm . Area of transverse section of ovary is smaller, lamellae lack muscle and connective tissue bundles and are not as elongate, germinal epithelium along margin of lamellae is thicker, ovarian wall is thinner.
Developing	Limited spermatogenesis in testes; elongation of lobules and some development of spermatozoa in testes, but no accumulation in lobules, efferent ducts, and spermatic ducts.	<u>Early</u> : Previtellogenic, with only primary growth and cortical alveolar oocytes. Cortical alveolar oocytes 140-200 μm in diameter. <u>Middle-Late</u> : Vitellogenic, most advanced oocytes in yolk-granule or yolk-globule stage. Oocytes 200-400 μm in diameter.
Spawning capable	<u>Early</u> : Spermatozoa evident in ducts; spermatogenesis amount in testes ranges from limited to extensive. Greater area of structural tissue in ducts compared to sinuses. <u>Middle (Storage)</u> : Spermatozoa storage within expanding ducts; >50% of sinuses' area densely packed with spermatozoa; amount of spermatogenesis in testes ranges from limited to extensive. <u>Late (Recent Spawn)</u> : large expanded ducts not as densely packed with spermatozoa. Area of sinuses greater than structural tissue. Empty lobules usually present towards center of testes.	Oocyte maturation in the most advanced oocytes: zona radiata becomes thin and oocytes are undergoing coalescence of yolk globules, germinal vesicle migration, germinal vesicle breakdown, hydration, or ovulation. Postovulatory follicle complexes sometimes present. Atresia of vitellogenic and/or hydrated oocytes may be present.
Regressing	Limited spermatogenesis in testes; some residual spermatozoa in shrunken ducts/lobules and sinuses. Overall number of ducts containing	More than 50% of vitellogenic oocytes with alpha- or beta-stage atresia.

spermatozoa small. Increase in connective tissue in testes, proliferating from center.

Regenerating Little or no spermatocyte development; empty ducts/lobules and sinuses. Large transverse section compared to immature male.

Primary growth oocytes only; traces of atresia. In comparison with immature female, most primary growth oocytes >60 um, area of transverse section of ovary is larger, lamellae have muscle and connective tissue bundles, lamellae are more elongate and convoluted, epithelium along margin of lamellae is thinner, ovarian wall is thicker.

Mature, phase unknown Mature, but inadequate quantity of tissue or postmortem histolysis prevent further assessment of reproductive phase.

Mature, but inadequate quantity of tissue or postmortem histolysis prevent further assessment of reproductive phase.

Spawning season in females was defined as extending from the first date to the latest date when late oocyte maturation was observed in a specimen. Females of unknown maturity were excluded from analysis. For males, tissue from the sperm duct was included in each gonad sample in addition to the testes in order to look at the amount of sperm storage, which informs the reproductive phase assessment.

Gonadosomatic index (GSI), which is an index of the gonad size relative to the fish's body size, was calculated for each mature female by the following equation: $(\text{whole gonad weight}/\text{whole fish weight}) * 100$. Mean values for GSI were calculated by month of collection for each island to examine trends in reproduction and peak spawning as related to the histology. Separate one-factor ANOVAs were used for each island to test the null hypothesis that no significant difference existed in monthly GSI (females). GSI values were log transformed to meet the assumptions of normality and Dunnett's T3 post-hoc comparisons were used to examine pairwise significant differences for GSI between months. The month with the significantly lowest GSI value was assumed to signal an end in peak spawning. Additionally, the percent of individuals assigned to each reproductive phase based on the month of collection were plotted separately for males and females to visually assess the spawning season duration.

Chi-square tests were used to determine if sex ratios of males to females differed between the two islands. Generalized linear models fitted to logistic curves were used to estimate the length at 50% maturity (L_{50}) for males and females from St. Thomas and St. Croix. We also used generalized linear models fitted to logistic curves to estimate the age at 50% maturity (A_{50}) for St. Thomas samples.

Chapter 3: Results

Between October 2015 and August 2017, a total of 617 queen triggerfish were purchased from commercial fishers in St. Thomas and 492 from commercial fishers in St. Croix (Table 2). Two individuals from St. Thomas and 5 from St. Croix were excluded from the size analysis since sex could not be determined histologically. Forty-four individuals from June and 39 from August in St. Croix were included in reproduction analysis to calculate GSI but were not included in the length and weight analysis. A hundred percent of St. Thomas queen triggerfish were caught by traps whereas in St. Croix, 14% (n=70) were caught in traps and 86% (n=422) were caught by spearfishing. Commercial fishers caught queen triggerfish samples from sites located around St. Thomas and St. Croix (Figure 4).

Table 2. Monthly sample sizes of queen triggerfish from each island.

Month	St. Thomas	St. Croix
January	53	29
February	53	38
March	49	52
April	47	56
May	73	39
June	30	58
July	79	76
August	46	39
September	29	27
October	44	33
November	35	45
December	79	0
Total	617	492

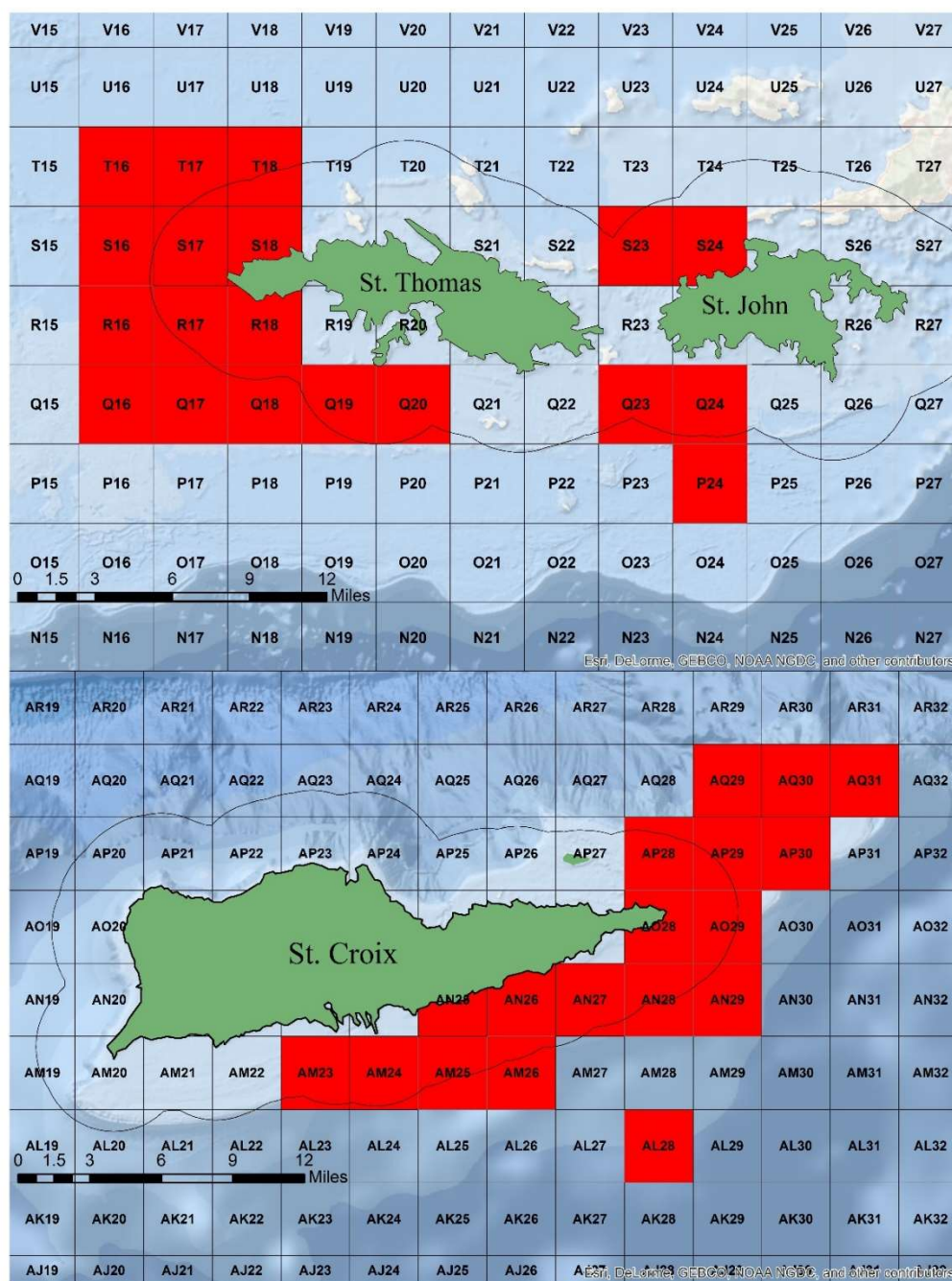


Figure 4. Locations of queen triggerfish samples from St. Thomas and St. Croix based on commercial fishing grids. The line around each island represents the 3 mile territorial boundary.

3.1 Size Distributions

Queen triggerfish from the commercial fishery were, on average, about 50 cm larger on St. Thomas ($343 \text{ mm} \pm 50 \text{ mm FL}$) than on St. Croix ($295 \text{ mm} \pm 40 \text{ mm FL}$) (Table 3). Across

the two islands mean fork length of males was about 20 mm larger than females; however, the maximum size of females exceeded the largest male on both islands (Table 3). Mean size differed significantly between islands and sexes (two-factor ANOVA, island: $F = 263.1$, $p < 0.001$; sex: $F = 69.3$, $p < 0.001$) but there was no significant interaction effect between the two factors ($p = 0.165$). A post-hoc Tukey test found significant differences between all four groups of queen triggerfish (Figure 5). Males were significantly larger on average than females in both St. Thomas ($p < 0.001$) and St. Croix ($p < 0.001$). The mean length of both sexes was significantly larger in St. Thomas than they were St. Croix.

