Final Report: Assessment of maturity in commercially and recreationally important reef fishes from the U.S. Virgin Islands

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Final Report:
Assessment of maturity in commercially and recreationally important reef fishes from the U.S. Virgin Islands

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Summary

Thirteen species of reef fish were sampled from commercial catches in St. Thomas, St. Croix and Puerto Rico. The primary objective was to characterize the catch – by island - in terms of sexual maturity, sex ratio, and size structure, and to use these data to explore the status of the stocks with respect to impacts of fishing mortality. Secondary goals included characterizing the seasonality of reproduction, and collecting hard parts for growth studies and tissue samples for genetic analysis. We studied six parrotfishes (Princess, Queen, Redband, Redtail, Redfin /Yellowtail, and Stoplight), three snappers (Mutton, Blackfin and Yellowtail), two groupers (Coney and Red hind), a grunt (White) and a triggerfish (Queen). For five of the parrotfish species, Coney, and Red hind, all of the specimens examined were sexually mature. Queen triggerfish had the lowest percentage of mature fish in the catch (86.4% mature). All other species had over 94.4% mature. This means the percentage mature will be close to 100% for any breakdown of the data by island, gear, season or fish size (caught in the commercial fishery) for those species for which the overall percentage mature is close to 100%. Sex ratios (females /males) for parrotfish (ignoring transitioning animals) were 0.30 for Redband, 0.58 (Princess), 0.73 (Redtail), 0.94 (Stoplight), 0.96 (Queen) and 2.03 (Redfin/Yellowtail). An unambiguous interpretation of these sex ratios is not available at present. For Coney and Red hind sex ratio was 0.73 and 1.46, respectively, ignoring transitioning animals. For the remaining five species, the sex ratio was fairly balanced, ranging from 0.82 (white grunt) to 1.07 (Blackfin snapper). Adequate data were obtained to describe seasonality of reproduction in Princess parrotfish, Stoplight parrotfish, Coney, and Queen triggerfish. Princess and Stoplight parrotfish spawn in all months. Coney spawn from December through April with the major activity occurring in January and February. Queen triggerfish spawn primarily from December through February but there is some spawning in every month except September, October and November.

Modeling work consisted of estimating total mortality from mean length and natural mortality from maximum age; fishing mortality was determined by subtraction. The implications of these findings were evaluated by computing spawning potential ratio. Queen triggerfish was used as an example because the data were extensive (but note there is uncertainty about growth rates). Total mortality appears quite low and this was consistent with an age-based catch curve. Natural mortality based on maximum age suggests fishing mortality is quite low (~ $F = 0.1$); calculated SPR for a variety of assumptions about longevity (natural mortality), age of first capture and age at maturity are all high (>0.62). For other species, uncertainty about longevity and growth parameters causes infeasible estimates in some cases ($L_\infty < \bar{L}$ or $Z < M$), and induces great uncertainty in the results for other species. But, where life history parameters are reliable, the approach offers a way to quantify heuristic results from maturity studies.

The fact that almost all fish caught in the commercial fishery for reef fish are sexually mature argues there is very little chance reproduction is being affected by recruitment overfishing and fishing mortality is probably quite low.

Outreach activities included a seminar by Hoenig on “Why do we care about fish maturity?” at the University of the Virgin Islands and three workshops on sampling gonads and collecting hard parts for studies of age and growth by Shervette given to personnel of the Virgin Islands Department of Parks and Natural Resources. An additional workshop on analyzing data was

planned for the winter of 2020 but was not conducted due to the coronavirus pandemic. This workshop will be given at a later date.

Introduction

The purpose of this project is to determine the maturity of 13 important reef fishes (Table 1) in the commercial catch in the US Caribbean and to model the implications of the findings for fishery management. The basic idea is that if a significant portion of the landings is comprised of immature fish then it is possible that overfishing will result in reduced recruitment (and possibly stock collapse). However, if most of the catch is comprised of mature fish then it is difficult to collapse a stock. A caveat to using this logic is that, if a population forms large spawning aggregations during restricted periods of the year and these aggregations are known to fishers, it could be subject to very high fishing mortality and it is possible that a large fraction of first time spawners could be harvested before they have a chance to reproduce. Therefore, this project aims to determine the composition of the commercial landings in terms of maturity status, delineate spawning times during the year, and model the implications of the findings for fisheries management. The modeling focused on estimating total mortality rate (from mean length) and natural mortality rate (from maximum age) and thus fishing mortality (by subtraction). The results were used to examine spawning potential ratio.

Table 1. Species collected for this project and number of fish examined histologically. Because very few silk snapper were collected, a decision was made to substitute White grunt for this species.

Group	species	common name	specimens examined
Parrotfish	*Scarus taeniopterus*	Princess parrotfish	587
Parrotfish	*Scarus vetula*	Queen parrotfish	300
Parrotfish	*Sparisoma aurofrenatum*	Redband parrotfish	374
Parrotfish	*Sparisoma chrysopterum*	Redtail parrotfish	819
Parrotfish	*Sparisoma rubripinne*	Redfin parrotfish/Yellowtail parrotfish	103
Parrotfish	*Sparisoma viride*	Stoplight parrotfish	1333
Snapper	*Lutjanus analis*	Mutton snapper	72
Snapper	*Lutjanus buccanella*	Blackfin snapper	387
Snapper	*Lutjanus vivanus*	Silk snapper	------
Snapper	*Ocyurus chrysurus*	Yellowtail snapper	251
Other	*Cephalopholis fulva*	Coney	381
Other	*Epinephelus guttatus*	Red hind	393
Other	*Haemulon plumierii*	White grunt	280
Other	*Balistes vetula*	Queen triggerfish	1439

Fish were purchased directly from commercial fishers and dissected to obtain gonads for assessing sexual maturity, hard parts to determine age, and genetic samples to examine connectivity of the populations in different areas. The hard parts and genetic samples have been archived for future studies. This project examined the gonadal samples. One species, silk snapper, was obtained in small numbers and a decision was made to examine white grunt (*Haemulon plumierii*) instead because it was more abundant in our sampling.

Previous reports from this project have reported on the sex composition and proportion mature for 10 of the species that are the subject of this research. Histological examination of the samples from the remaining three species has been completed and are presented in this report along with all previous findings.

Field and Laboratory Methods

SAMPLE COLLECTION – The main research goal for the 13 species is to determine sex ratios, reproductive seasonality, size at maturity, proportion of catch that are reproductively mature in U.S. Caribbean waters and assess if significant differences occur in various life history parameters between/among the major areas where each species occurs in the catch: St. Croix, Puerto Rico, and St. Thomas/St. John. To do this, for each of the 13 species in each of the areas where they occur as a part of the catch, we hoped to collect a minimum of 50 individuals per sampling season. Based on the first year's sampling numbers, some species do not contribute to the fisheries in all three of the major areas so the final number of samples was anticipated to be less than 7800 (13 species x 3 major areas x 4 main sampling seasons x 50). In the end, we were able to collect 6696 specimens, sampling in all seasons.

It is important to understand that the purpose of this study is to determine what the commercial fishery is doing to the stocks. This is in contrast to another possible goal of studying the composition (in terms of sex and maturity) of the population in the sea. The idea is that if the fishery harvests immature fish there is the potential for reproductive overfishing whereas if the fishery targets mature fish it is difficult to cause recruitment failure. (An exception is if the fishery targets spawning aggregations because then there is the potential to remove fish before they have had the chance to spawn at least once.)

Thus, this project focused on obtaining representative samples of the commercial catch. This turns out to be a difficult task for several reasons. First, some fishers may process some of the catch at sea, may sell directly to restaurants, and may drop off parts of the catch to buyers at various places before returning to the point of departure. Second, some fishers take special orders for customers and that portion of the catch is not available to be sampled. Third, sampling at the retail markets does not necessarily provide a representative sample, even if one arrives at the market before selling begins. This is partly because some fish are sold before the catch reaches the market. But, also, fish can arrive at the market throughout the day and be added to coolers of fish containing those fish from the previous day that have not yet been sold. To the extent that the buyers are selective in what they purchase, sampling the coolers in the market may provide biased results.

It appears the least biased sampling would be obtained by randomly selecting landing sites and remaining there all day to purchase fish as they are brought in. This is very inefficient because long periods of time may be spent waiting for fishers to land. Most fishers are open to selling fish to the port sampler but some may refuse because they are in a hurry to bring fish to regular customers or for other reasons.

We attempted to reach a compromise between random sampling and selective sampling by waiting at the dock to meet incoming boats, then asking the fishers for phone numbers and arranging to buy (unspecified) fish the day before the fisher goes out. Many fishers wanted to help and offered to bring us what we wanted. We told them we wanted a variety of what they normally catch, and we declined to say which species we sought. When we reached a desired number of fish for a species we stopped purchasing that species so the fishers couldn't conclude we wanted any particular species because we might buy a species one day but not the next.

REPRODUCTION – Reproductive studies of fishes, such as assessment of size at maturity and duration and peak of spawning season, requires knowledge of the stage of gonadal development in an individual fish. The following describes the basic methods that were used for all of the species. Reproductive tissues were examined microscopically and assigned a sex and stage of maturity. Whole gonads were removed from each specimen and then weighed to the nearest 0.01 g. Gonadosomatic Index (GSI) was calculated using the following formula: GSI = (gonad weight)/(body weight – gonad weight). Month-specific GSI was calculated for males and females independently for each species.

The posterior portion of the gonads (when possible, the whole gonad) were saved and fixed in Davidson's fixative for histological processing for a minimum of 48 hours, then transferred to 70% ethanol for 1-2 weeks. Gonad samples were processed, sectioned, and stained using standard procedures. Briefly, the tissue samples were processed in a Modular Vacuum Processor, vacuum infiltrated, and blocked in paraffin wax. After processing, tissue samples were sectioned on a rotary microtone (5-7 um) and three sections of each gonad sample were mounted on a slide, which was stained with double-strength Gill hematoxylin and counter-stained with eosin-y. Stained sections were viewed under a compound microscope at 40-400x magnification to determine sex and reproductive state. Two readers independently assigned sex and reproductive phase to all samples. Date of capture, specimen length, and specimen age were unknown to the readers to prevent bias. If differences in maturity assignments occur, both readers re-read the slide simultaneously. If no decision could be reached, that specimen was eliminated from the analyses. All gonad histology slides were photographed in order to maintain a digital register of the slides.

Gonad samples were classified according to the phase/stage of maturation for males and females using Tables 2, 3 and 4 which combine the histological classification system we have previously developed for Caribbean fish species with updated terminology and organization. Terms and conditions used in the tables are illustrated in Figures 1 – 4 for Princess parrotfish and Figures 5 – 6 for Queen triggerfish. To ensure that immature and resting specimens were assigned correctly, the frequencies of immature, definitely mature (developing, spawning, and spent), and resting fish for each length class were compared separately for each species. If little or no overlap was identified in length of immature and resting specimens, it was assumed that the stages were assessed correctly. For each species, the estimated mean length at first maturity (L_{50}) for females was determined by fitting the logistic curve to the percentage of mature individuals using a routine statistical method if possible. (This requires that there be a variety of different sizes in the sample with both mature and immature fish occurring in the sample.) The L_{50} is defined as the smallest size class in which 50% of the individuals are sexually mature.

Table 2. Reproductive Classes of Princess Parrotfish CA = cortical alveolar oocytes, GVBD = germinal vesicle break-down, GVM = germinal vesicle migration, HO = hydrated oocytes, Og = oogonia, PG = primary growth oocytes, POC = post-ovulatory complex, Sc1 = primary spermatocytes, Sc2 = secondary spermatocytes, Sg = spermatogonia, Sz = spermatozoa, Vtg1 = primary vitellogenic oocytes, Vtg2 = secondary vitellogenic oocytes, Vtg3 = tertiary vitellogenic oocytes. See Figures 1 – 4.

	Reproductive Class/Phase	Histological Features
1	Immature Female	Only Og or PG oocytes. No atresia, muscle bundles, or signs of previous vitellogenic activity.
2 and 2^+	Developing Female	PG, CA, and Vtg1/Vtg2 may be present. No POCs nor Vtg3. Some oocytes possibly atretic. *Early subclass*: Only PG and CA oocytes present. 2^+ denotes that the gonad was functionally a developing ovary, but also contained spermatogenic/testicular tissue. Spermatocytes are few or absent.
3 and 3^+	Spawning capable Female	Vtg3 present. POCs and evidence of early oocyte maturation (i.e. GVM) may be present. 3^+ denotes that sample was functionally a spawning capable female but gonad also contained spermatogenic/testicular tissue. Spermatocytes are few or absent.
4 and 4^+	Actively spawning Female	Technically a subclass of spawning capable. Oocytes in various stages of oocyte maturation, including GVM and GVBD. HOs and POCs likely. 4^+ denotes that sample was functionally an actively spawning female but with possible spermatogenic/testicular tissue. Spermatocytes are few or absent.
5	Regressing/Regenerating Female	Only PG oocytes or few atretic vitellogenic oocytes. Unlike immature phase, POCs and signs of previous vitellogenic activity possible. Muscle bundles may be present. No spermatogenic tissue.
6	Transitioning	Majority of gonad is PG oocytes and/or atretic vitellogenic oocytes. No Vtg 1, Vtg2, Vtg3, GVM, GVBD, or HO. Early spermatogenesis evident with presence of Sg and/or spermatogenic cysts (Sc1/Sc2, no Sz). Neither an active male nor female.
7 and 7*	Developing Male	Proliferation of Sg. Cysts of spermatocytes may be extensive. Early stages of spermatogenesis (i.e. Sc1/Sc2) prevalent. No pooling of Sz in lumen of lobules or ducts. 7* denotes that sample was functionally a developing male but with evidence of oocytes or ovarian tissue still present.
8 and 8*	Spawning capable Male	All stages of spermatogenesis (especially later ones) may be present. Significant pooling of Sz in lumen of lobules and ducts. 8* denotes that sample was functionally a spawning capable male but with evidence of oocytes or ovarian tissue still present.
9 and 9*	Regressing/Regenerating Male	Lumen of lobules and ducts may be empty with minimal residual Sz. Proliferation of Sg possible with few/no cysts of spermatocytes. 9* denotes that sample was functionally a regressing/regenerating male but with evidence of oocytes or ovarian tissue still present.

Table 3. Descriptions of Red Hind reproductive phases.

Phase	Male	Female
Immature (never spawned)	No primary males found. Juveniles are either females or, infrequently, simultaneous or transitional (see below)	Previtellogenic oocytes only; no evidence of atresia. In comparison with resting female, most previtellogenic oocytes <70 um, 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	Development of cysts containing primary and secondary spermatocytes through some accumulation of spermatozoa in lobular lumina and dorsomedial sinuses.	Early: Previtellogenic, with only primary growth and cortical alveolar oocytes. Cortical alveolar oocytes 140-200 um in diameter Middle-Late: Vitellogenic, most advanced oocytes in yolk-granule or yolk-globule stage. Oocytes 170-400 um in diameter.
Spawning capable	Predominance of spermatozoa in lobules and dorsomedial sinuses; little or no occurrence of spermatogenesis	Completion of yolk coalescence and hydration in most advanced oocytes. Zona radiata becomes thin. Postovulatory follicles sometimes present.
Regressing	No spermatogenesis; some residual spermatozoa in lobules and sinuses	More than 50% of vitellogenic oocytes with alpha- or beta-stage atresia.
Regenerating	Little or no spermatocyte development; empty lobules and sinuses.	Previtellogenic oocytes only; traces of artresia. In comparison with immature female, most previtellogenic oocytes >70 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 specimen, stage unknown	Mature, but inadequate quantity of tissue or postmortem histolysis prevent further assessment	Mature, but inadequate quantity of tissue or postmortem histolysis prevent further assessment of reproductive stage
Transitional	Proliferation of spermatogonia through limited spermatogenesis within lamellae of resting ovary accompanied by peripheral sinuses development in musculature of ovarian wall	

Table 4. Histological criteria for Queen Triggerfish gonads during each phase of the reproductive cycle. See Figures 5 and 6.

Reproductive Phase	Male	Female
Immature (never spawned)	Small transverse section compared to regenerating male; little or no spermatocyte development.	Small ovaries. Primary growth oocytes only; no evidence of atresia. In comparison with regenerating female, most primary growth oocytes <60 um. 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. Oogonia are abundant along margin of lamellae.
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.	Early: Previtellogenic, with only primary growth and cortical alveolar oocytes (CA). Middle-Late: Vitellogenic, most advanced oocytes in yolk-granule (Vtg1) or yolk-globule stage (Vtg2). Oocytes 170-400 um in diameter.
Spawning capable	Early: Spermatozoa evident in ducts; spermatogenesis amount in testes ranges from limited to extensive. Greater area of structural tissue in ducts compared to sinuses. Middle (Storage): Spermatozoa storage within expanding ducts; >50% of sinuses' area densely packed with spermatozoa; amount of spermatogenesis in testes ranges from limited to extensive. Late (Recent Spawn): 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 (Vtg3), germinal vesicle migration (GVM), germinal vesicle breakdown (GVBD), hydration, or ovulation. Postovulatory follicle complexes sometimes present. Atresia of vitellogenic and/or hydrated oocytes may be present. Actively Spawning Subphase: Presence of hydrated oocytes (HO), late GVM, GVBD
Regressing	Limited spermatogenesis in testes; some residual spermatozoa in shrunken ducts/lobules and sinuses. Overall number of ducts containing spermatozoa small. Increase in connective tissue in testes, proliferating from center.	More than 50% of vitellogenic oocytes with alpha- or beta-stage atresia.
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 specimen, 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.

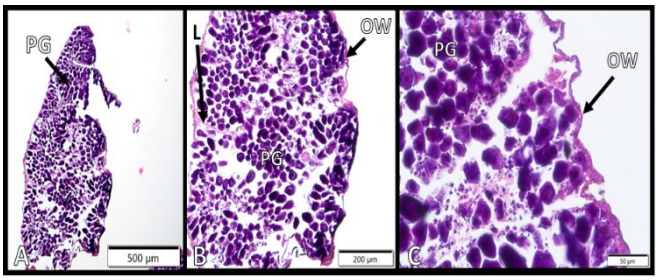
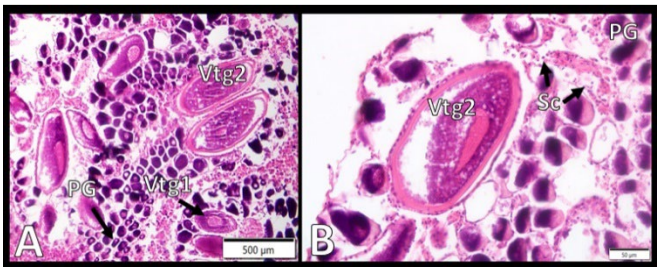
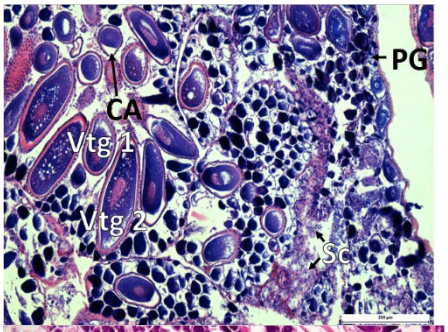


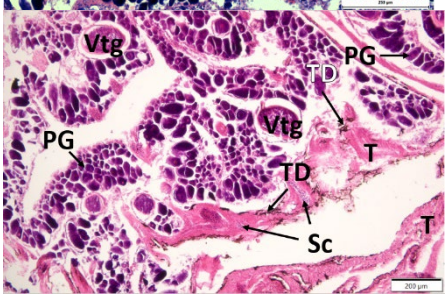
Figure 1. Princess parrotfish female gonads, Class 1. (A) Primary growth oocytes (PG) are the most advanced oocyte stage in immature females. Oogonia may also be present. (B)(C) Notice the thin ovarian wall (OW), lack of muscle or vessel bundles, and absence of vitellogenesis. PG are arranged in lamellae (L), or thin membranes that bound clusters of previtellogenic oocytes.



Developing female gonads, Class 2 and 2+. (A) Note the presence of primary growth oocytes (PG) early vitellogenic oocytes (Vtg 1 and 2). (B) Note the presence of PG and Vtg 2 with pockets of spermatocytes (Sc), which are indicative of a 2^{+} individual.

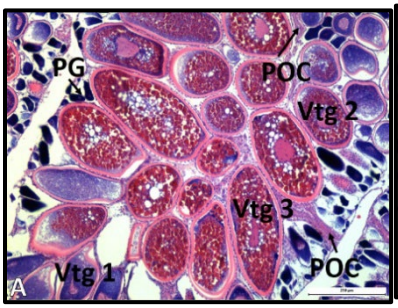


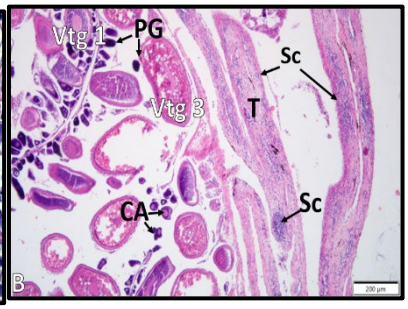
Developing female gonad with cortical alveolar oocytes and spermatocytes, Class 2^{+}. Note the presence of primary growth oocytes (PG), cortical alveolar oocytes (CA), and primary and secondary vitellogenic oocytes (Vtg 1 and 2). Also note the presence of spermatocytes (Sc).



Developing female gonad with spermatocytes and tissue degeneration, Class 2^{+}. Note the presence of primary growth oocytes (PG), vitellogenic oocytes (Vtg), and pockets of spermatocytes (Sc). Also note the presence of presumptive male tissue (T), which is associated with male and transitioning fish, and tissue degeneration (TD).

Spawning capable female gonads, Class 3 and 3^{+}. (A) Note the presence of tertiary vitellogenic oocytes (Vtg 3), which indicate spawning capability. Post-ovulatory complexes (POC) are also evidence of spawning capability. Primary growth oocytes (PG) and early vitellogenic oocytes (Vtg 1 and 2) are still present. (B) In addition to Vtg 3, note the pockets of spermatocytes (Sc) which are indicative of a 3^{+} individual.





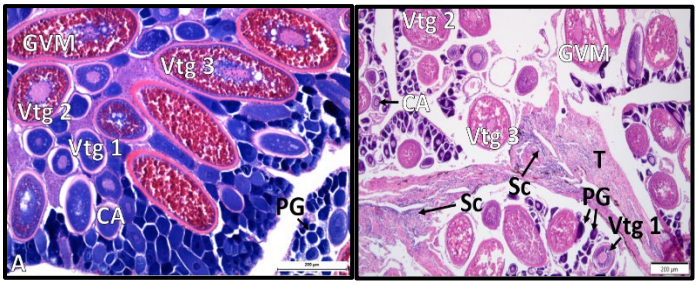
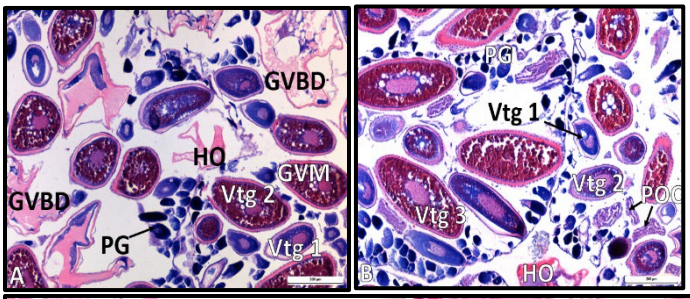
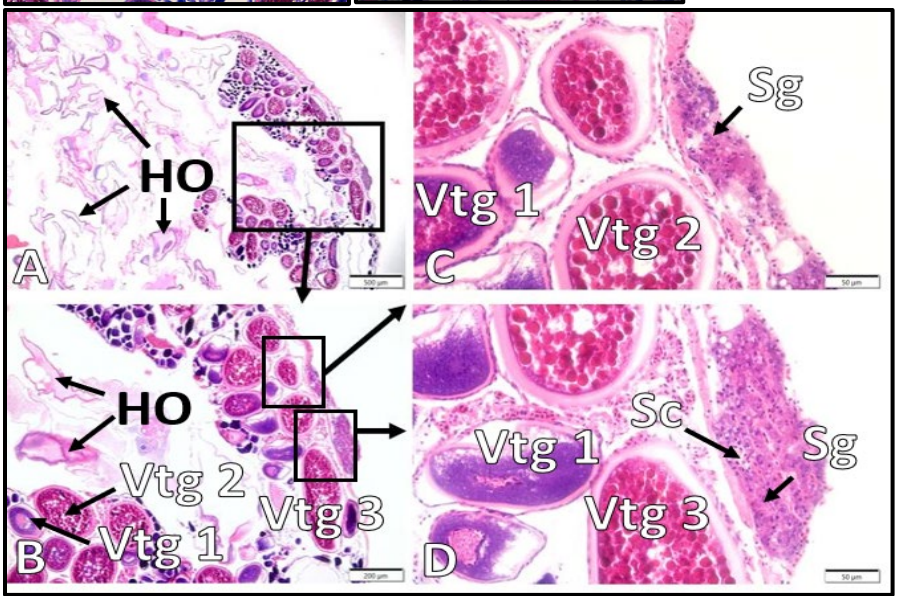


Figure 2. Princess parrotfish spawning capable female gonads with germinal vesicle migration, Class 3 and 3^{+}. (A) Early germinal vesicle migration (GVM) seen in limited abundance is indicative of spawning capability. Also note the presence of primary growth oocytes (PG), cortical alveolar oocytes (CA), and primary, secondary, and tertiary vitellogenic oocytes (Vtg 1, 2, and 3). (B). GVM and Vtg oocytes are present with presumptive male tissue (T) and pockets of spermatocytes (Sc) which are indicative of a 3^{+} individual.

Actively spawning female gonads, Class 4. No evidence of spermatogenic tissue is apparent in either gonad. (A) Stages of mid/late oocyte maturation including widespread germinal vesicle migration (GVM), germinal vesicle breakdown (GVBD), and hydrated oocytes (HO) are indicative of active spawning. Note the continued presence of primary growth oocytes (PG) and early vitellogenic oocytes (Vtg 1 and 2). (B) Post-ovulatory complexes (POC) are observed and indicate recent spawning. The POC occur with HO that indicate active spawning.





Actively spawning female gonad with spermatogenic tissue, Class 4^{+}, at increasing magnification levels. (A) Abundant hydrated oocytes (HO) are visible with a box representing a region of higher magnification. (B) The magnified view of the box in photo A show HO and primary, secondary, and tertiary vitellogenic oocytes (Vtg 1, 2, and 3). Two boxes represent regions of higher magnification. (C)(D) The magnified views of boxes from photo B show Vtg 1 and 3 as well as spermatogonia (Sg) and spermatocytes (Sc) which are indicative of a 4^{+} individual.

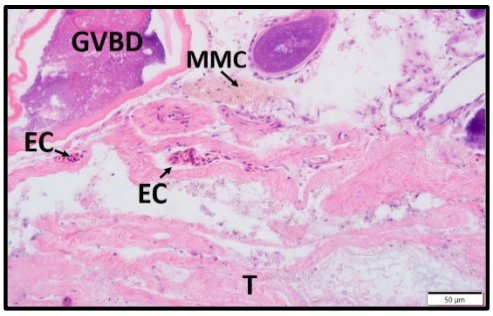
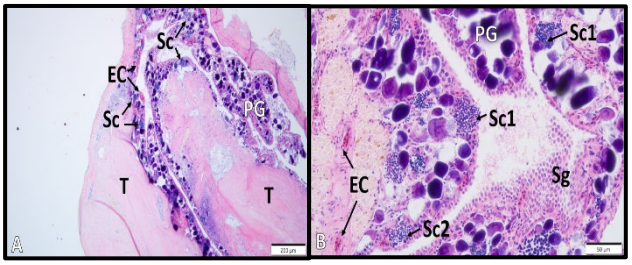
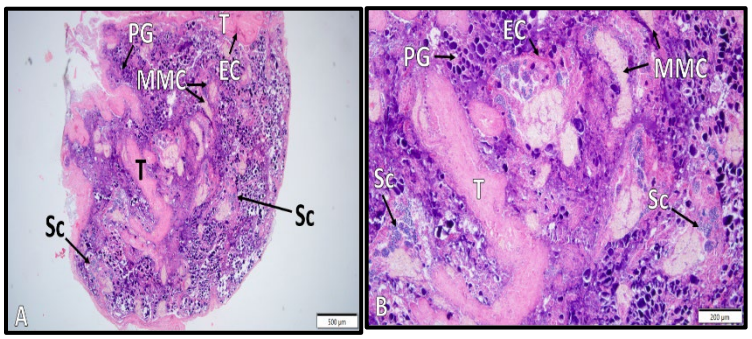


Figure 3. Princess parrotfish actively spawning female gonad with possible male tissue and likely degeneration, Class 4^{+}. Notice the germinal vesicle breakdown (GVBD) that is indicative of an actively spawning female and the presumptive male tissue (T). Eosinophilic cells (EC) and melanomacrophage centers (MMC) are observed and can be associated with processes of oocyte degeneration. EC and MMC are common in known transitioning fish

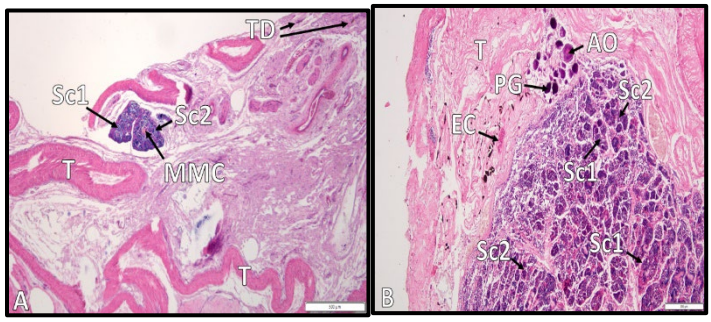


Early transitioning gonads, Class 6. (A) Most of the gonad is dominated by primary growth oocytes (PG) with small, isolated pockets of spermatocytes (Sc). Notice the eosinophilic cells (EC) and abundant amount of presumptive male tissue (T). (B) Most of the gonad is characterized by PG with isolated pockets of primary and secondary spermatocytes (Sc 1 and 2) interspersed. A nest of spermatogonia (Sg) is apparent. EC are also present.