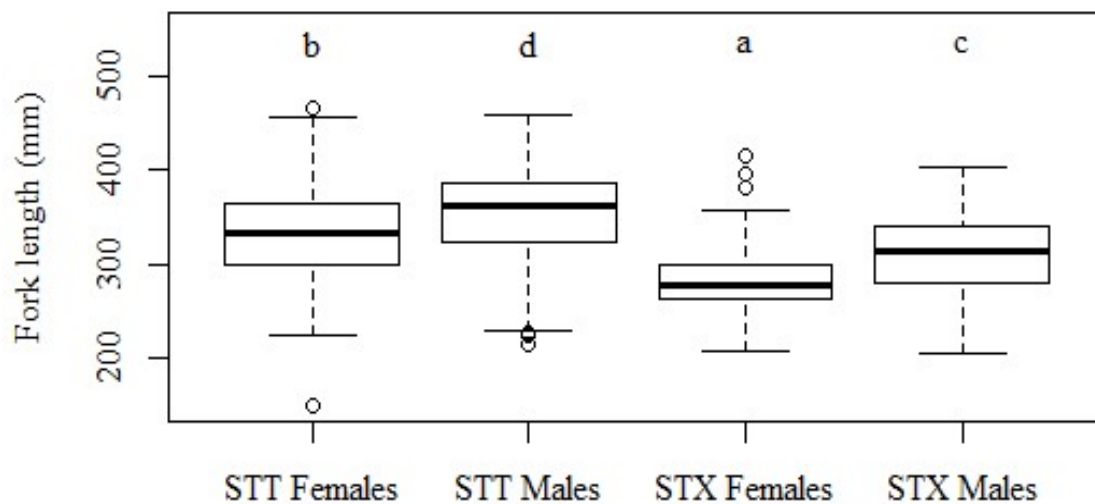


Figure 5. The fork length distributions of St. Thomas and St. Croix females and males. Letters represent significant differences.

The mean weight of queen triggerfish was $1,082 \text{ g} \pm 442 \text{ g}$ in St. Thomas and $699 \text{ g} \pm 275 \text{ g}$ in St. Croix (Table 3). Mean weight differed significantly between islands and sexes (two-factor ANOVA, island: $F = 231.0$, $p < 0.001$; sex: $F = 49.5$, $p < 0.001$) but there was no significant interaction effect between the two factors ($p = 0.334$). A post-hoc Tukey test showed that males weighed significantly more than females in both St. Thomas ($p < 0.001$) and St. Croix ($p < 0.001$). Furthermore, St. Thomas queen triggerfish weight was significantly greater by about 300 g than St. Croix queen triggerfish for both females and males. A positive relationship was seen between length and weight; as fork length increased so did weight (Figure 6).

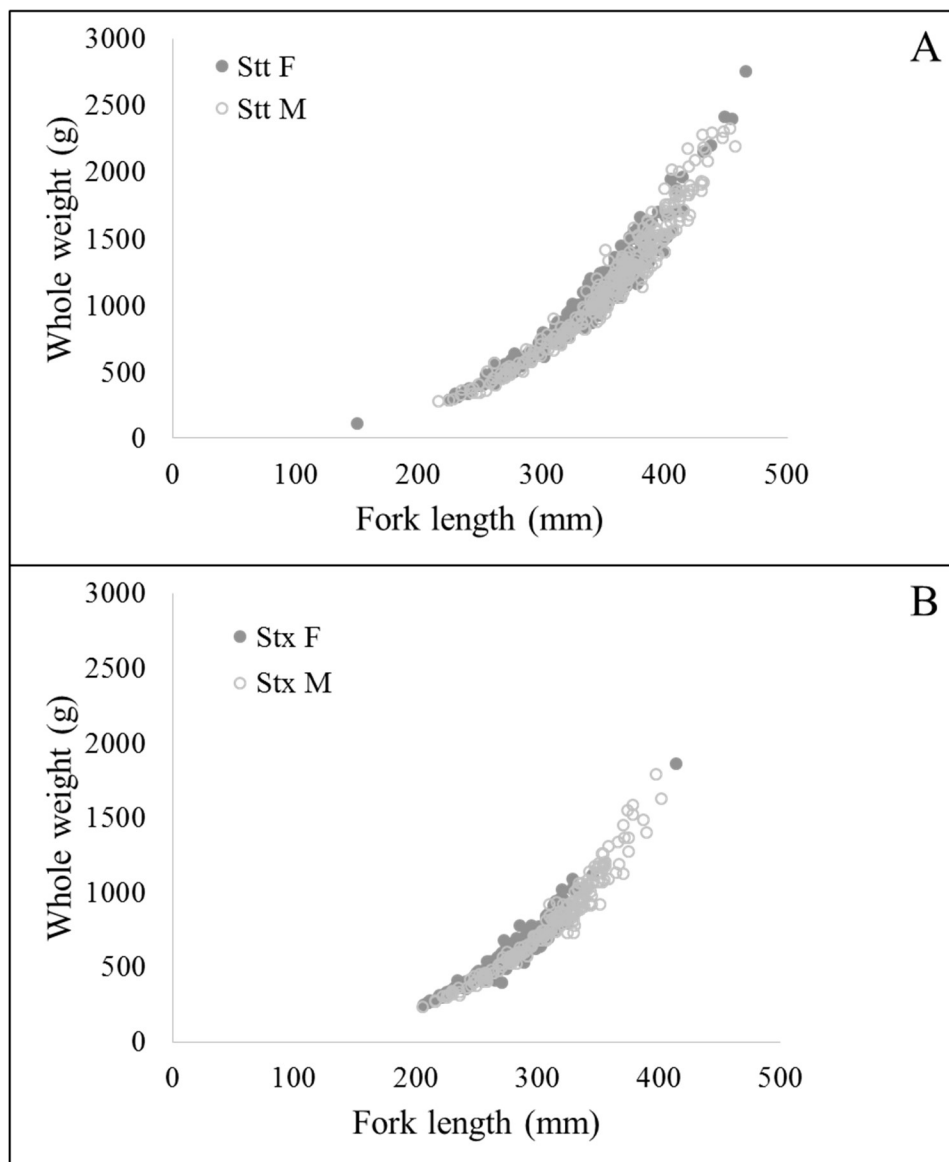


Figure 6. Scatter plots of whole weight vs. fork length of queen triggerfish in St. Thomas (A) and St. Croix (B).

Table 3. Summary statistics of queen triggerfish by island and sex. Two fish from STT and 5 fish from STX were excluded from analysis due to missing data.

	STT		STX	
	Males	Females	Males	Females
n	315	300	204	193
Mean FL (mm)	353	331	308	281
Min FL (mm)	216	150	206	207
Max FL (mm)	458	466	402	414
Mean Weight (g)	1,170	988	786	609

Size frequency distributions by island were compared for males and females (Figure 7). Male and female size distributions were significantly different from each other on both St. Thomas and St. Croix (K-S test: STT $K = 2.88$, $p < 0.001$, STX $K = 3.9$, $p < 0.001$). Females were more frequent in the smaller size classes while males were more frequent in the larger size classes for both islands.

A nonparametric K-S test comparing the size distributions of fish collected in St. Thomas versus St. Croix, with males and females combined for each island, was also significant ($K=7.54$, $p < 0.001$). Therefore, the size distributions of the two islands were also significantly different from each other.

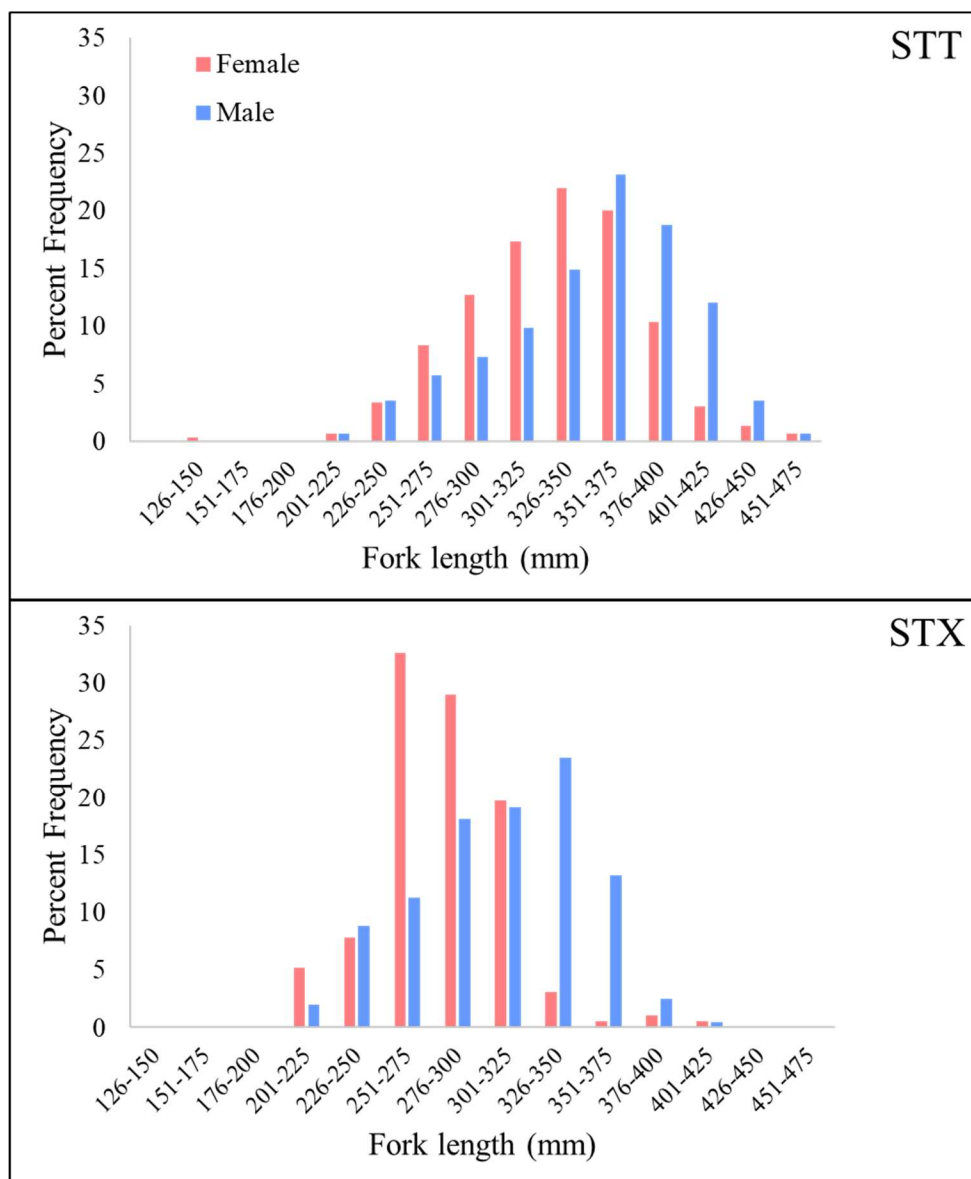


Figure 7. Size frequency distributions for male and female queen triggerfish in St. Thomas (STT, n=615) and St. Croix (STX, n=397).

3.2 Age and Growth

In St. Thomas, starting December 2015 through June 2017, a total of 617 queen triggerfish were processed. Increments were identified and counted for 89% (547 of 617) of the samples. The remaining specimens were excluded from age estimation because their spines were missing, broken, or unreadable. In order to determine the precision of age estimates, a total of 28% of STT triggerfish dorsal spines were assessed by two independent readers (n=153). Exact agreement between readers occurred for 44% of the spine sections, and age estimates were

within one year of each other for an additional 32%. We had an APE of 7%. The quality and clearness of spines varied (Figure 8).

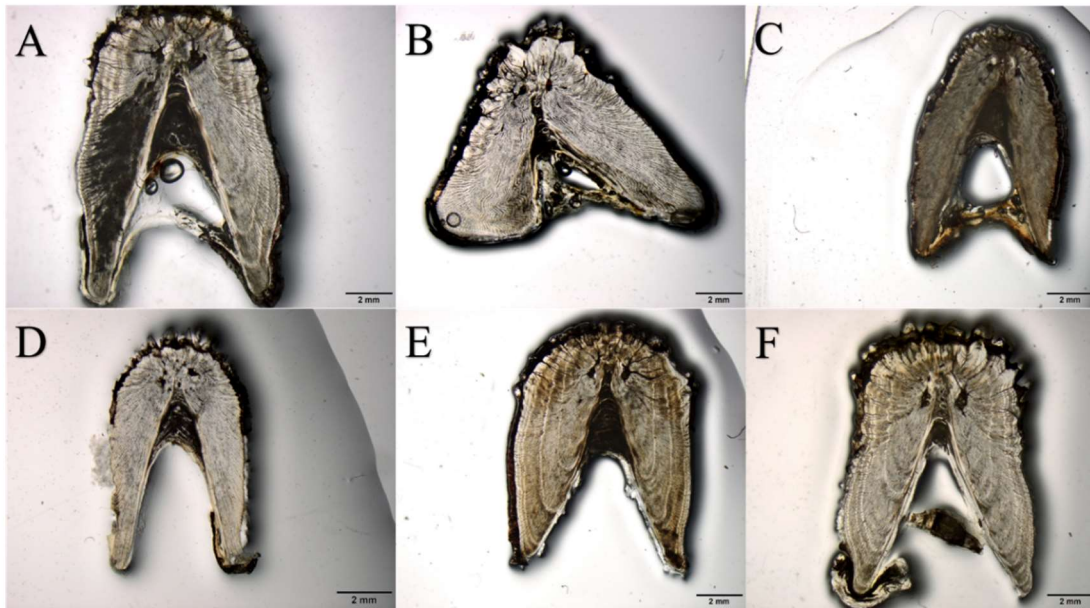


Figure 8. Images of dorsal spines with varying quality and clearness. Spines A and B have damage making them difficult to read or unreadable, spines C and D are opaque and show no clear increments, and spines E and F have very clear, distinct increments.

The percentage of spines with translucent edges was over 50% from February to July and then dropped to less than 50% in August and to less than 30% in September through December (Figure 9). Age frequency distributions were significantly different between St. Thomas males and females, with a higher proportion of older females (K-S test: $Z = 1.8$, $p = 0.014$; Figure 10). Mean ages of females and males were 6.0 and 5.5 y, respectively (Student's t-test: $t = 3.17$, $p = 0.002$). The oldest female caught was 13 y and the youngest was 1 y. The oldest male was 14 y and the youngest was 2 y. Ninety-four percent of our sample size was accounted for in the age range of 3 to 10 y.

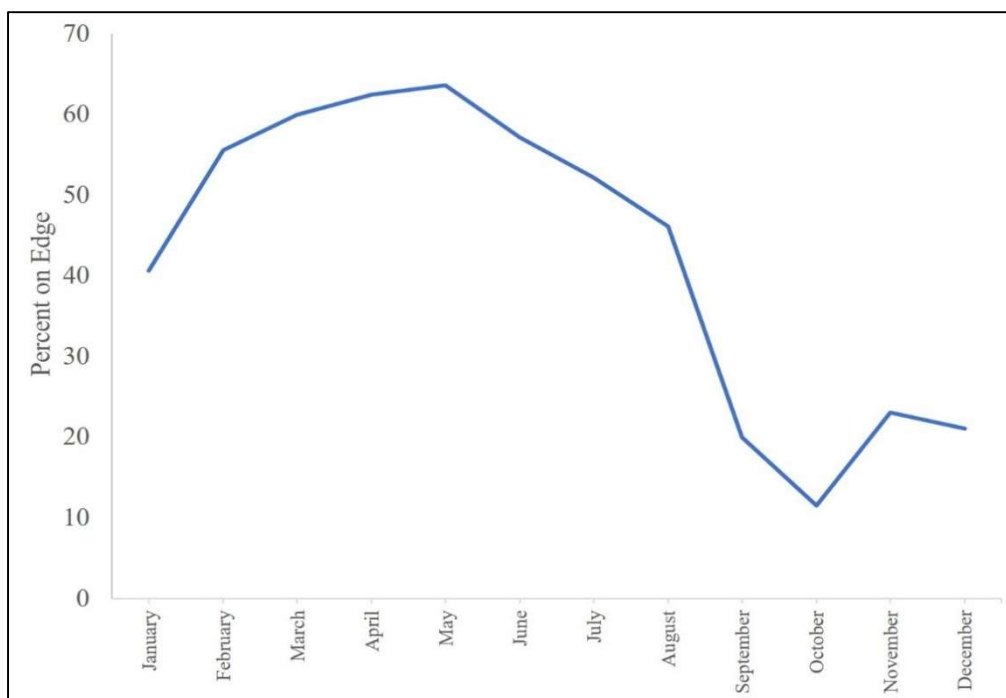


Figure 9. Percent of dorsal spines with translucent edges by month for St. Thomas queen triggerfish using age-3 through age-6 fish.

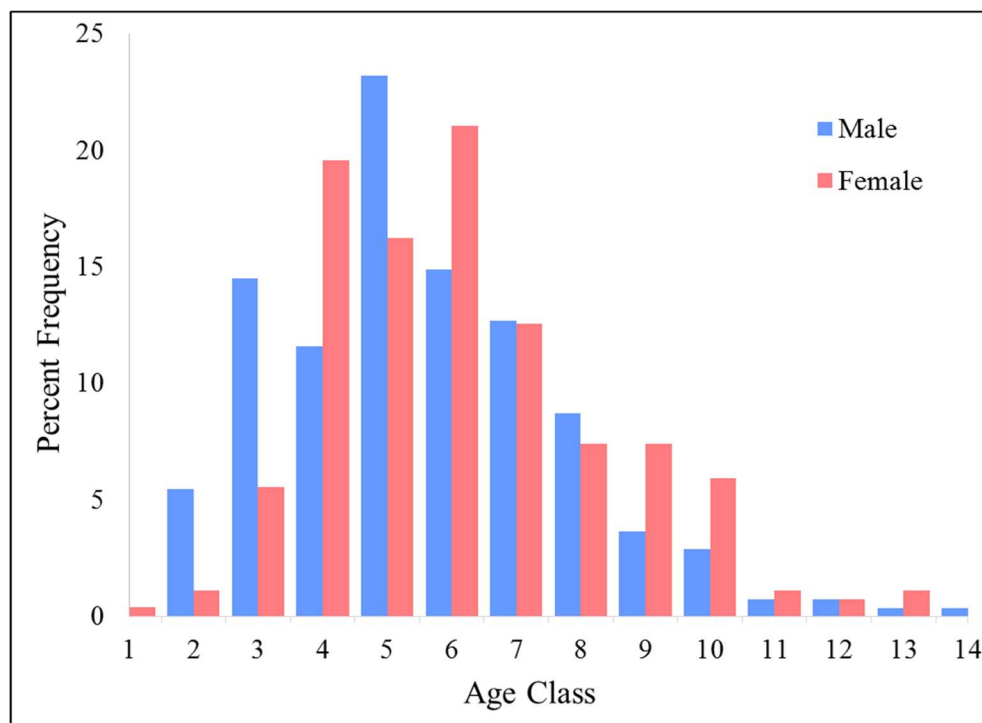


Figure 10. Age class frequency distributions for male and female queen triggerfish from St. Thomas (n=547).

A significant difference was found between the von Bertalanffy growth models for males and females (analysis of RSS: $F_{2, 539} = 199.5$, $p < 0.001$). Sex-specific growth curves were fitted, yielding the following von Bertalanffy equations (Figure 11; Table 7): $FL_t = 426[1 - e^{-0.42(t + 0.65)}]$ for males and $FL_t = 430[1 - e^{-0.28(t + 0.34)}]$ for females.