Mid transitioning gonads, Class 6. (A) Primary growth oocytes (PG) still dominate the gonad and spermatocytes (Sc) are spreading throughout the gonad. Presumptive male tissue (T), melanomacrophage centers (MMC), and eosinophilic cells (EC) are present. (B) Pockets of Sc are becoming larger and more widespread throughout the gonad, most of which is dominated by PG. MMC and EC are present and T is abundant.

Developing male gonads with residual female tissue, Class 7*. (A) The gonad consists of primary spermatocytes (Sc1) and secondary spermatocytes (Sc2) which have smaller diameters relative to Sc1. Most of the gonad demonstrates presumptive male tissue (T). The tissue degeneration (TD) and melanomacrophage centers (MMC) likely indicate the breakdown of oogenic material. (B) Sc 1 and 2 dominate the gonad. Some primary growth oocytes (PG) and atretic oocytes (AO) are present. Eosinophilic cells (EC) can be seen interspersed with abundant T.



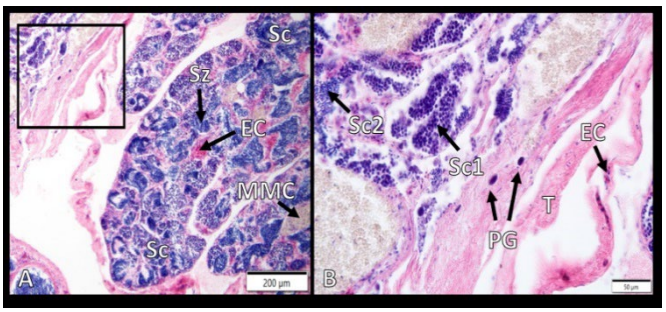
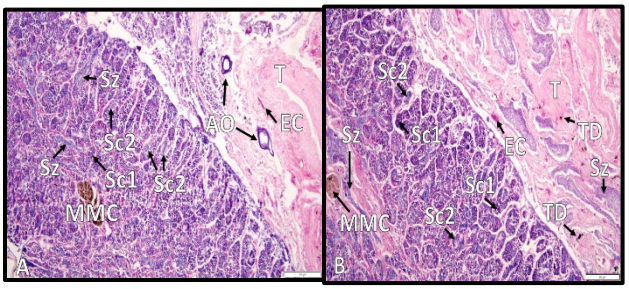
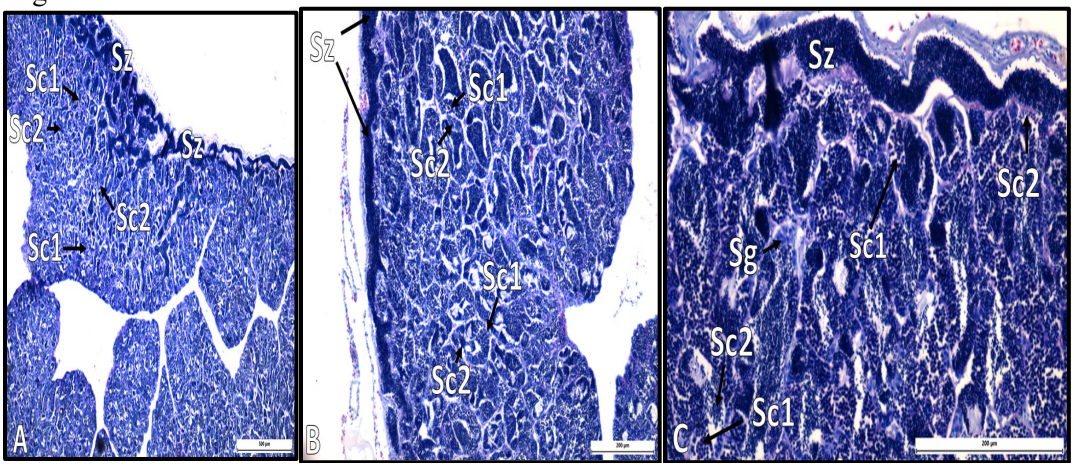


Figure 4. Princess parrotfish spawning capable male gonad, Class 8*, for the smallest initial male in this study. The smallest initial male measured 159 mm TL and had an unknown age. (A) The presence of spermatocytes (Sc) and the pooling of spermatozoa (Sz) indicate spawning capability. The presence of melanomacrophage centers (MMC) and eosinophilic cells (EC) likely indicate degeneration of oogenic material. The box in the upper left represents a gonad region for higher magnification. Notice the lamellar-like structure of the male gonad. (B) The magnified view of the boxed region in photo A show Sc 1 and 2 as well as primary growth oocytes (PG) that are likely degenerating. The presence of PG with EC indicates residual female tissue (Class 8*).



Spawning capable male gonads with residual female tissue (Class 8*). (A) Primary spermatocytes (Sc1) and secondary spermatocytes (Sc2), which have smaller diameters relative to Sc1, are prevalent. The pooling of spermatozoa (Sz) indicates spawning capability. Melanomacrophage centers (MCC) and eosinophilic cells (EC) are common and presumptive male tissue (T) is widespread. The presence of atretic oocytes (AO) in the process of breaking down indicates that residual female tissue is present (Class 8*). (B) Sc 1 and 2 are widespread and there is significant pooling of Sz. There is abundant T. The presence of tissue degeneration (TD) and MMC may be indicative of degenerating oogenic material.



Spawning capable gonads with no residual female tissue, Class 8. (A)(B)(C) Primary spermatocytes (Sc1) and secondary spermatocytes (Sc2), which have smaller diameters than Sc1, are widespread. The pooling of spermatozoa (Sz) is particularly apparent in the peripheral sinuses. No residual female tissue is apparent.

Figure 5. *Histological examples of reproductive phases for the gonads of female Queen Triggerfish as described in Table 2: (A) Immature – primary growth oocytes (PG) and thin ovarian wall (OW): (B) Developing (early) – cortical alveolar oocytes (CA); (C) Developing (mid-late) – primary and secondary vitellogenic oocytes present (V); (D) Spawning capable – Oocyte maturation in the most advanced oocytes: zona radiata becomes thin and oocytes are undergoing coalescence of yolk globules; (E, F) Actively spawning subphase – presence of postovulatory follicle complexes (POF) and oocytes show late germinal vesicle migration (GVM) and germinal vesicle breakdown (GVBD); (G) Regressing – more than 50% of vitellogenic oocytes with atresia (A); (H) Regenerating phase PG and thick OW; (I) Whole gonads of a female – note that the two ovaries fuse together in Queen Triggerfish.*

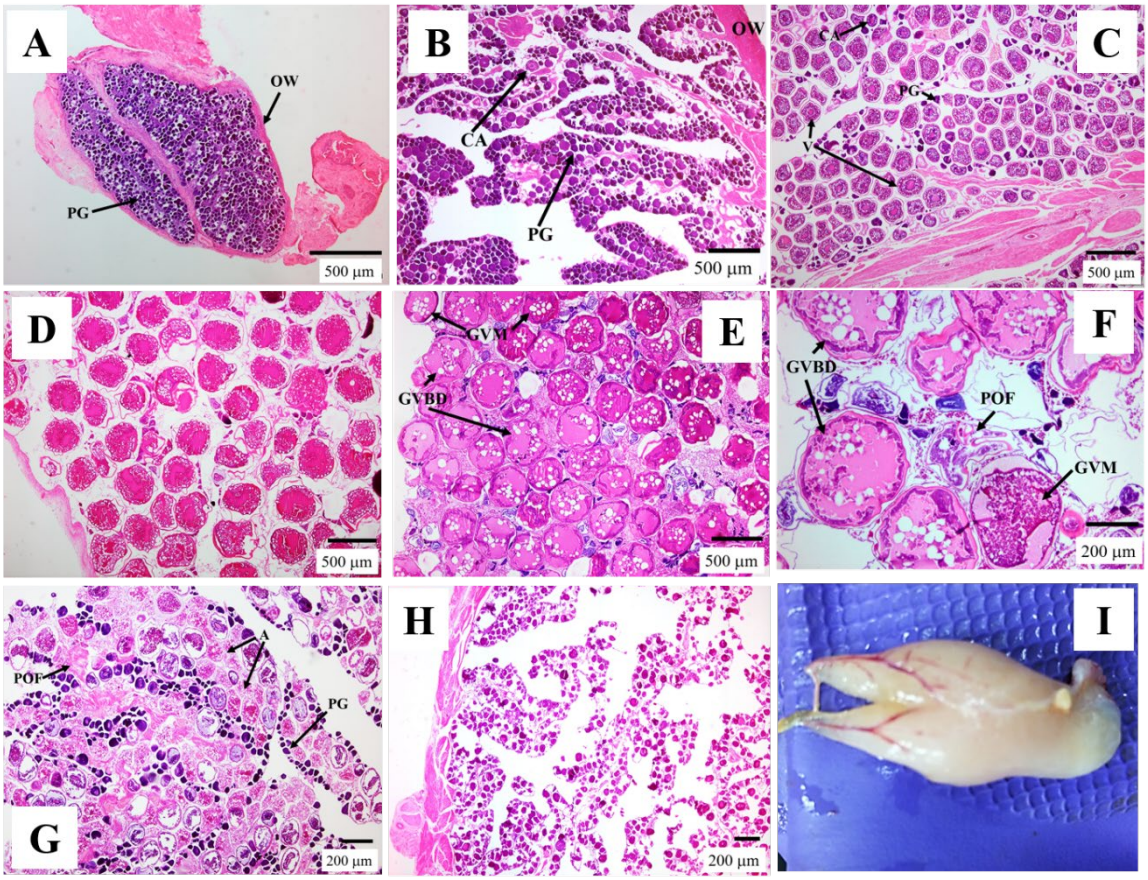
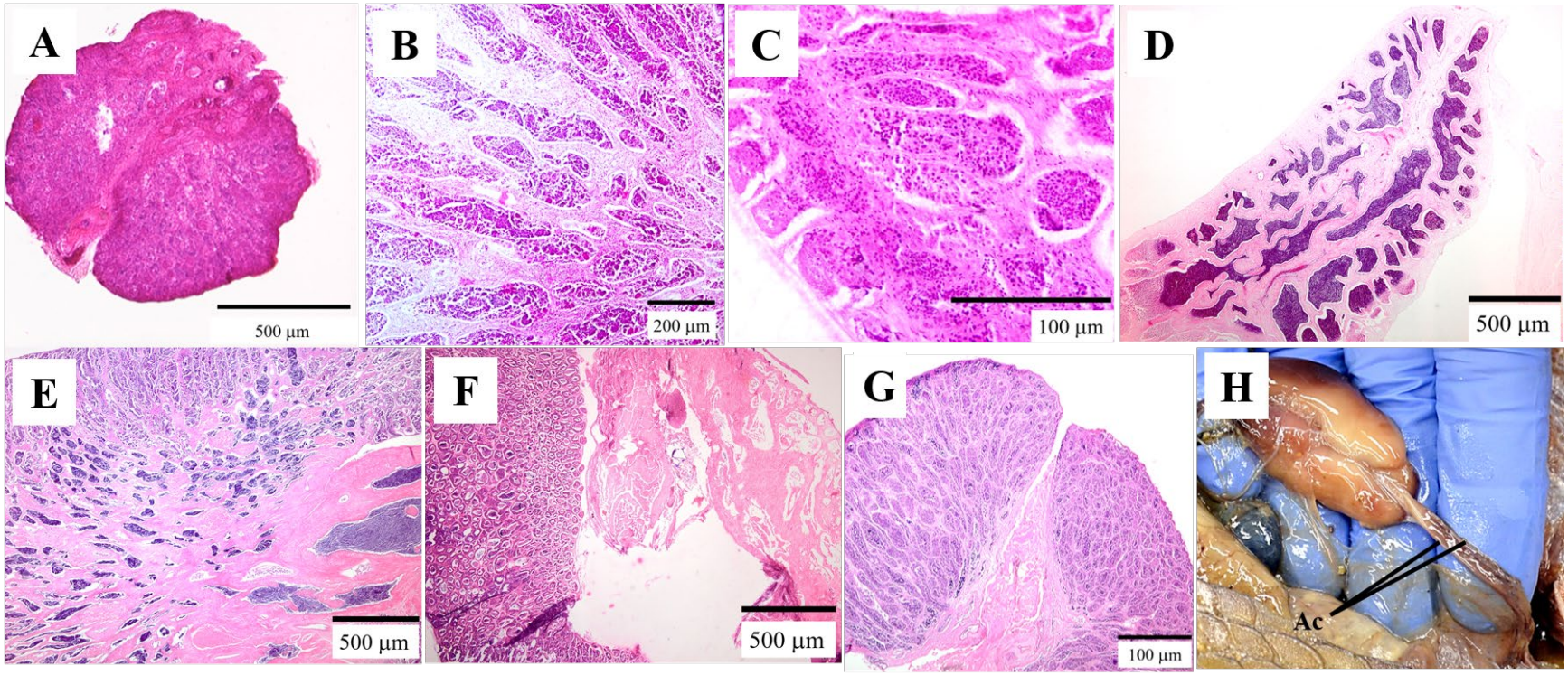


Figure 6. *Histological examples of reproductive phases for the gonads of male Queen Triggerfish as described in Table 2: (A) Immature – no spermatocysts with spermatocytes developing in testes; (B) Developing – limited spermatogenesis in testes; elongation of lobules and some development of spermatozoa in testes, but no accumulation in lobules, efferent ducts, and spermatic ducts; (C) Developing – note the development of spermatozoa; (D) Spawning Capable – accessory gland with spermatozoa storage in its expanding ducts; (E) Spawning Capable – large expanded ducts not as densely packed with spermatozoa; (F) Regressing – limited spermatogenesis in testes, some residual spermatozoa in shrunken ducts and sinuses; (G) Regenerating – little to no spermatocytes development, empty lobules/ducts and sinuses; (H) Queen Triggerfish male gonad with spermatic duct and accessory glands (Ac).*



Results of Maturity Study

PRINCESS PARROTFISH –

All 587 Princess parrotfish examined in this study were mature. The breakdown of the catch by phase is as follows:

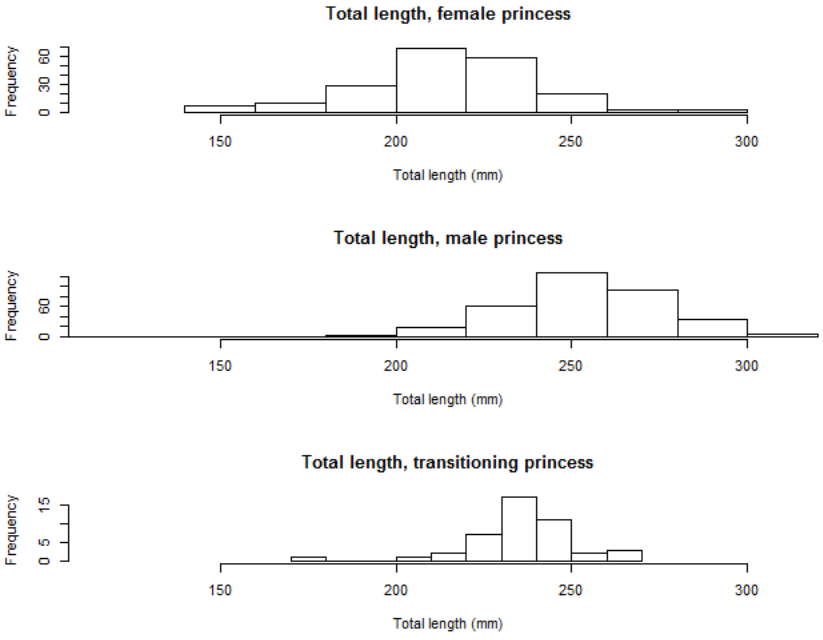
phase	initial	intermediate	Terminal
number	244	1	342

Roughly 42% of the catch is initial phase. Further breakdown by phase and sex is shown in the table below.

	female	male	transitional
initial	198	4	42
intermediate	0	1	0
Terminal	1	339	2

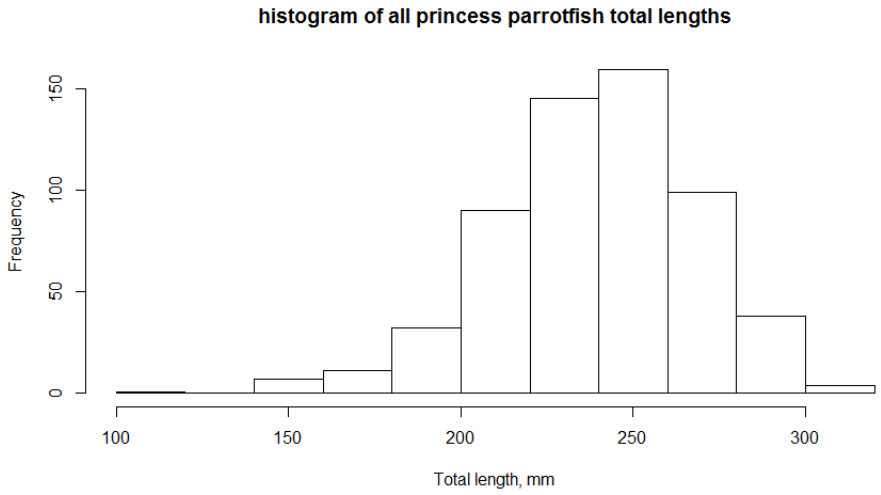
The sex ratio (female/male) is 199/344 = 0.58 (ignoring the 44 transitional fish).

The males caught in the fishery tend to be considerably larger than the females, as shown in the figure below.

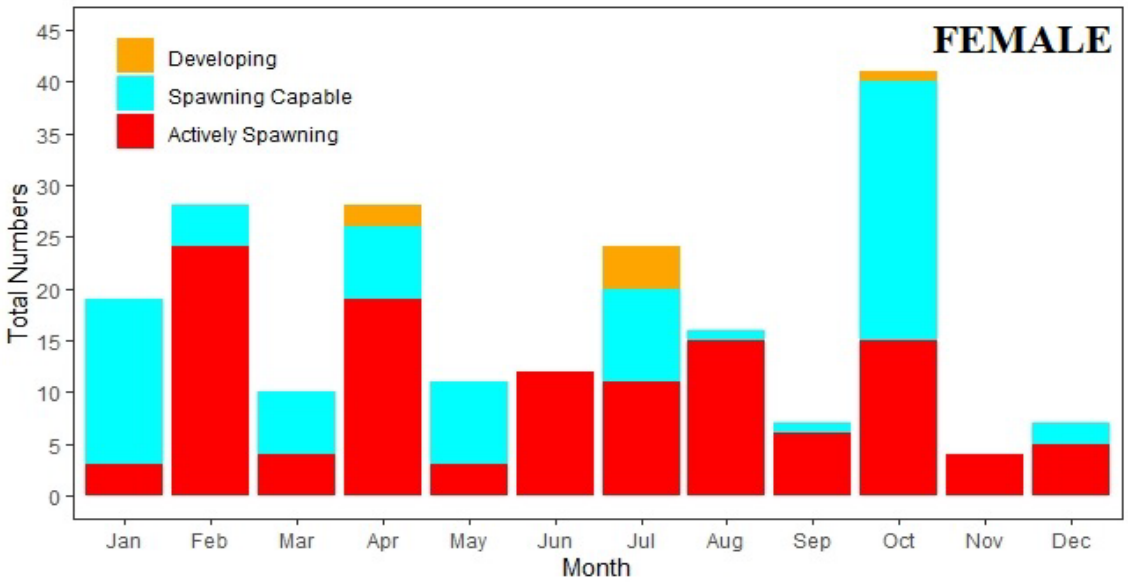


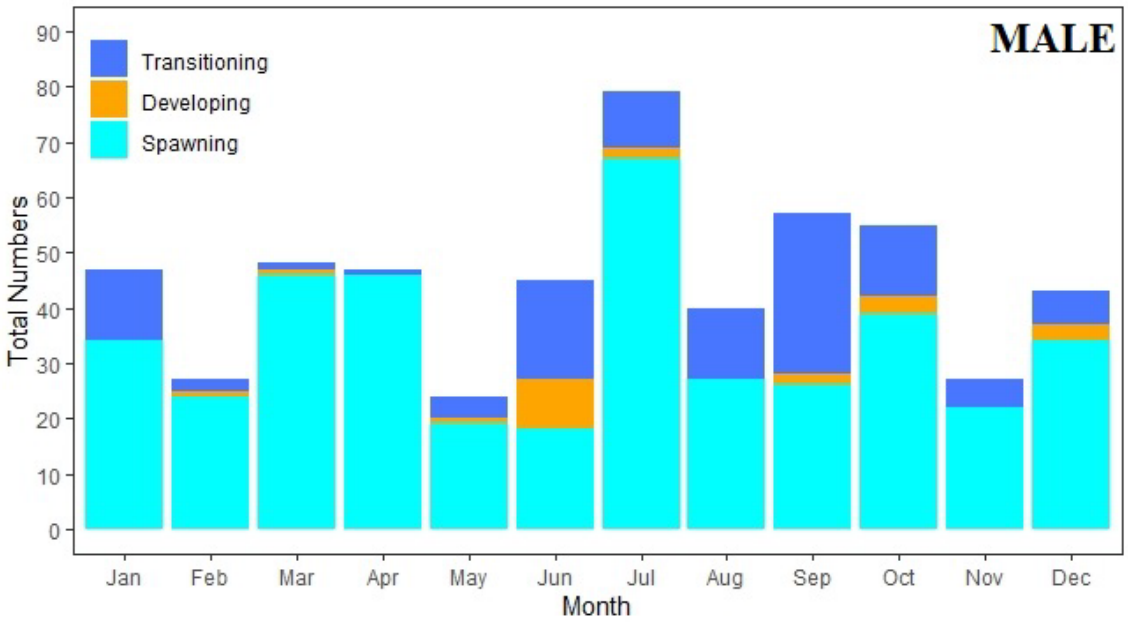
For the purpose of estimating total mortality rate from mean length it is necessary to specify a length of entry into the fishery, L_c, and the mean length of those fish greater in size than , L_c. From the histogram below, L_c appears to be around 220 mm.

Species	mean length	L_c	mean > L_c
Princess	240.4	220	252.7

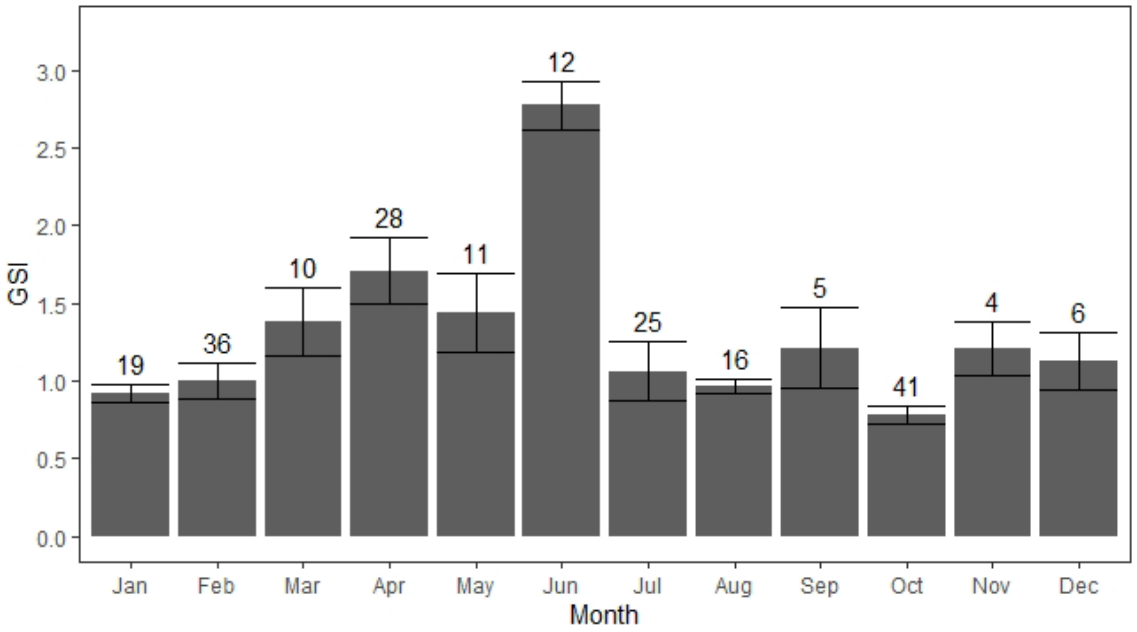


From the bar graphs below, it appears that Princess parrotfish spawn throughout the year. They become mature around age 1.5 (50%) and virtually all are mature by age 2.





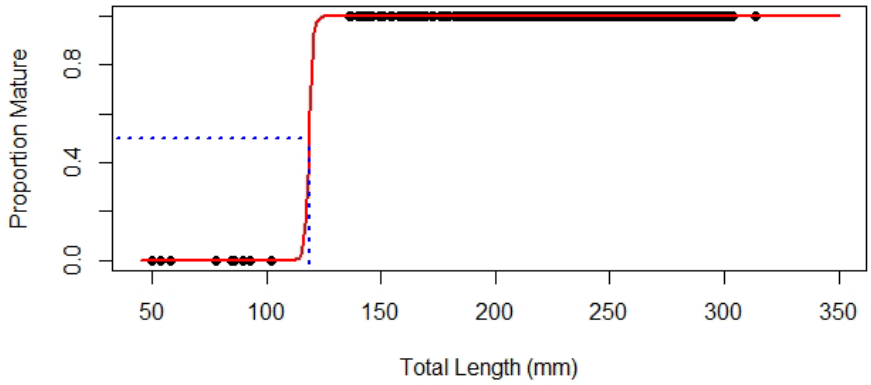
Monthly numbers of female Princess parrotfish (above) in developing, spawning capable, and actively spawning classes and monthly numbers of males (below) in the developing and spawning classes relative to the monthly numbers of transitioning fish.



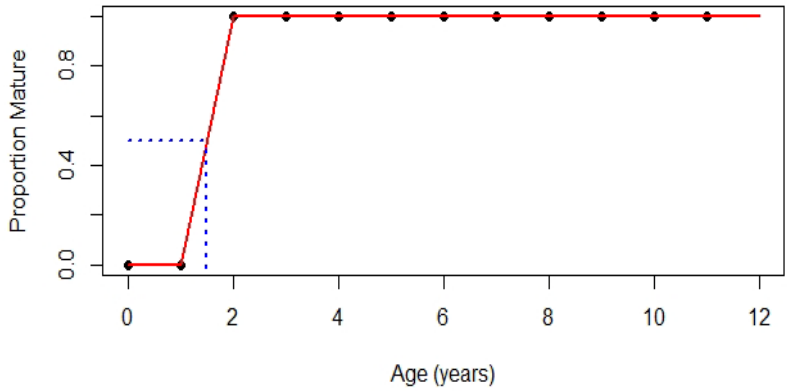
Monthly mean GSI of female princess parrotfish. GSI was defined by the equation $\frac{gonad\ weight\ in\ g}{total\ body\ weight\ in\ g} X\ 100$. *Numbers above each bar represent monthly sampling size and the error bars represent standard error.*

An estimate of age-at-maturity is needed for purposes of modeling the status of the population using spawning potential ratio. Maturity data for Princess parrotfish is presented here for

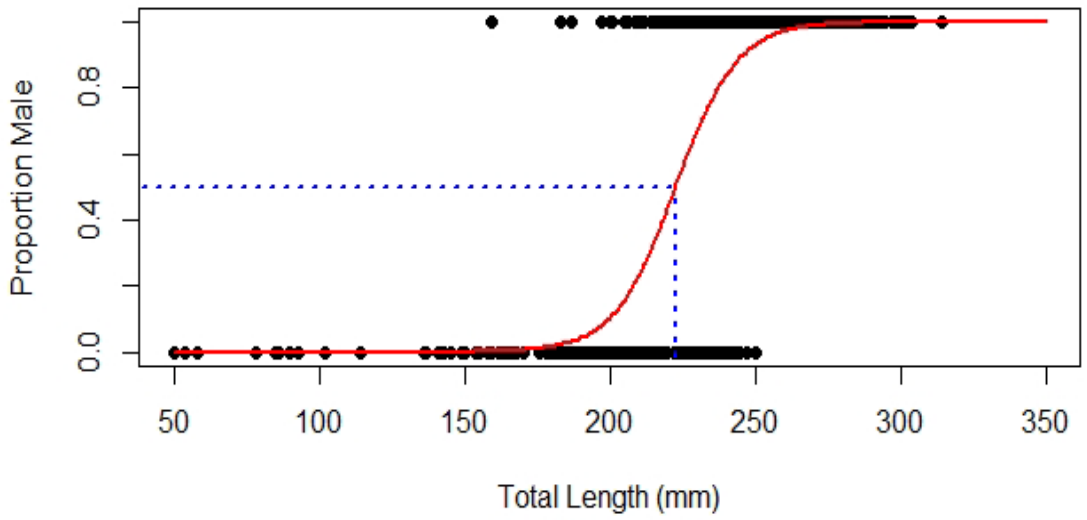
reference and came from a co-occurring investigation under the direction of V Shervette. For specific information on these data, refer to: Jones (2020).



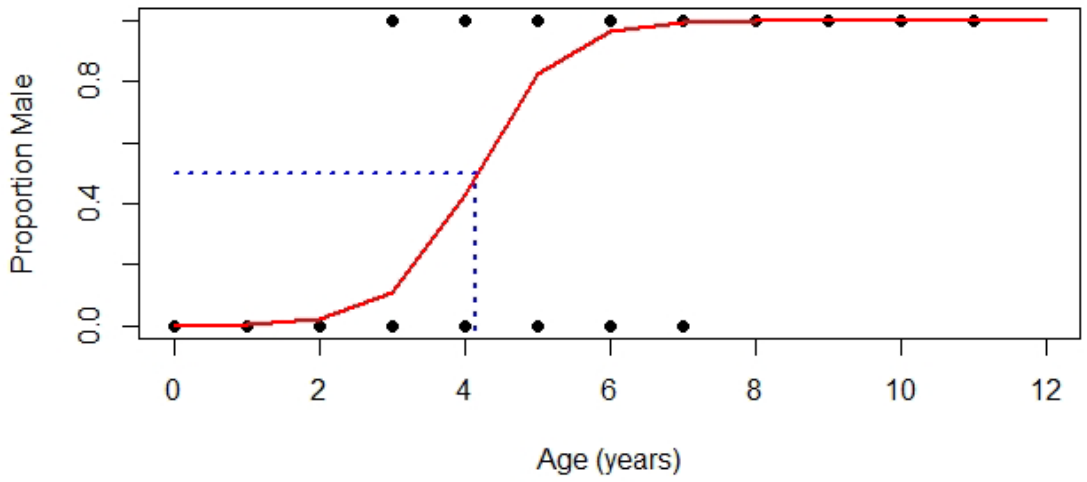
Total length at median sexual maturity in princess parrotfish. The length at median sexual maturity (LM_{50}) was 119 mm (n = 756). (from Jones 2020)



Age at median sexual maturity in princess parrotfish. The age at median sexual maturity (AM_{50}) was 1.5 years (n = 712). (from Jones 2020)



Total length at median sexual transition in princess parrotfish. The length at median sexual transition (LS_{50}) was 223 mm (n = 643).



Age at median sexual transition in princess parrotfish. The age at median sexual transition (AS_{50}) was 4.2 (n = 601).

QUEEN PARROTFISH –

Examination of the data for 300 Queen Parrotfish revealed all 300 were mature fish.

The breakdown of the catch by phase shows that roughly half of the fish are initial phase and half are terminal:

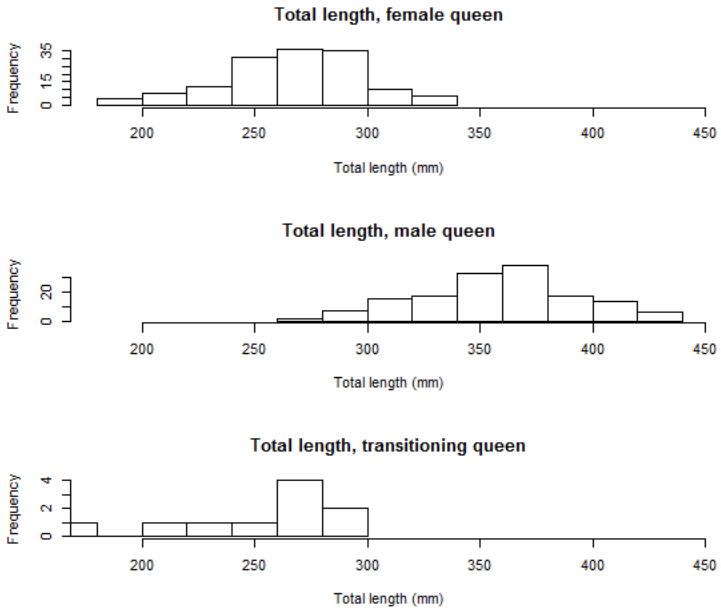
Phase:	Initial	Terminal
Number:	154	146

The breakdown by phase and sex is as follows:

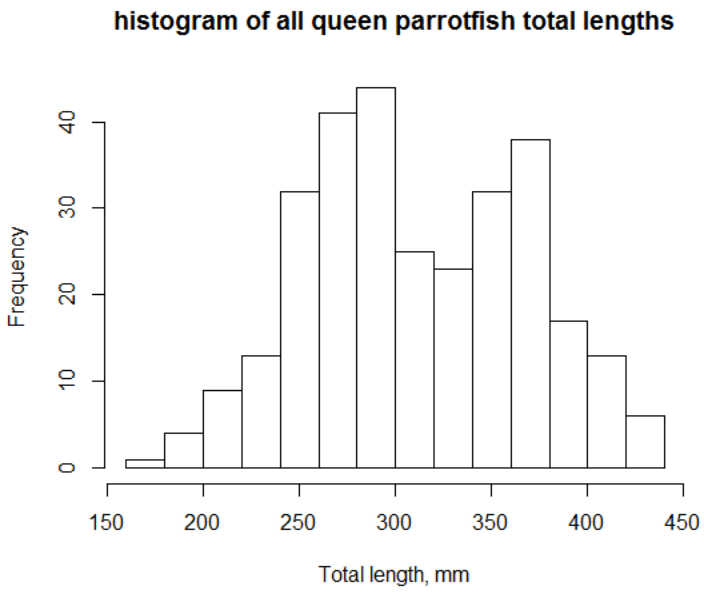
	Female	Male	Transitional
Initial	142	2	10
Terminal	0	146	0

Thus, the sex ratio (females/males) is 142/148 = 0.96 (ignoring the 10 transitional animals).

The males caught by the fishery tend to be larger than the females, as shown in the histograms below.



The length frequency distribution for all fish is:



The mean length of fish greater in length than L_c is as follows for various values of L_c:

Value of Lc	240	250	260	270	280
Mean length	321.3	325.6	330.6	337.1	342.9

This can be used as input to the Beverton-Holt mean length-based mortality estimator.

REDBAND PARROTFISH –

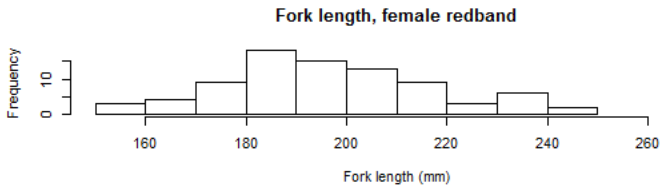
Examination of the data for the 374 Redband parrotfish collected from the commercial fishery reveals that all specimens were sexually mature. The breakdown by phase and by sex and phase are as follows:

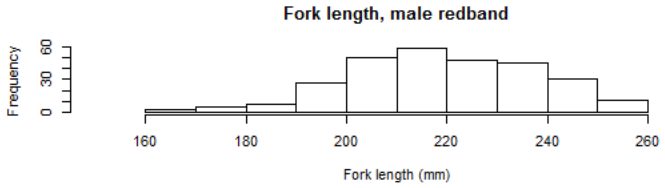
```
Phase:       Initial   Intermediate     Terminal
Number:           89              4          281
```

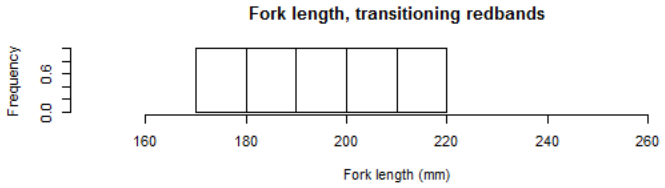
```
  phase        female    male    transitioning
  Initial          84       0                5
  Intermediate      0       4                0
  Terminal          0     280                1
```

Thus, the sex ratio (female/males) is 84/284 = 0.30 (ignoring the 6 transitioning animals).

The males caught by the fishery tend to be larger than the females, as shown in the histograms below.

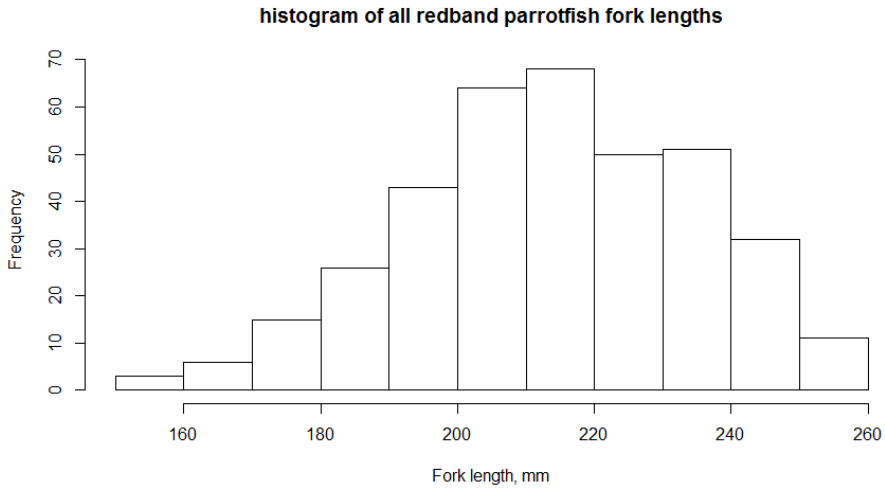


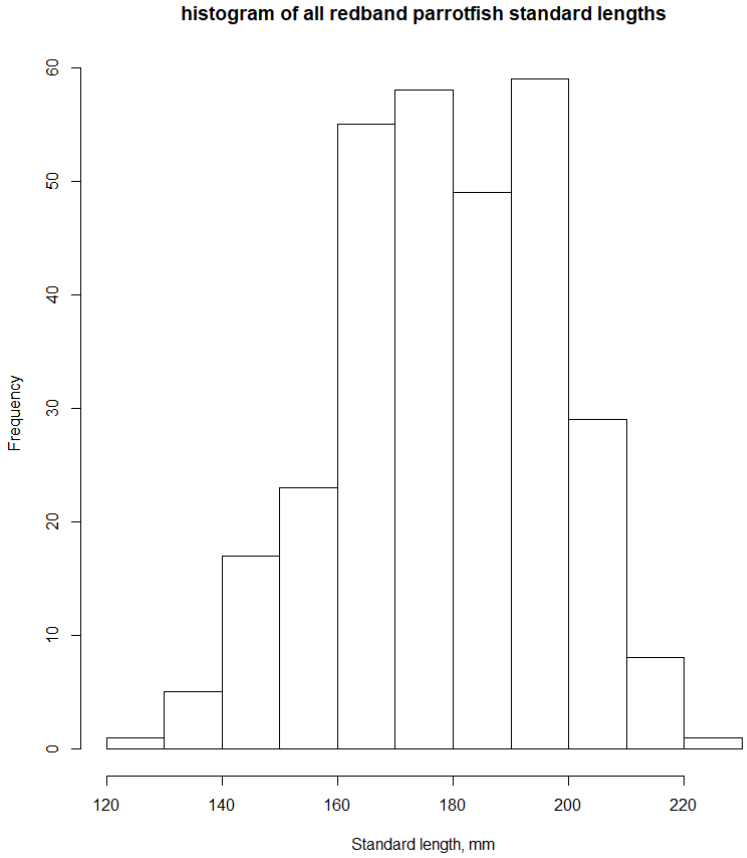




For purposes of estimating total mortality rate from the length-frequency distribution, the mean length of those animals greater than or equal to L_c is:

Species	mean length	L_c	mean > L_c
Redband	214.6 FL	200 FL	224.0 FL
Redband	179.2 SL	160 SL	184.5 SL





REDTAIL PARROTFISH –

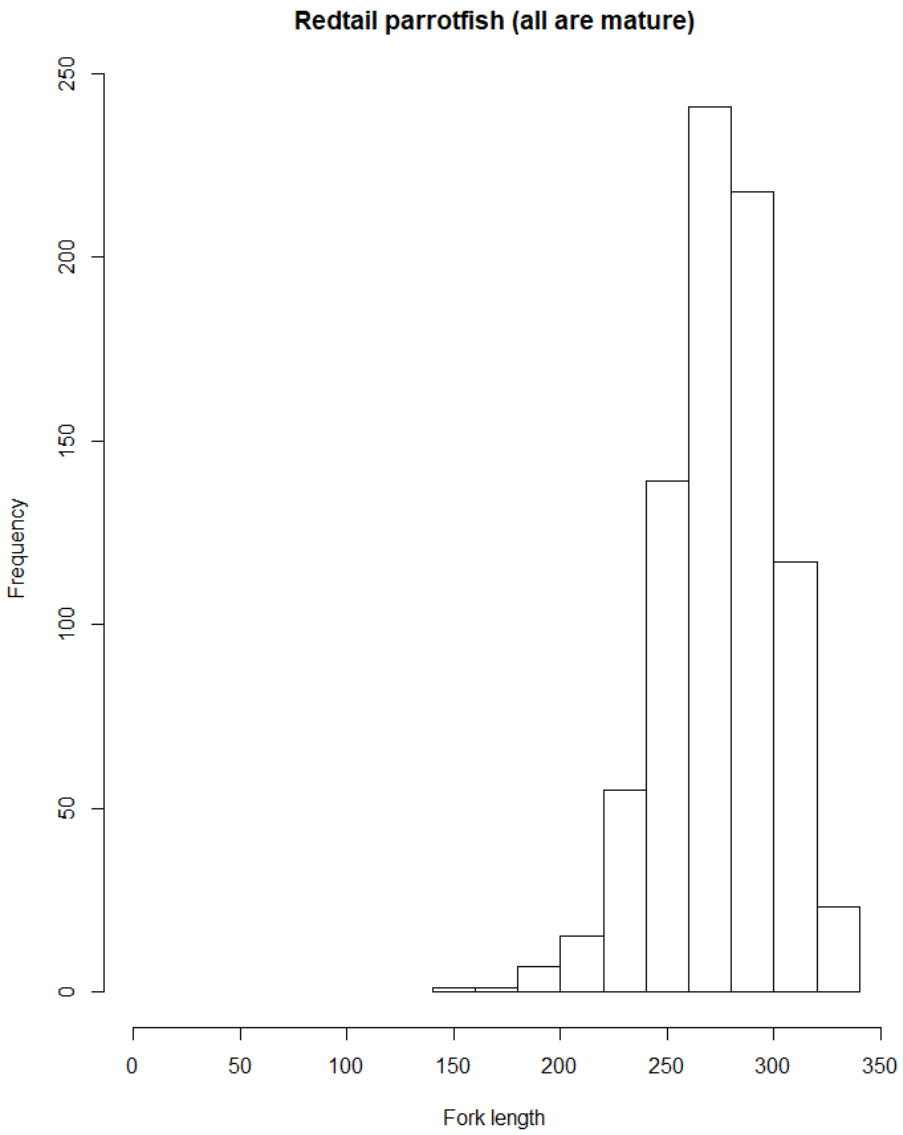
All of the 819 Redtail parrotfish obtained from commercial fishermen were mature fish. The breakdown by phase is:

initial	intermediate	terminal
425	12	382

The phase categories relate to the sex categories as follows:

Phase	sex			
	female	male	simultaneous	transitional
initial	308	29	1	86
intermediate	1	11	0	0
terminal	0	382	0	0

Here, simultaneous refers to one fish that had one gonad that was clearly male and another that was clearly female. The sex ratio (female/male) is 309/422 = 0.73 (ignoring the 86 transitional animals).