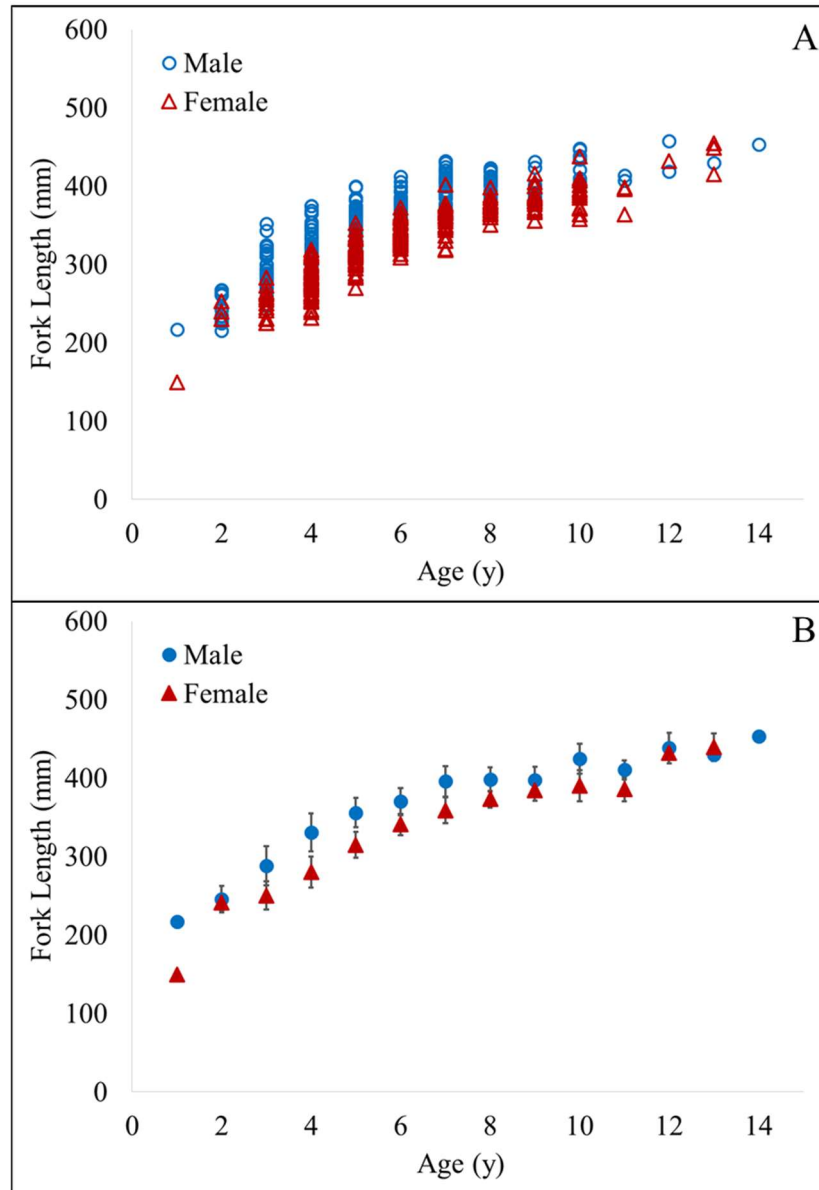


Figure 11. Fork lengths at age (A) and mean fork length at age with standard error (B) for male and female queen triggerfish from the St. Thomas trap fishery.

3.3 Reproduction

Of the 1,019 histological samples collected and processed, sex and reproductive state were assigned to 1,000 (98.1%). The earliest date of spawning capable females occurring in St. Thomas was observed on December 14, indicating the beginning of the spawning season. The end of spawning season was August 25, which was the latest date spawning capable females occurred. In St. Croix samples, the presence of spawning capable females was seen between February 17 and July 21. However, two females with GSI values indicative of spawning activity were collected August 25 in St. Croix, but histological analysis is not yet completed for those samples.

There was a significant difference in the mean GSI value across the months for both St. Thomas ($p < 0.001$) and St. Croix ($p < 0.001$, Table 4). In St. Thomas, mean GSI peaked in December and January compared to the rest of the year (Figure 12). A second spike in GSI was seen in August. In St. Croix, average GSI was significantly higher in February and similar to St. Thomas, there was a second peak in GSI in July and August. September through November had significantly lower mean GSI values than the surrounding months in both islands.

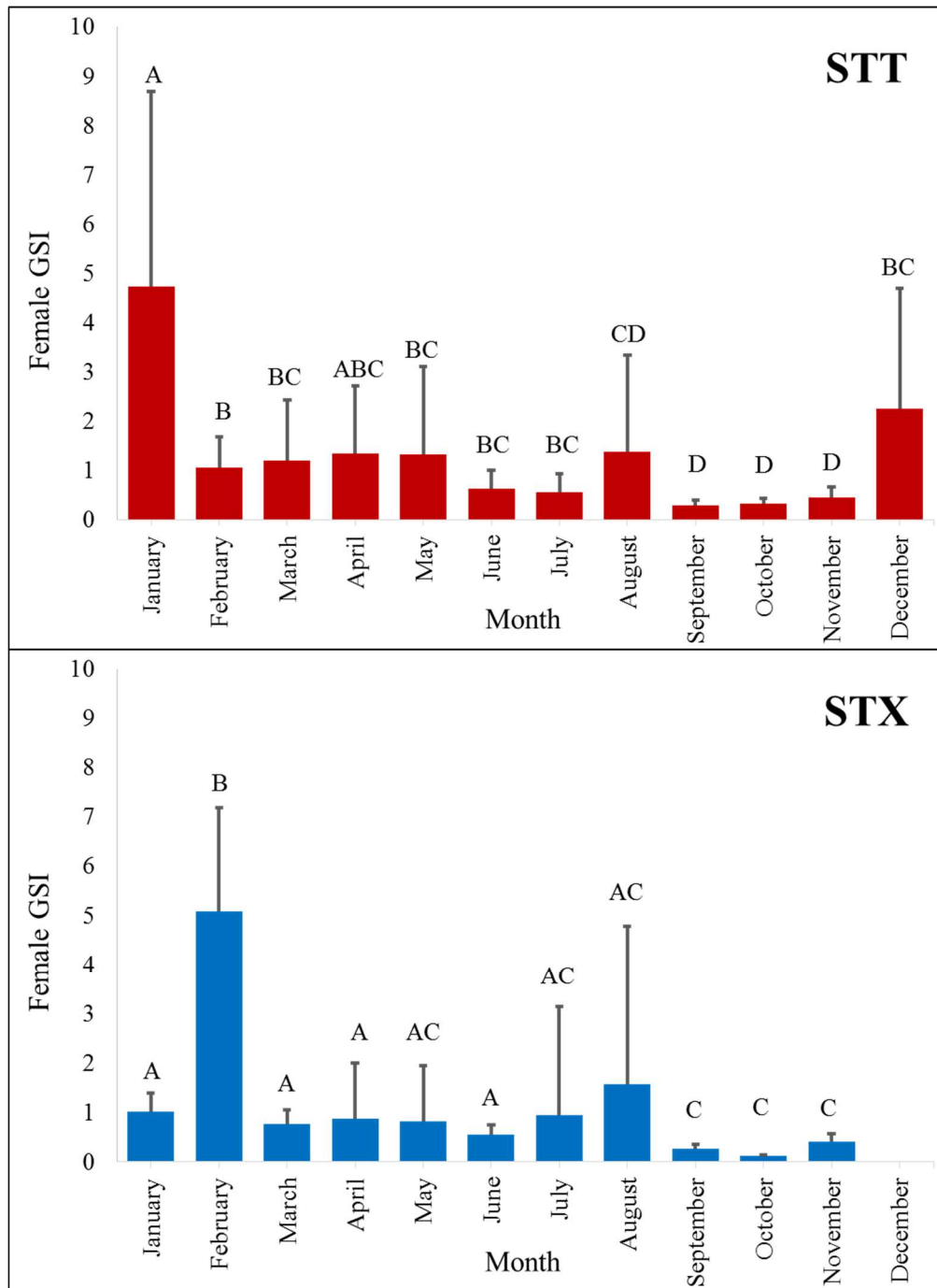


Figure 12. Monthly mean GSI (error bars represent standard deviation) for mature female queen triggerfish sampled in St. Thomas (STT) and St. Croix (STX). Letters indicate significant differences in monthly mean GSI for pairwise comparisons ($\alpha = 0.05$).

Table 4. One factor ANOVA results for differences in mean GSI among months for female queen triggerfish. Separate ANOVAs were run for the two islands.

Source	Sum of Squares	Degrees of Freedom	Mean Square	F	Significance
St. Thomas					
Month	7.14	11	0.65	14.93	p < 0.001
Error	13.74	319	0.04		
Total	36.32	328			
St. Croix					
Month	4.66	10	0.47	22.09	p < 0.001
Error	3.61	171	0.02		
Total	15.38	182			

The highest percent of spawning capable females in St. Thomas was seen in December (25.8%) and January (51.9%) (Figure 13). In the month of August, which is outside the peak spawning season, the percent of spawning capable females was 15.4% and regressing females was 61.5%. Comparatively, males were more than 50% spawning capable in every month except three. For the months of July, September, October, and November over 50% of females were in the regenerating stage of reproduction. Regenerating was the least frequent stage seen in St. Thomas male queen triggerfish (Figure 13). The percent of developing females was highest in February (56.0%), June (64.3%) and December (54.8%). The highest percent of developing males was in November at 59.1%.