The mean length of fish greater than or equal to 260 mm FL is 287. The mean length of fish greater than 220 mm SL is 246. Note, however, that 209 out of 819 fish have no standard length measurement.

REDFIN/YELLOWTAIL PARROTFISH –

All 103 Redfin/Yellowtail parrotfish examined were mature. The breakdown by phase is:

phase	initial	intermediate	Terminal
number	95	4	4

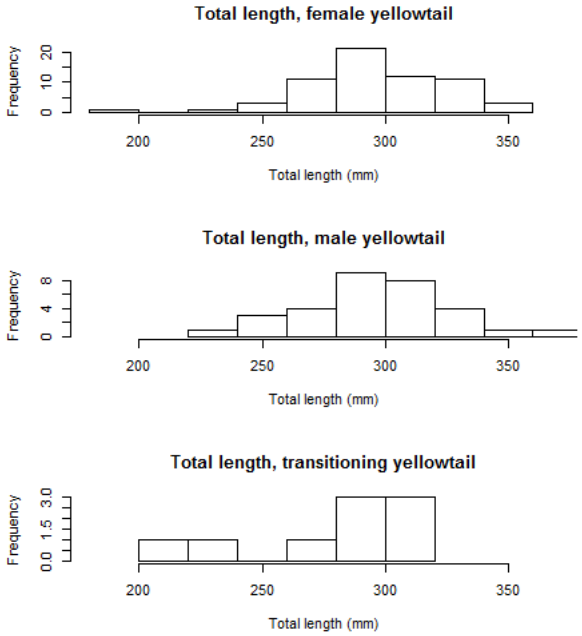
and the breakdown by phase and sex is:

	female	male	transitional
initial	63	23	9
intermediate	0	4	0

```
Terminal          0     4              0
```

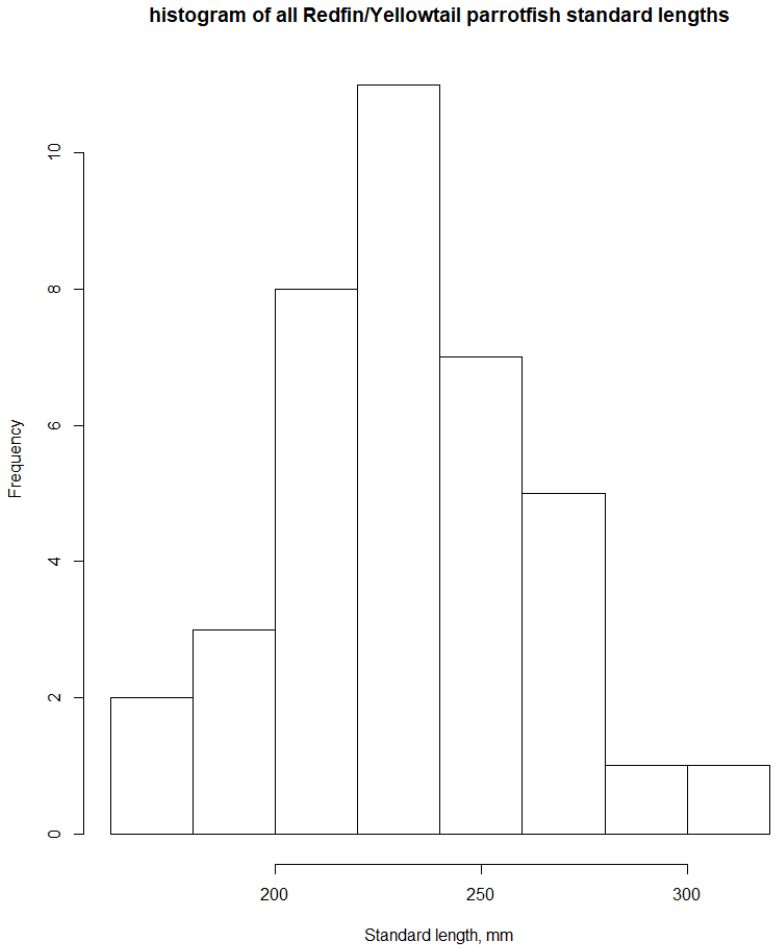
Thus, the sex ratio is 63/31 = 2.03 (ignoring the 9 transitional animals).

The size distribution of the males is similar to that of the females, as shown below.



The mean size is:

Species	mean length	Lc	mean > Lc
Yellowtail	294.4 mm FL	270	306.2
Yellowtail	233 mm SL	210	245.3



STOPLIGHT PARROTFISH –

Examination of the data for 1333 stoplight parrotfish revealed that all but one fish were mature fish. An additional 110 samples were received from the Virgin Islands fishery department but these were not well preserved and maturity of these specimens could not be determined. The breakdown of the catch by phase shows that roughly half of the fish are initial phase and half are terminal:

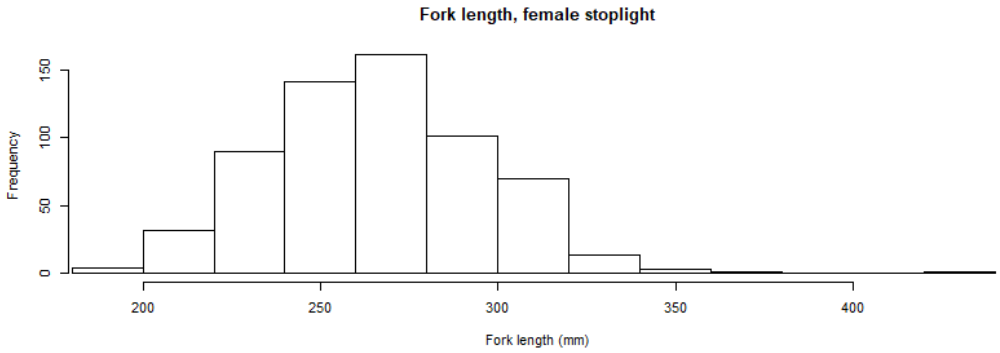
Initial	Juvenile	Terminal	Transitional
675	1	634	22

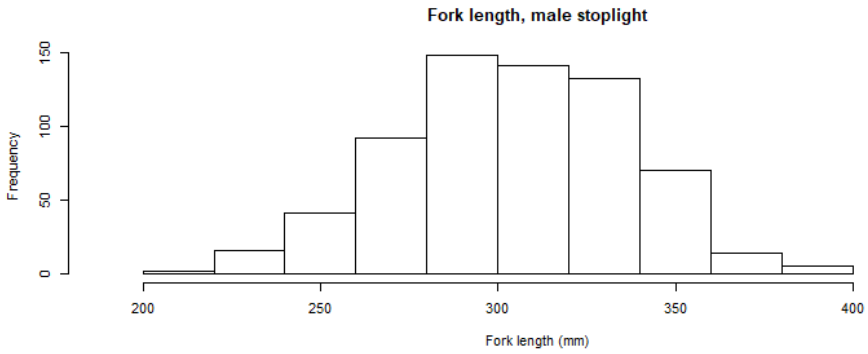
The breakdown by phase and sex is as follows:

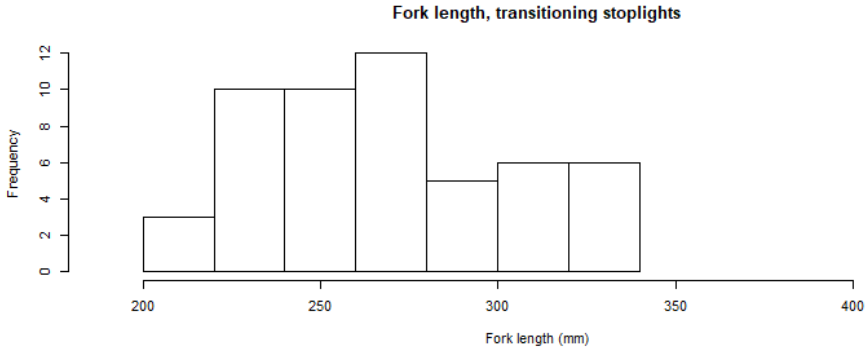
Phase	Female	Male	Transitional
Initial	616	11	48
Juvenile	1	0	0
Terminal	0	632	2
Transitional	2	18	2

Thus, the sex ratio (female/male) is 619/661 = 0.94 (ignoring the 52 transitional-sex animals).

The males caught by the fishery tend to be larger than the females, as shown in the histograms below.

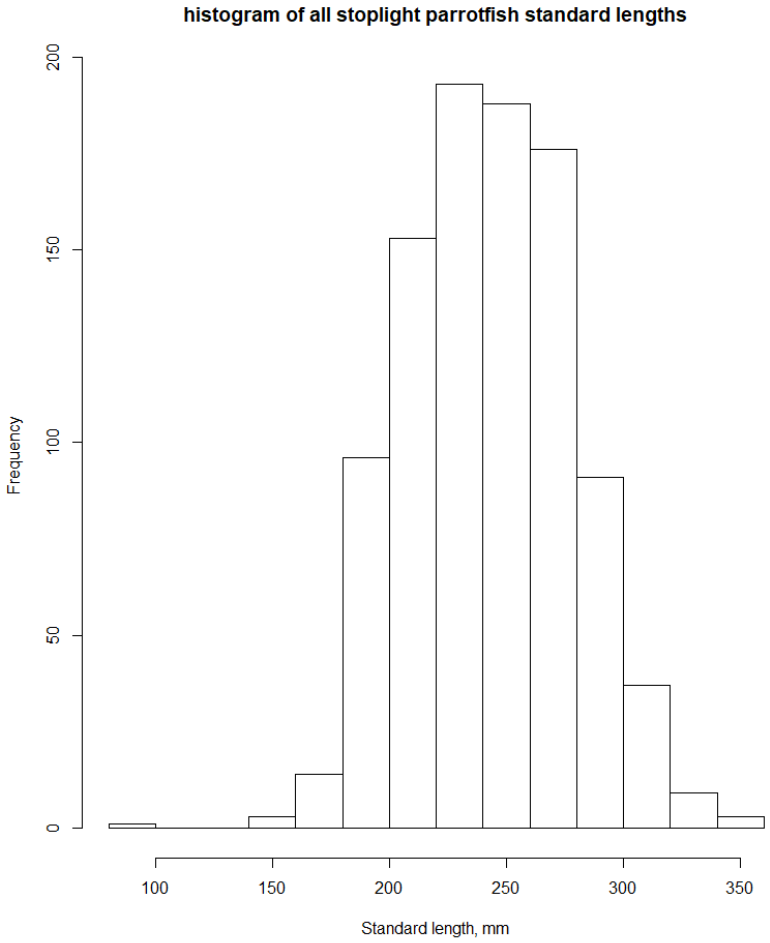




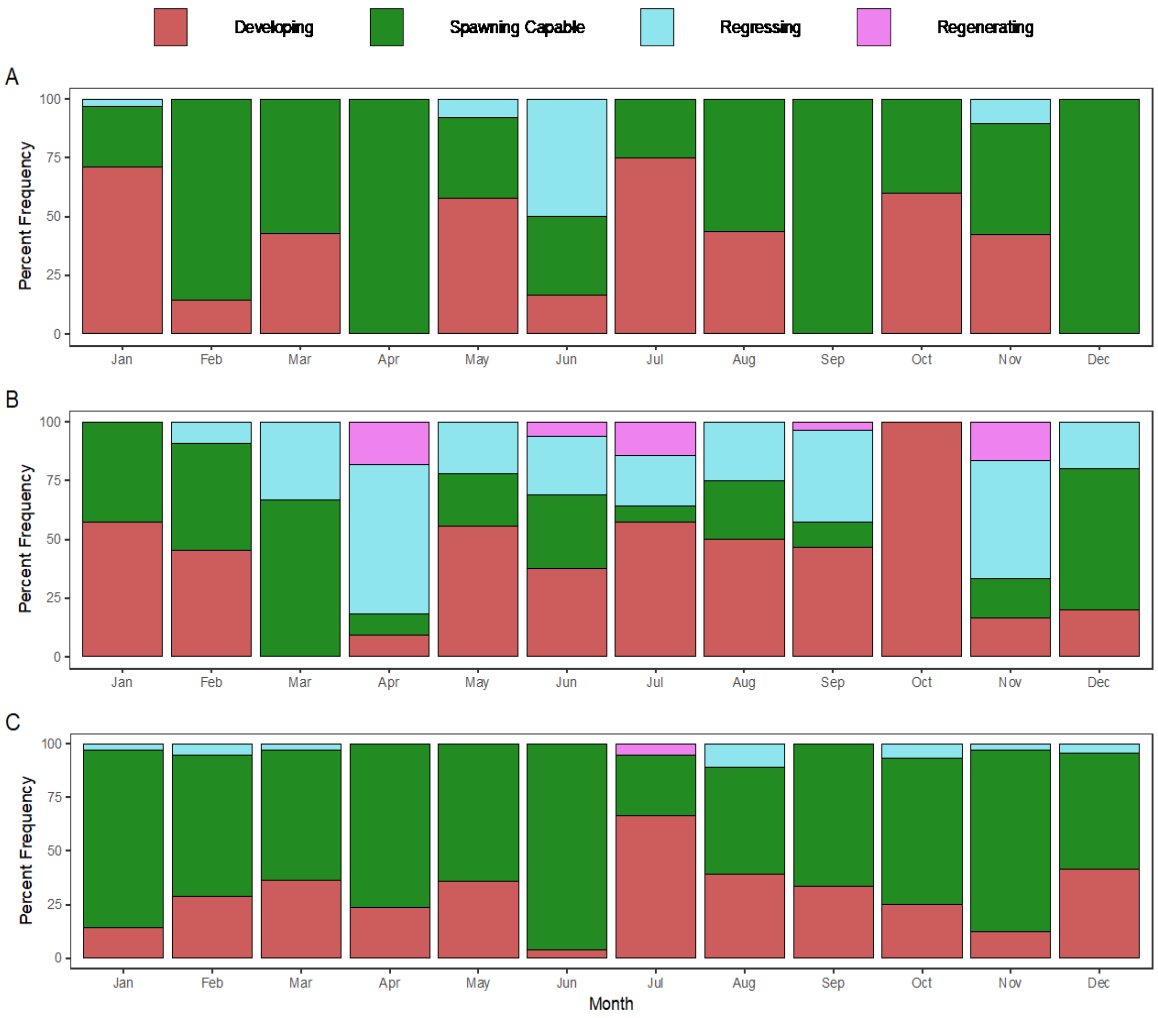


For purposes of modeling the dynamics of the population, it is convenient to work with standard length because von Bertalanffy growth parameters are available for measurements of standard length.

From the histogram of standard lengths below it appears the size of entry into the fishery is about 210 mm SL. The mean length above 210 mm is 254 mm SL.

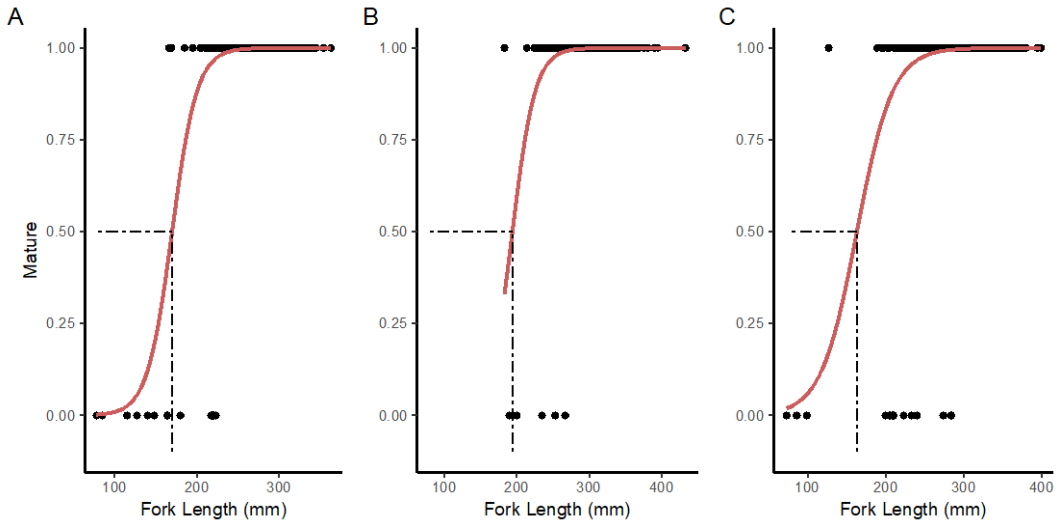


Spawning takes place in every month of the year (see figures below). There appear to be inter-island differences in spawning patterns but it is not clear if this is because of small sample sizes.

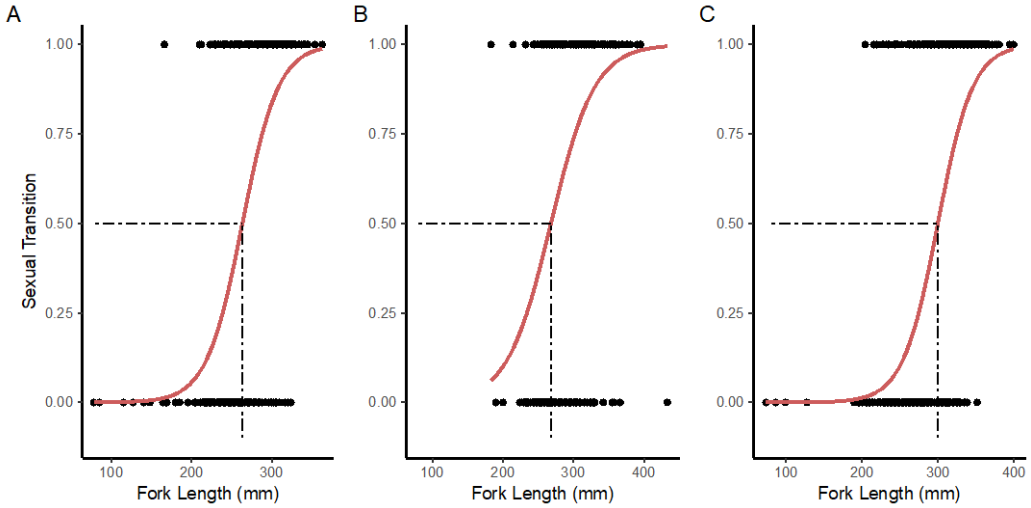


Proportions of female Stoplight Parrotfish in different reproductive phases throughout the months of the year in Puerto Rico (A), St. Thomas (B), and St. Croix (C).

An estimate of proportion mature at age is needed in order to compute spawning potential ratio. Maturity data for stoplight parrotfish is presented here for reference and came from a co-occurring investigation under the direction of V. Shervette. For specific information on these data, refer to: Wagner (2019).

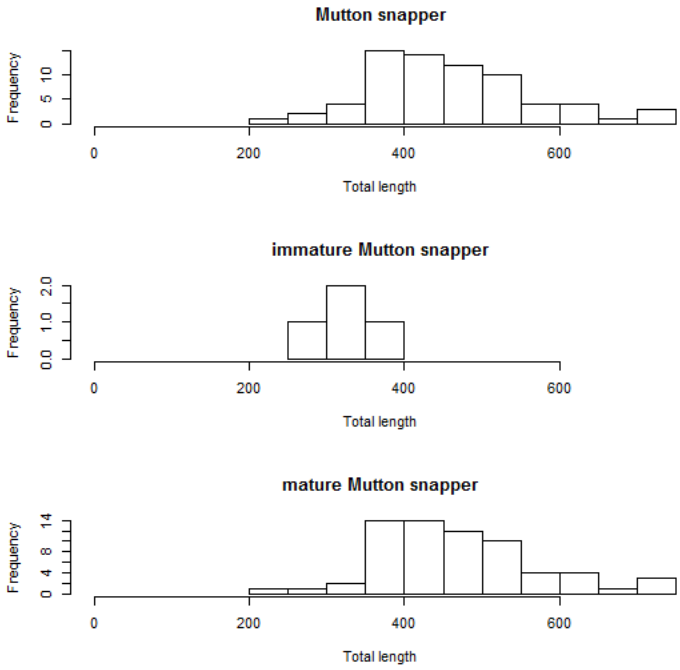


Length at 50% maturity for Stoplight Parrotfish in Puerto Rico (A), St. Thomas (B), and St. Croix (C). From Wagner (2019).



Length at 50% sexual transition for Stoplight Parrotfish in Puerto Rico (A), St. Thomas (B), and St. Croix (C). From Wagner (2019).

MUTTON SNAPPER –



Histograms of all fish, immature fish and mature fish for mutton snapper for all three islands combined.

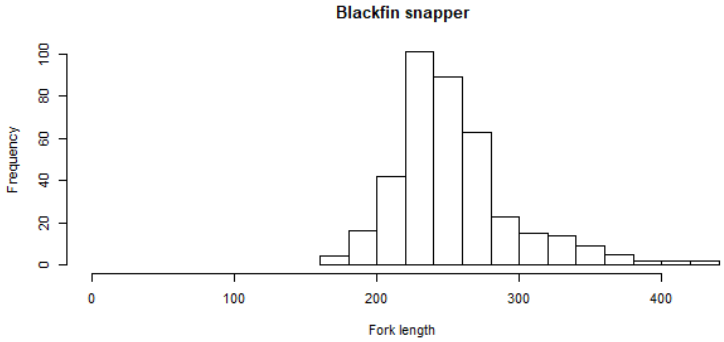
Out of 72 specimens of mutton snapper, 4 (5.6%) were immature.

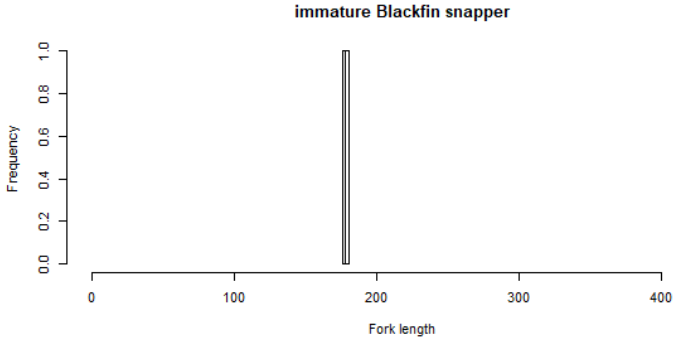
The sex ratio (female/male) is 0.89:

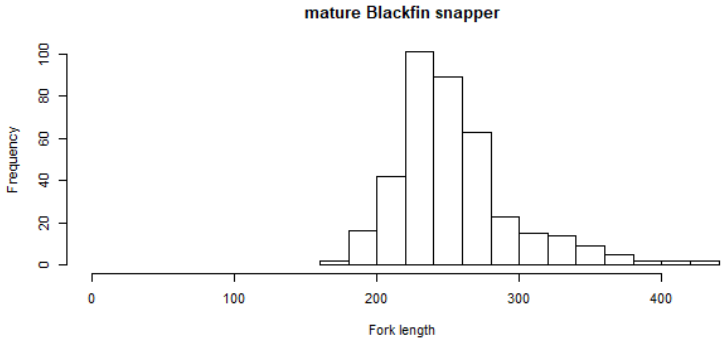
```
female   male
    34     38
```

The mean length of fish greater than or equal to 350 mm TL is 480.

BLACKFIN SNAPPER –





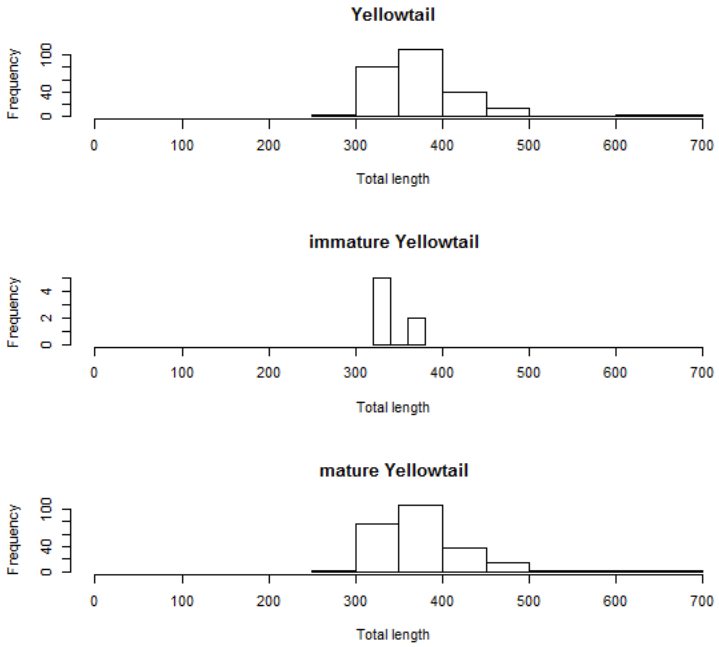


Length frequency distribution of all blackfin snapper (n=387), immature fish (n=2), and mature fish (n=385).

There were 200 females and 187 males for a sex ratio (females to males) of 1.07.

The mean length of those fish greater than or equal to 220 mm FL is 264.

YELLOWTAIL SNAPPER –



Histograms of all fish, immature fish and mature fish for yellowtail snapper for all three islands combined.

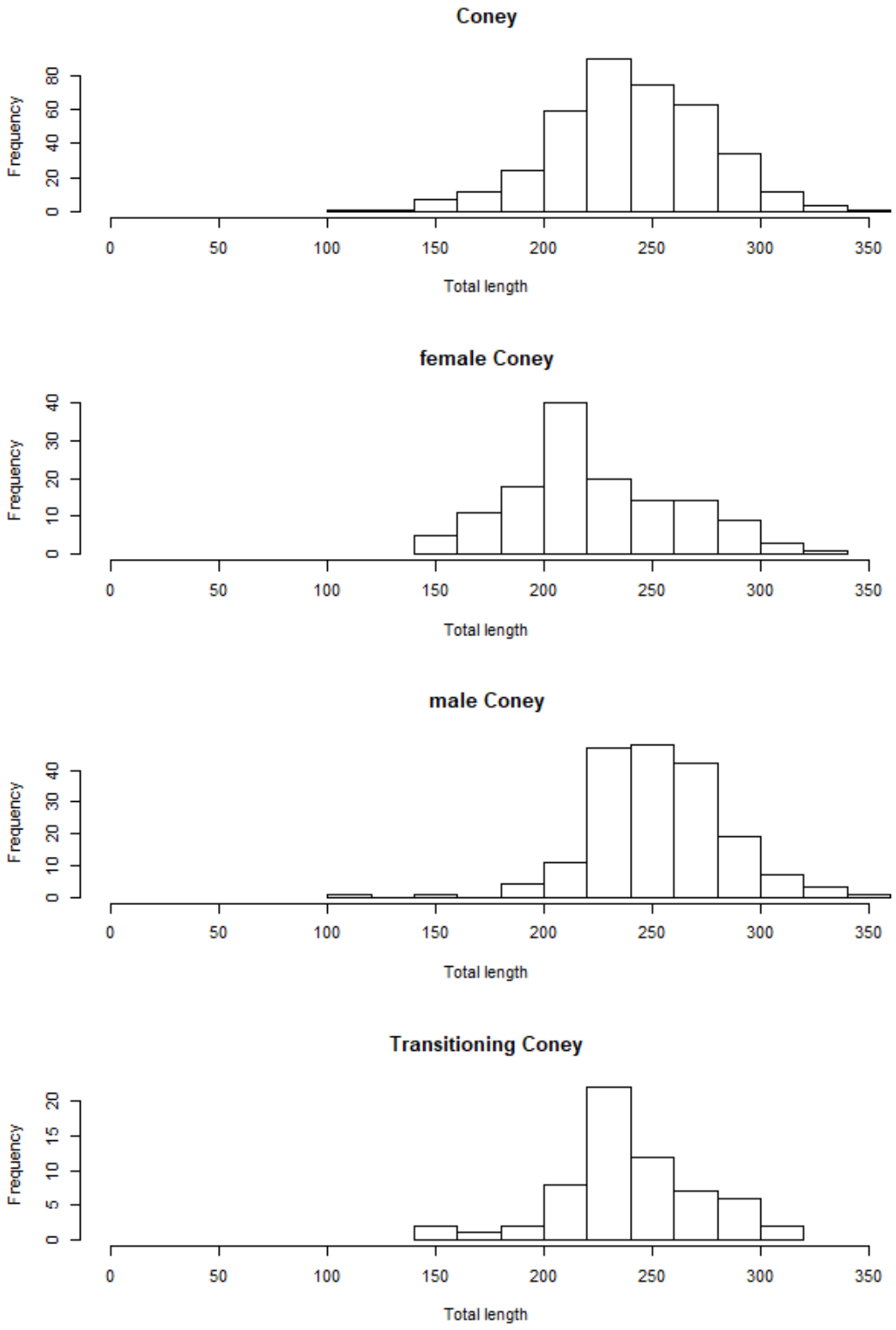
Out of 251 specimens of yellowtail, 7 (2.8%) were immature.

The sex ratio (female/male) was 1.04 as follows:

```
female   male
   128    123
```

The mean length of yellowtail snapper greater than or equal to 300 mm TL is 381mm.

CONEY –



Length-frequency distribution for 381 Coney.

All fish were mature.