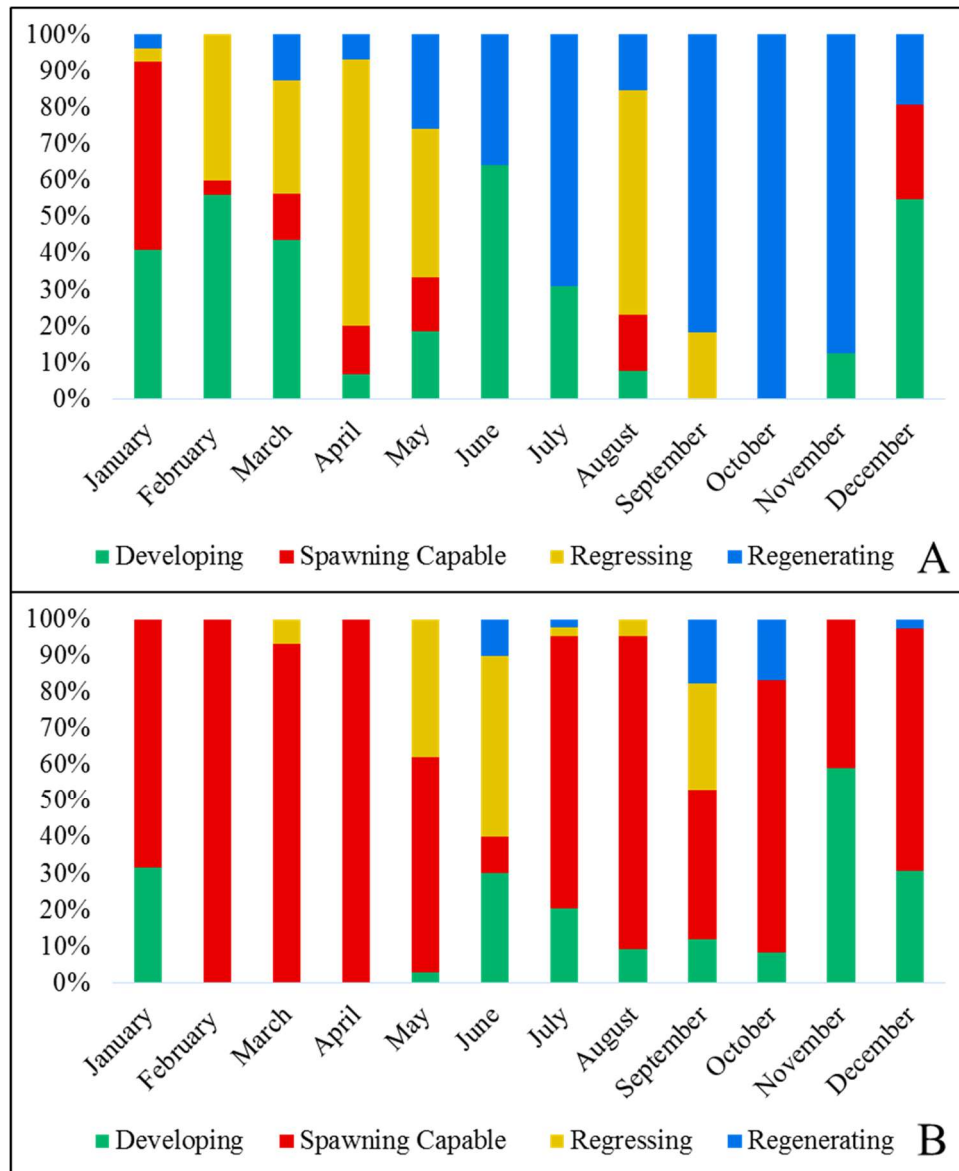


Figure 13. The composition of reproductive stages for St. Thomas females (A) and males (B) throughout the year.

The highest percent of spawning capable females in St. Croix was observed in February at 72.7%. Based on our samples, the St. Croix peak spawning season is February-May; however, no spawning capable females were observed in March (Figure 14). There was a small portion of females that were spawning capable in July (7.7%), outside the peak spawning months, similar to what was found in August females in St. Thomas. Another similarity between the islands was that spawning capable males dominated the reproductive composition of almost every month. Regressing females were not seen as frequently in St. Croix as in St. Thomas; only samples from March (5.3%), May (38.5%), and July (7.7%) captured any regression of oocytes. Regression in

males was also infrequently captured, and regeneration even less so (Figure 14). Developing females comprised over half the reproductive stage composition of January (100%), March (94.7%), April (67.6%), and June (75.0%). Developing males were seen in the highest percentage in June (50%) and November (64.7%).

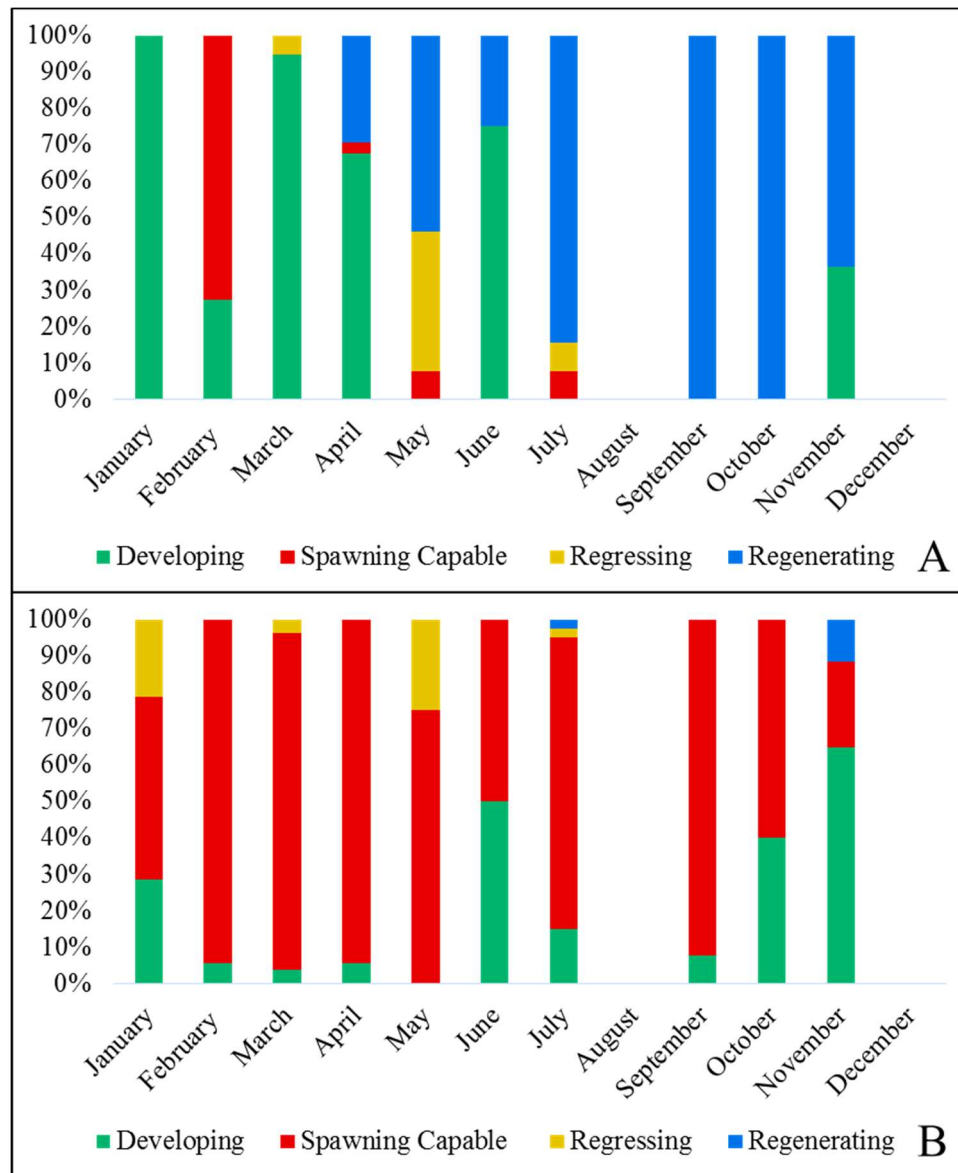


Figure 14. The composition of reproductive stages in St. Croix females (A) and males (B) throughout the year.

The proportion of mature queen triggerfish in each size-class (25 mm FL bins) and age-class was examined by using binary logistic regression. Queen triggerfish females reached 50% maturity at 287 mm FL (95% confidence interval [CI] = 279-294 mm) in St. Thomas and at 265 mm FL in St. Croix (95% CI = 256-272). Despite the difference in size at 50% maturity in

females between the two islands, 100% maturity was reached at 375 mm FL for both St. Thomas and St. Croix (Figure 15). Females attained maturity at a minimum of 241 and 230 mm FL in St. Thomas and St. Croix, respectively. The age at 50% maturity for St. Thomas females was 3.4 y (95% CI = 3.0-3.6 y). Since only one immature male was collected over the study period, we did not calculate L_{50} and A_{50} for males. All males from both islands were 100% mature by 225 mm FL, with the exception of the one immature male we observed at 242 mm FL.

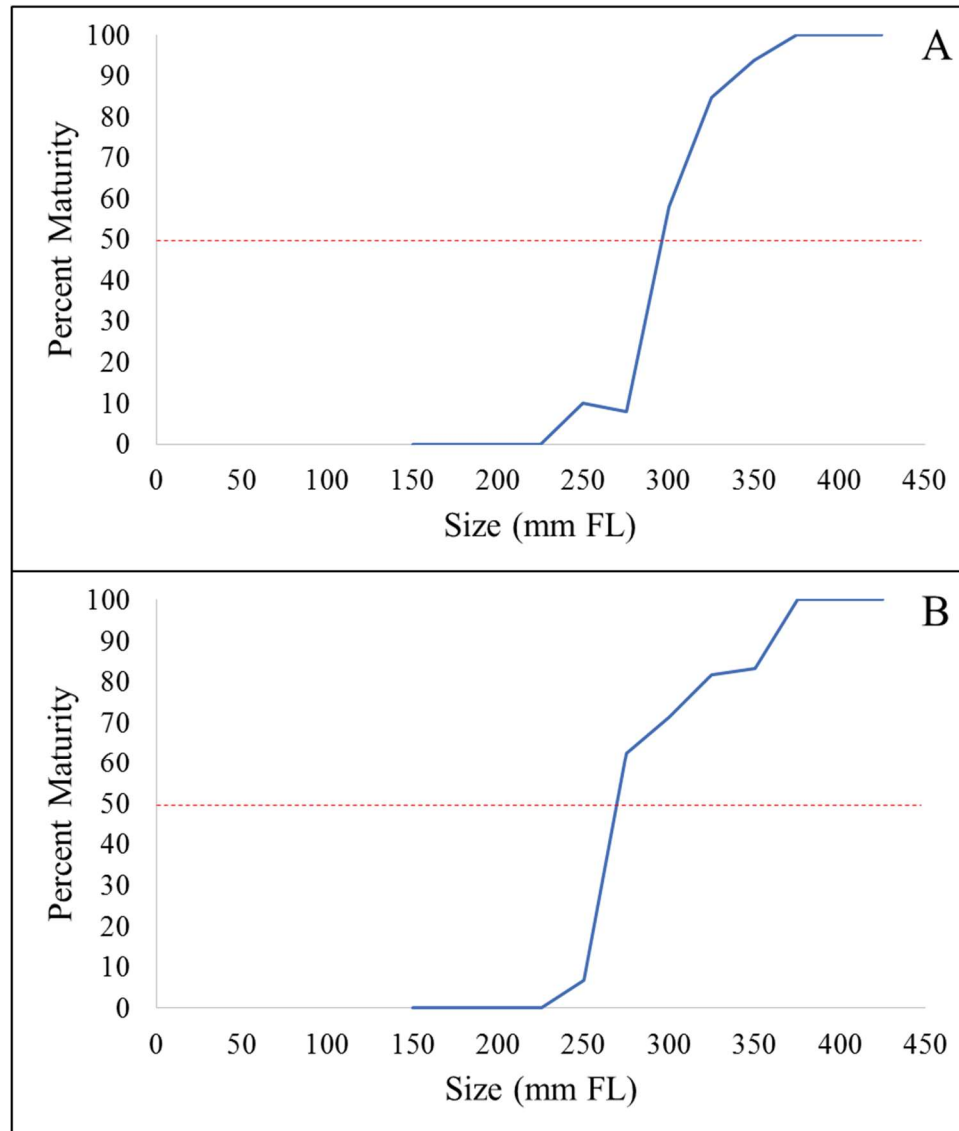


Figure 15. The percent maturity by length in female queen triggerfish from St. Thomas (A) and St. Croix (B). The red dotted line represents the length at 50% maturity.

The male: female ratio for queen triggerfish collected in St. Thomas was 1.00:0.95 (315:300) and did not differ significantly from a 1:1 ratio ($p=0.55$). The male: female ratio in St.

Croix was 1.00:0.94 (204:193) and also did not differ significantly from a 1:1 ratio ($p=0.58$). However, upon further chi-square tests of individual size classes, we found that St. Thomas females were significantly more abundant in the smaller size class 301-325 mm FL while males were significantly more abundant in larger size classes of 376-400 and 401-425 mm FL (Table 5). St. Thomas females were more abundant in size classes 276-300 and 326-350 mm FL as well, but resulted in p-values that were just over the 0.05 threshold. The same trend was found in St. Croix, where females were significantly more abundant in small size classes of 251-275 and 276-300 mm FL and males were significantly more abundant in larger size classes 326-350 and 351-375 mm FL (Table 5).

Table 5. Sex ratios within 25 mm FL size classes for queen triggerfish from St. Thomas and St. Croix. Significant p-values are shown with an asterisk.

	FL (mm)	Total n	M:F ratio	p-value
St. Thomas				
	226-250	21	1:0.91	0.83
	251-275	43	1:1.39	0.29
	276-300	61	1:1.65	0.055
	301-325	83	1:1.68	0.02*
	326-350	113	1:1.40	0.07
	351-375	133	1:0.82	0.26
	376-400	90	1:0.53	0.003*
	401-425	47	1:0.24	<0.001*
St. Croix				
	226-250	33	1:0.83	0.60
	251-275	84	1:2.74	<0.001*
	276-300	93	1:1.51	0.049*
	301-325	77	1:0.97	0.91
	326-350	54	1:0.13	<0.001*
	351-375	28	1:0.04	<0.001*

Analysis of individual age classes showed males were significantly more abundant in age classes 2 and 3 while females were significantly more abundant in age class 4 (Table 6). No

other age classes had a sex ratio that differed significantly from 1:1. Chi-square analyses for ages 1 and 11-14 were not performed due to low sample sizes.

Table 6. Sex ratios within each age class for age-2 to age-10 queen triggerfish from St. Thomas. Significant p-values are shown with an asterisk.

Age (y)	# of females	# of males	M:F ratio	p-value
2	3	15	1:0.20	0.004*
3	14	36	1:0.39	0.002*
4	51	31	1:1.65	0.03*
5	44	61	1:0.72	0.10
6	57	41	1:1.39	0.11
7	34	34	1:1.00	1.00
8	20	21	1:0.95	0.88
9	18	11	1:1.64	0.19
10	13	6	1:2.17	0.11

The smallest mature female in St. Thomas was 241 mm FL and the youngest mature female was 3 y. The largest immature female was 333 mm FL. All females were mature by 7 y. The smallest mature male in St. Thomas was 216 mm FL and 2 y. Only one immature male was observed in St. Thomas and was 242 mm FL and 2 y. In St. Croix, the smallest mature female was 230 mm FL and the largest immature female was 329 mm FL.

Chapter 4: Discussion

This study presents new and specific life history information for the commercially popular and previously data-poor queen triggerfish, *Balistes vetula*. Our results comprehensively describe the age, growth, and reproduction for this Caribbean *Balistes* species in the U.S. Virgin Islands.

4.1 Population Size Structure, Age, and Growth

The mean length and weight of queen triggerfish caught by commercial fishers in St. Thomas was significantly greater than in St. Croix. There are multiple reasons why this difference could exist in the fishery. Historical length data collected between 1983 and 2011 demonstrates that the lengths of queen triggerfish showed fairly similar trends among the islands of St. Thomas/St. John, St. Croix, and Puerto Rico with a steady decline in mean length up to about 1996. After 1996, mean length seemed to increase for Puerto Rico and St. Thomas but continued to decline in St. Croix. The St. Croix pot and trap fishery also shows less variability in mean length than St. Thomas/St. John and Puerto Rico series until around 2001. After 1996, St. Croix lengths also appear to be consistently smaller than the other islands, despite data gaps in the time series. This could be due to the profound effects of Hurricanes Hugo and Marilyn on the fishing gear types in St. Croix, which led to fishers using spear and line fishing more than trapping. While our results are based predominantly on the St. Croix spear fishery, the same trend holds true. The distribution and population dynamics of a species are influenced by numerous factors, including substrate type, food availability, water depth, and water movement (Lowe-McConnell 1987), which are in part determined by the shelf characteristics associated with each island (Walsh 1988). There may be two distinct populations of queen triggerfish within the territory which are subjected to differing hydrological conditions across the disparate island shelf geographies. St. Croix has less shallow reef habitat than St. Thomas and consequently less area for a fish's population to forage over. The level of recruitment to the population in St. Croix may differ compared to St. Thomas since less shelf area could also mean less viable areas for spawning (Kadison et al. 2017).

However, the differences in gear types used and their exploitation intensity between the northern USVI islands and St. Croix could also help explain our findings. The narrower and

shallower shelf of St. Croix, with much less fishable area than St. Thomas, makes it more vulnerable to intense fishing efforts, especially when fishing strategies like spearfishing are used. It has been shown that spearfishing has a very efficient CPUE and a high selectivity, which is only increased when used on scuba (Frisch et al. 2008, Lindfield et al. 2014). It has also been shown that intense spearfishing can cause declines in the density and mean size of target species (Frisch et al. 2012), which is why this fishing methodology has been banned in certain parts of the world (Lindfield et al. 2014). In comparison, the St. Thomas shelf has more fishable area in depths greater than 25 meters than St. Croix (Kadison et al. 2017), which is why no level of commercial spearfishing in the northern USVI has been established. Smaller sized fish in St. Croix than in St. Thomas has also been confirmed by long-term fisheries-independent monitoring in the territory. The Territorial Coral Reef Monitoring Program (TCRMP) collects data by fixed site belt transect surveys on scuba in St. Thomas, St. John, and St. Croix annually. Kadison et al. (2017) analyzed the abundance of large bodied commercially important snappers and groupers using TCRMP data and found most of those species to be greatly reduced in abundance and smaller in size in St. Croix. From our fisheries-dependent data, our conclusions are limited to the portion of the population that is exploited. However, fisheries-independent data seems to suggest that there are differences in whole reef fish populations, not just the exploited portions, across the islands shelves.

Despite the across island differences, males were significantly larger than females on both islands. This finding is similar in other studies for *Balistes* species. Aiken (1975) reported male queen triggerfish from Jamaica to be larger than females, although no statistical tests were conducted on the sizes. Significantly larger males have been reported in gray triggerfish in the Atlantic as well (Kelly-Stormer et al. 2017). The reproductive behavior of triggerfish species may explain why males attain a larger size than females. As males of queen and gray triggerfish have been observed patrolling nesting territories, a larger size would be advantageous in defending nests and subsequently increasing the survival of fertilized eggs. While females can reach larger sizes, their biparental care is not necessarily augmented by size. However, the overall reproductive success of a population is partially dependent on female size because larger females can be more fecund than their younger and smaller counterparts (Birkeland and Dayton 2005).

The range of ages seen in the present study differs, but not drastically, from that reported in the literature (Menezes 1985, Manooch and Drennon 1987, Albuquerque et al. 2011). In Brazil, the combined fishery-dependent and -independent samples ranged in age from 2 to 14 y (Albuquerque et al. 2011). Menezes (1985) reported a maximum age of 12 y from Brazil. Our present study and the current literature do not report any ages above 14 y for any queen triggerfish based on spine increment analysis. We managed to catch an individual that was 1 y, whereas the youngest queen triggerfish caught in Brazil was 2 y. However, it should be noted that our 1 y specimen was not collected from a commercial fisherman; it was speared on scuba and is therefore a fisheries-independent sample. Ninety-seven percent of queen triggerfish collected from Brazil ranged from 3 to 10 y, while 94% of individuals in our study from St. Thomas ranged from 3 to 10 y. The presence of older individuals than the mean age, which was between 5 and 6 y in our study for St. Thomas males and females, suggests that fishing effort may not have induced changes in the age structure of the USVI queen triggerfish population (Albuquerque et al. 2011). Manooch and Drennon (1987) collected fishery-dependent individuals up to 7 y in the USVI, but also caught an age 0 queen triggerfish of 215 mm FL in their study. Kelly-Stormer et al. (2017) observed ages 0-10 in the conspecific gray triggerfish. These differences in age ranges between this study and previous ones may be due to a combination of reasons, including the difficulty of using dorsal spines to estimate ages in *Balistes* species (Burton et al. 2015, Kelly-Stormer et al. 2017, Shervette and Dean 2015); differences in what time of year samples were collected (Pope and Willis 1996); and differences in the sample sources for triggerfish such as fisheries-dependent or -independent (Allman et al. 2017)

Dorsal spine growth does not occur in isolation from the physical environment of the fish, giving it a disadvantage over other aging structures such as otoliths (Campana and Thorrold 2001). Due to the small size of triggerfish otoliths and difficulty finding them, spines have been relied on in age and growth studies in triggerfish species (Künzli and Tachihara 2012, Smart et al. 2016, Kelly-Stormer et al. 2017, Allman et al. 2017), however gray triggerfish sagittal otoliths do form annual increments and should be evaluated as an ageing structure (Shervette and Dean 2015). Queen triggerfish sagittal otoliths are similar to gray triggerfish and also form annual increments (V. Shervette, unpublished data). The reliance on dorsal spines for estimating age in triggerfish over the past 30 years, means standardized methods currently do not exist in the

published literature for processing triggerfish sagittal otoliths in order to estimate age (Shervette and Dean 2015).

Other studies have reported difficulties in using dorsal spines. Our exact agreement between two readers was 44%, which was quite similar to the results of Kelly-Stormer et al. (2017), which had 43% for gray triggerfish spines. Both in our study and in Kelly-Stormer et al. (2017), the overall percent agreement increased to over 75% when estimates within 1 year were included. Our study had an APE of 7% indicating that we had a smaller amount of between reader error compared to Albuquerque et al. (2011) which reported an APE of 11%. Despite these issues with age estimation, the first dorsal spine is the currently accepted aging structure for triggerfish species. Whether or not this method represents the true age is still unclear and needs to be investigated further.

Queen triggerfish from St. Thomas appear to form increments from February through June, depending on when individuals spawn within those months. Manooch and Drennon (1987) reported a similar finding from their marginal increment formation analysis on queen triggerfish from the USVI and Puerto Rico. Their analysis indicated increment formation occurred from February to March. Spawning capable females were seen in St. Thomas from December to May and again in August. This supports the timing of increment formation because during spawning individuals are expending less energy on somatic growth and more on reproductive input, which is represented in the dorsal spines' thinner, translucent zones. Albuquerque et al. (2011) found that queen triggerfish off the coast of central Brazil form increments during summer, which corresponds with the spawning season in that region. Gray triggerfish form increments in late spring to summer, also corresponding to their spawning season of May to August (Kelly-Stormer et al. 2017).

Age-0 queen triggerfish do not seem to occur in the fishery-dependent samples from St. Thomas. Other studies focused on *Balistes* species that used fish and lobster traps for collection reported scarce numbers of age-0 individuals (Manooch and Drennon 1987, Kelly Stormer et al. 2017). A few studies have documented habitat-use in juvenile *Balistes* species. Gray triggerfish early life stages are associated with *Sargassum*, which serves as nursery habitat for many species that recruit to commercial fisheries as adults (Wells and Rooker 2004). *Sargassum* mats that drift throughout the Caribbean could potentially provide a transport method and nursery habitat for

pelagic queen triggerfish juveniles. Bean et al. (2002) studied the relationship between microhabitat specialization and distribution patterns of juveniles and adults of five triggerfish species in Papua New Guinea. Preference for habitat with higher topographic complexity was greater in juveniles, due to their increased susceptibility to predators. Differences in diet, such as omnivores or planktivores, between species also influenced the distributions in adult and juvenile triggerfish (Bean et al 2002). Therefore, the co-occurring species in a habitat can affect what microhabitats are available to individual species. Queen triggerfish juveniles may have higher survival in certain locales they settle in based on the reef community composition. Robertson (1988) reported a mass settlement of queen triggerfish juveniles in Panama in early April 1985, which led to a 1.5-fold increase in the adult population at that location. The habitat these juveniles settled in was shallow back reef, 1-3 m in depth, composed of a mixture of sand, sparse seagrass, and small coral growths on a rock base that provided numerous holes for the triggerfish to shelter in. They ranged in size from 49-70 mm FL and were on average 75 days old. The low sample sizes of queen triggerfish in that size class and less than 1 year represent a data gap for fully understanding their life history. Since commercial fishing gear only targets a limited number of these smaller individuals of ages 0 to 1, fisheries-independent sampling is required to supplement current datasets.

We compared our results to the two other studies of queen triggerfish age and growth: Manooch and Drennon (1987) and Albuquerque et al. (2011). The von Bertalanffy parameters, sample sizes, size and age ranges, and sample types are shown in Table 7. Note that the sample size for our study only reflects the number of samples for which we were able to obtain an age reading, not the overall number of samples collected. Additionally, we plotted our overall growth curve, with both sexes combined, alongside the other studies' growth curves (Figure 16).

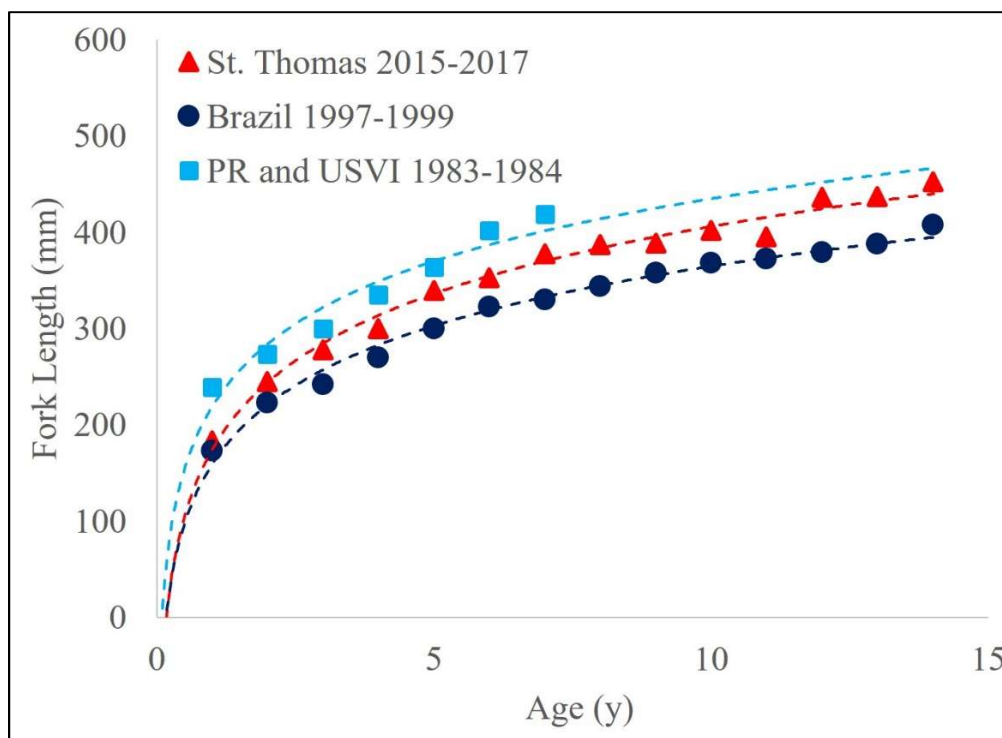


Figure 16. Comparison of mean size-at-age for queen triggerfish from three studies: the current study, St. Thomas 2015-2017 trap fishery; Queiroz de Albuquerque et al. (2011), Brazil central coast 1997-1999 scientific surveys and commercial fisheries using bottom longline and handlines; Manooch and Drennon (1987), Puerto Rico and U.S. Virgin Islands 1983-1984 trap and hook-and-line fisheries. See Table 7 for supplementary information.

Our study is the first to examine growth rates of male and female queen triggerfish separately. The previous two studies reporting growth only examined growth rates for males and females combined (Manooch and Drennon 1987, Albuquerque et al. 2011). However, growth in queen triggerfish is sexually dimorphic with females' growing slower and attaining a smaller asymptotic length (L_{∞}). Our overall growth rate, for male and females combined, was $k=0.33$, which was similar to what Manooch and Drennon (1987) found for fisheries-dependent U.S. Caribbean queen triggerfish samples from 1983-1984 (Table 7; Figure 16). Comparatively, a combination of fishery-dependent and -independent queen triggerfish in Brazil had slower growth rates of 0.14-0.15 (Menezes 1985, Albuquerque et al. 2011). The highest reported growth rate for queen triggerfish is 0.57, but was calculated indirectly based on length distributions instead of age estimates (Aiken 1975). Fishery-independent sample of the conspecific gray triggerfish has been shown to exhibit moderately rapid growth rates of $k=0.67$ (Kelly-Stormer et al. 2017). However, the sampling source can influence the aging and growth results, even within the same species. Allman et al. (2017) examined if fishery selectivity could potentially influence

growth estimates and found that growth functions computed with fishery-dependent samples tend to overestimate size-at-age. Not only was the effect of sample source on size-at-age significant, but so was the effect of sex. Therefore, there is a difference in size-at-age for both males and females between fishery-independent and -dependent data sources. The differences in sample source results can be akin to the different gear types used in each source and the depths they are deployed in. There is limited evidence that queen triggerfish move deeper offshore as they mature (Aiken 1975). Size-selective capture methods can also favor fast-growing individuals, which would affect the resulting growth estimate. Allman et al. (2017) also compared growth estimates between models that included juvenile age data (age-0 individuals) and found a significant difference between models that did not include that data. Similarly, when Kelly-Stormer et al. (2017) did not include age-0 gray triggerfish in their growth model, the growth rate decreased by half from 0.67 to 0.30. Our sex-specific growth rates do not include juvenile individuals and therefore represent the growth rates of the local commercial fishery rather than the U.S. Caribbean queen triggerfish population as a whole.

Table 7. Summary of studies reporting on age and growth of queen triggerfish.

Study Location and Source	Time Period	Sample Size	Size Range (FL mm)	Age Range (years)	L_{inf}	k	t_0	Sample Type
St. Thomas Current Study	2015-2017	All: 547 Male: 276 Female: 271	150-466	1-14	Observed All: 428 Male: 426 Female: 430	Observed All: 0.33 Male: 0.42 Female: 0.28	Observed All: -0.48 Male: -0.65 Female: -0.34	Fisheries-dependent samples from traps
U.S. Caribbean (Manooch and Drennon 1987)	1983-1984	494	214-425	0-7	Back-cal All: 415 Observed All: 392	Back-cal All: 0.30 Observed All: 0.64	Back-cal All: -0.60 Observed All: -0.81	Fisheries-dependent samples from traps and hook-and-line
Brazil (Queiroz de Albuquerque et al. 2011)	1997-1999	476	180-460	2-14	Back-cal All: 441 Observed All: 384	Back-cal All: 0.14 Observed All: 0.34	Back-cal All: -1.80 Observed All: -0.41	Combination of fisheries-dependent and -independent samples

4.2 Reproduction

Our study provides a clearer and more detailed understanding of when queen triggerfish spawn in northern Caribbean waters. Our results indicate that St. Thomas female queen triggerfish spawn from December to August. In St. Croix, we still have two months without histology data; therefore, we have not yet identified all of the months in which spawning capable females occur. A study from Jamaica, that examined gonads macroscopically, reported that ripe females occur January-February and August-October (Aiken 1975). Similar to what we found in St. Thomas and St. Croix, Puerto Rico queen triggerfish female spawning occurs from December to August (V. Shervette, unpublished data).

Off the central coast of Brazil, *B. vetula* spawns during the summer months (Albuquerque et al. 2011). This difference in spawning season from the subtropical, Atlantic waters of Brazil and eastern Caribbean is most likely explained in part by the average temperature differences. Temperature is an influential environmental factor, in addition to the lunar cycle, that affects spawning in fishes, most markedly seen in the difference between temperate and tropical species (Pauly 1980, Lam 1983, Fromentin and Fonteneau 2001). Other regional variations such as fish community composition, fishing pressure, and habitat complexity could also cause the differences in spawning season (Kelly-Stormer et al. 2017). However, none of the published studies on queen triggerfish reproduction conducted histological samples of gonadal tissue, but rather macroscopically staged gonads. This difference in methodologies for determining reproductive stage gives rise to caution when comparing results found in our study. Macroscopic evaluation of gonads sometimes overestimates the proportion of mature females (Vitale et al. 2009). Other methodologies of the studies, such as sample sources (fisheries-dependent versus independent), sample sizes, and sampling duration also differ from ours. Lastly, Munro et al. (1973) and Aiken (1975) reported collection numbers but did not conduct any statistical evaluation of the data to determine significance in their findings.

Many large-bodied Caribbean reef fishes, such as Nassau grouper (*Epinephelus striatus*), red hind, lane snapper (*Lutjanus synagris*), and mutton snapper (*Lutjanus analis*), form spawning aggregations that occur in relationship to the lunar cycle (Colin et al. 1987, Beets and Friedlander 1992, Domeier and Colin 1997, Claro and Lindeman 2003). An ongoing study on spawning aggregations at Lang Bank, east of St. Croix, documented that queen triggerfish start

aggregating as early as the full moon in January (R. Nemeth, unpublished data). Queen triggerfish abundance begins to increase the day before the full moon and tapers off around 7-8 days after. Unfortunately, in our study, St. Croix queen triggerfish sample collection was not timed to the lunar cycle: January 2017 samples were caught 12+ days after the full moon; February 2016 samples were caught 3-5 days prior to the full moon; March 2017 samples were caught 8-10 after the full moon; April 2017 samples were caught 13+ days after the full moon; May 2017 samples were caught the day of the full moon. Additional sampling in St. Croix is planned for 2018 so that female fish are collected each day for a week after the full moon in order to address this data gap. Interestingly, all St. Thomas female queen triggerfish in spawning condition were collected as early as 2 days prior to the full moon and as late as 8 days after. This may indicate that a queen triggerfish spawning aggregation exists near St. Thomas. Further investigation is needed to confirm the location of that aggregation.

Males had less variation in monthly reproductive phases throughout the year compared to females. Spawning capable males occurred in every month of the year in St. Thomas, suggesting that mature males may be ready to spawn year-round. A similar trend was also seen in gray triggerfish where spawning capable females were only observed from April to August but spawning capable males were found in all months of the year (Moore 2001). Regeneration in males was the least captured phase, whereas the percent of females in regeneration began to increase once the spawning season ended in May. In St. Thomas from September to November, almost all females had gonads in the regenerating phase even though the majority of male gonads were spawning capable. It is possible that the duration of reproductive phases such as development and regeneration for males is much shorter than it is for females, since the energetic cost of female gonad development is greater than males' (Yong and Grober 2014).

The length at 50% maturity for female queen triggerfish differed between the two USVI islands. Sampling biases may explain this difference since we relied on fisheries-dependent samples and the main methods of fishing are different on each island. Another possibility is that St. Croix may have a smaller population size of queen triggerfish, due to the smaller size and shallow nature of the island's shelf. Low density and population size can be a signal to mature earlier (Morgan and Colbourne 1999), which would be influenced by the area of habitat available to a species. Fishing pressure has the potential to exacerbate such a difference and has been

shown in another study to significantly alter the population size structure of marine fishes (Buxton 1993). Increased mortality in adult individuals of a population can also cause declines in size at maturity because a smaller maturation favors the chance of reproducing before death (Morgan and Colbourne 1999). However, uniform, fisheries-independent sampling of queen triggerfish in the waters of both islands is needed in order to truly determine if a difference exists in size at maturity.

4.3 Management Implications

Our results provide new information and a more comprehensive understanding of the life history of queen triggerfish populations in the U.S. Virgin Islands of St. Thomas and St. Croix. This information is directly applicable and essential for local and federal fisheries managers in the Caribbean. Our study has documented that differences exist between the fish that are part of the catch for each island. This year local management bodies such as the St. Thomas Fishermen's Association (STFA), the Caribbean Fishery Management Council (CFMC), and the Department of Planning and Natural Resources Division of Fish & Wildlife have begun the process of developing island based fishery management plans for St. Thomas/St. John, St. Croix, and Puerto Rico. Currently, all three areas are under a broad management plan with the same regulations that does not take into account differing physical and spatial conditions. Each island has individual needs and demands that influence the intensity of fishing and landings composition. Documented differences in the reef fish assemblages exist between the northern and southern USVI island platforms (Kadison et al. 2017); fisheries management goals should take those differences into consideration.

Queen triggerfish do not have regulations in place beyond annual catch limits (ACLs) and accountability measures (AMs). The ACL currently differs by island. If the ACL for a reef fish group, such as triggerfish and filefish, is exceeded based on prior years' landings, then the fishing season length is reduced for the next year. The amount of time that the reduction includes is based on how far the ACL was exceeded. For example, based on average landings during the 2012-2014 fishing years, the commercial ACL in Puerto Rico was exceeded for spiny lobster, triggerfish and filefish, and three other management units (NMFS 2016). Therefore, the National Marine Fishery Service closed those species groups for a portion of the 2016 fishing year. The rule went into effect for commercial triggerfish and filefish on October 16, 2016 and was closed

through December 31, 2016. The AMs are designed to protect reef fish in the exclusive economic zone (EEZ) of each U.S. Caribbean territory.

Unlike other reef fishes such as groupers and snappers, there are no minimum sizes or seasonal closures specifically for queen triggerfish. While there are no size limits, there is a degree of self-regulation among local fishers because “plate-size” fish are more desirable to some customers than the largest individuals, which are usually the targeted individuals in commercial fisheries. A plate-size fish is valued by Virgin Island customers, because fish are traditionally gutted, skinned/descaled, and cooked whole in a pot, otherwise called “pot-fish,” rather than filleted. Fishers from St. Thomas indicated that they often throw back larger triggerfish pulled from their traps that would be too big to fit into a pot. However, no studies have documented the commercial discards of St. Thomas fishers and no studies have quantified the mortality of queen triggerfish discarded because they were deemed too large or small. It has been reported for gray triggerfish in the snapper-grouper fishery off the coast of the southeastern U.S. that nearly all discarded individuals experienced immediate release mortality (Stephen and Harris 2010). That kind of information is critical before further speculation can occur on any potential benefits of a plate-size fishery. Fishery-independent sampling would also aid in better understanding any plate-size influence because the trap funnel entrance size determined by fishers might skew size frequencies and exclude certain size classes from a fishery-dependent dataset.

To truly assess the queen triggerfish fisheries in the USVI and determine the stock status for the queen triggerfish populations, the life history parameters we have presented need to be incorporated into the analysis used by federal fishery managers under the Magnuson-Stevens Act, to establish new baselines for ACLs, AMs, and when applicable, seasonal closure and size restrictions to prevent overfishing. This is especially relevant as island based management plans are being developed. One of the biggest issues discussed in CFMC meetings is the lack of fisheries-dependent data available for informing decisions on commercially important species like queen triggerfish. Data-limited assessments that rely on mean sizes are often the only resource available, but may not accurately define the true status of a fishery without key information such as spawning season, age and size at maturity, and growth rates. Our study aimed to fill in data gaps in life history for one of the most commercially popular reef fishes in the USVI so that managers have the necessary data for future assessments.

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