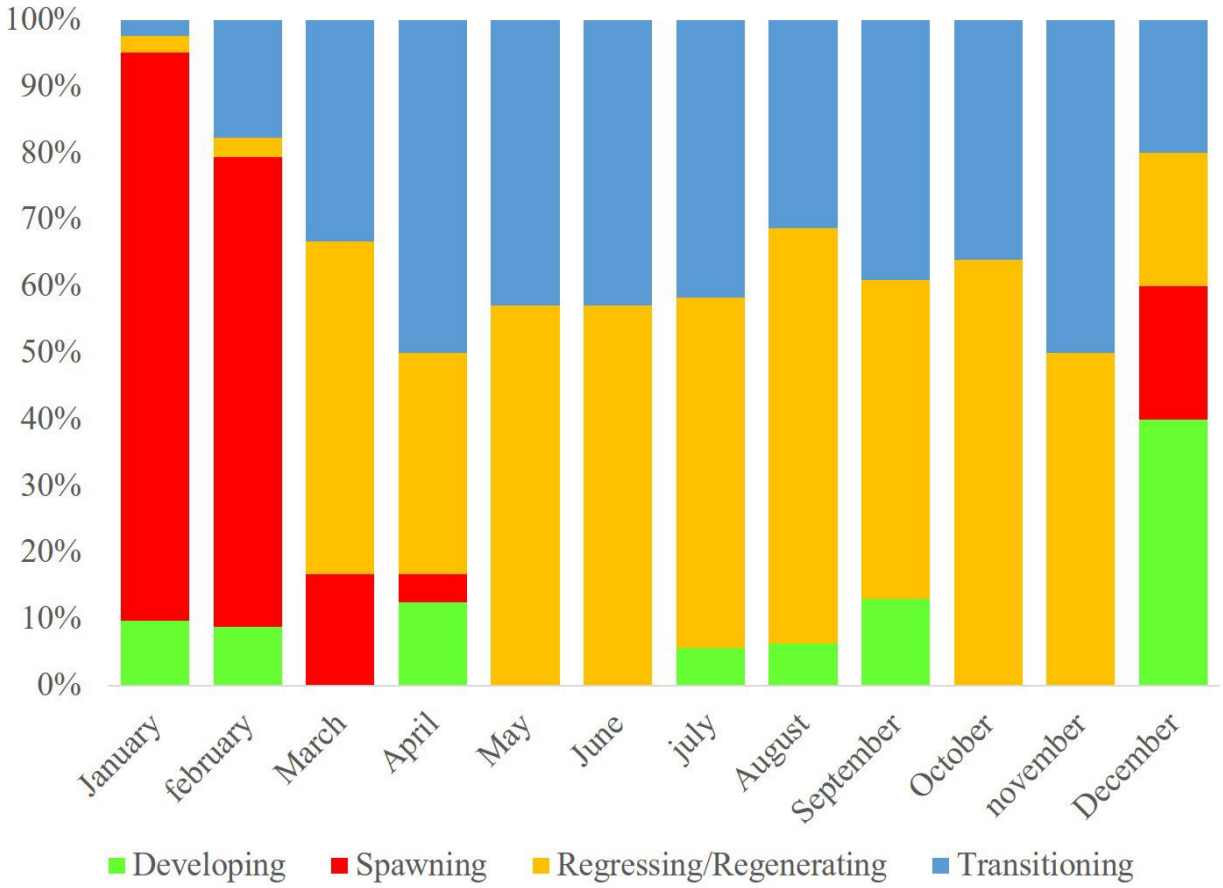
The sex ratio was as follows:

female	male	transitioning
135	184	62

The sex ratio (female/male) is 135/184 = 0.73 (ignoring the 62 transitioning animals).

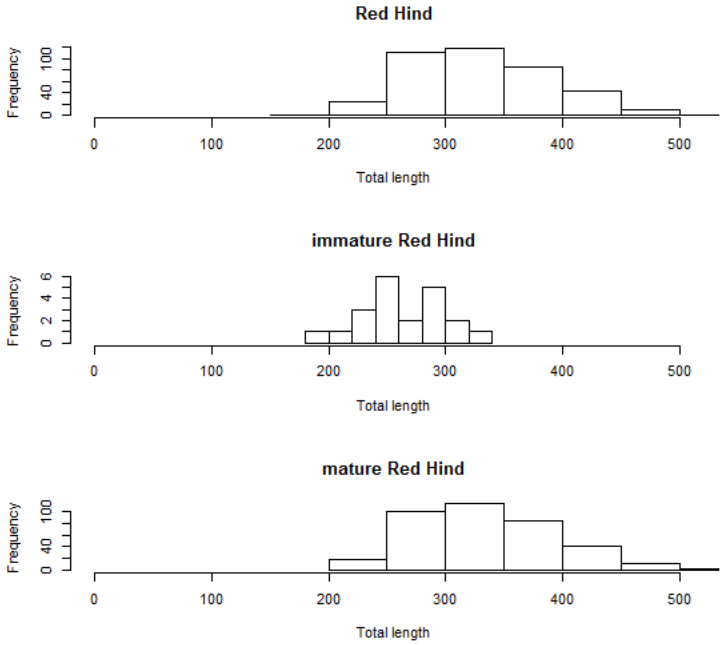
The mean length of fish greater than or equal to 220 mm TL was 257 mm.

Coney appear to have a distinct spawning season from December through April, with most activity occurring during January and February.



Spawning activity of coney.

RED HIND –



Histograms of all fish, immature fish and mature fish for red hind for all three islands combined.

Out of 393 specimens of red hind, 21 (5.3%) were immature.

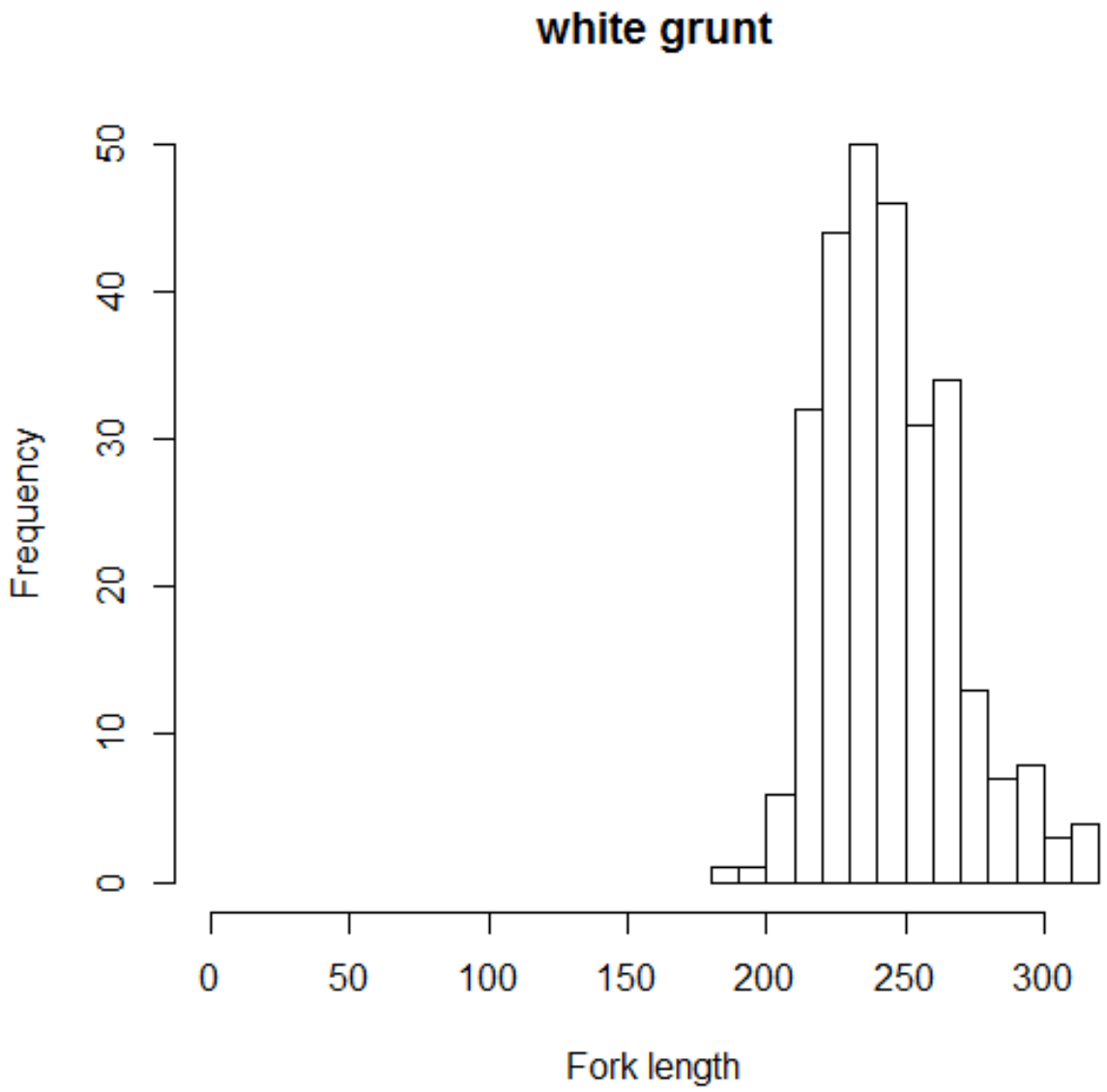
The sex composition was as follows:

female	male	Transitional	Unknown
187	128	76	2

The sex ratio (females/males) is 187/128 = 1.46 (ignoring the 76 transitional animals).

The mean length of fish greater than or equal to 250 mm TL is 337.

WHITE GRUNT –



Histogram of lengths of all white grunt for all three islands combined.

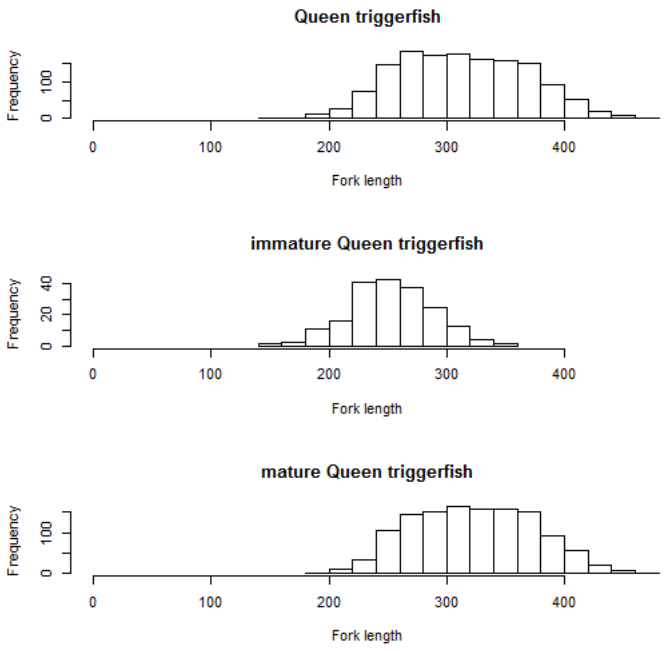
Out of 280 specimens of white grunt, none (0 %) were immature.

The sex ratio (female to male) is 0.82:

```
female   male
   126    154
```

This is not significantly different from a 1:1 sex ratio (exact binomial test, p=0.11. The mean length of fish greater or equal to 220 mm FL is 250.

QUEEN TRIGGERFISH –



Histograms of all fish, immature fish and mature fish for Queen triggerfish for all three islands combined.

Out of 1439 specimens of queen triggerfish, 195 (13.6%) were immature.

Because 13.6% of the landings were immature, the spatial variation in maturity needs to be explored because it is possible that one of the islands could have a considerably higher fraction of the catch that is immature.

	PR	STT	STX
immature	66	63	66
mature	391	537	316
% immature	14.4	10.5	17.2

As it turns out, the percent immature in the catch varies by island from 10 to 17%.

The sex ratio is as follows:

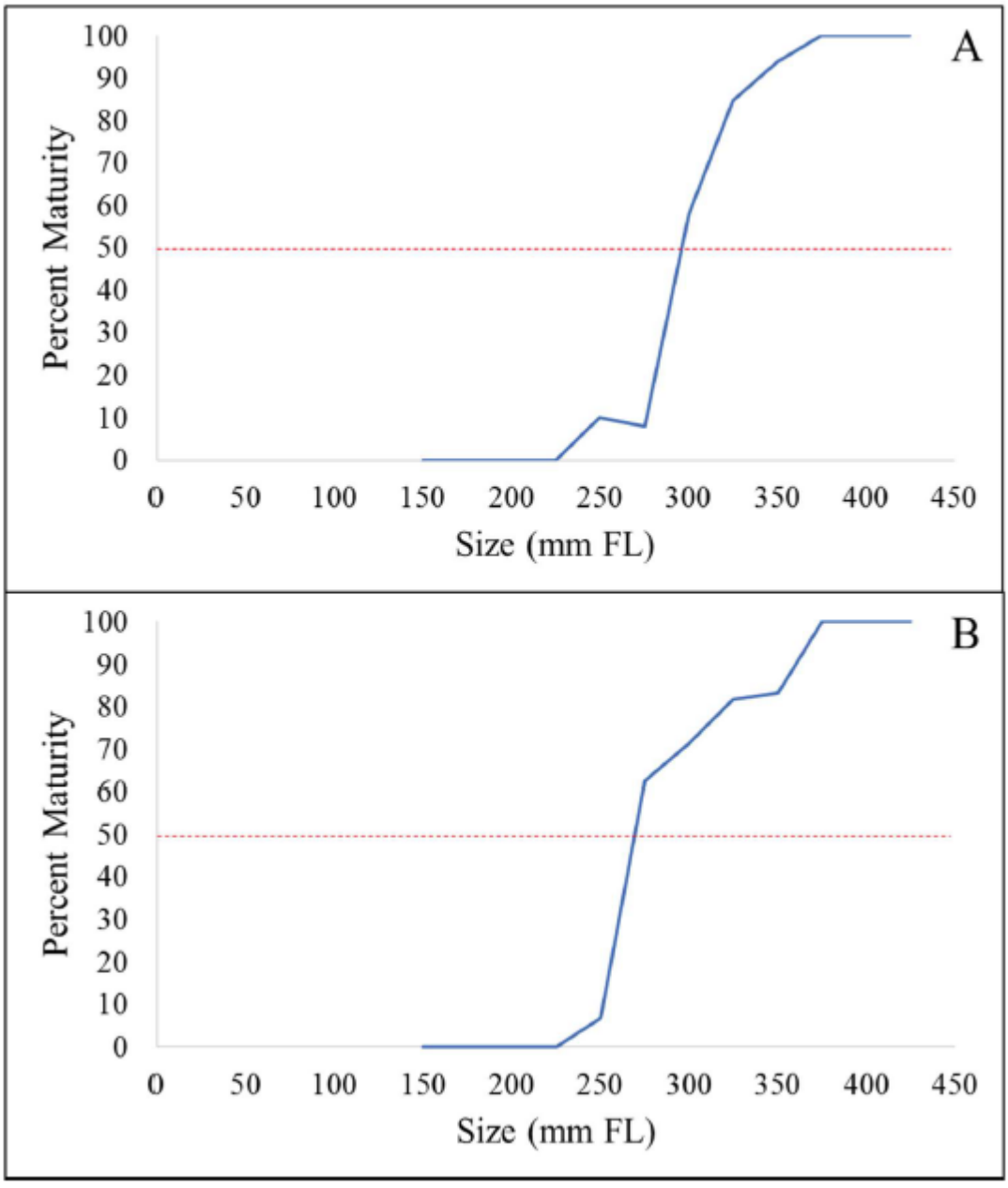
female	male
698	741

for a sex ratio (female/male) of 0.94.

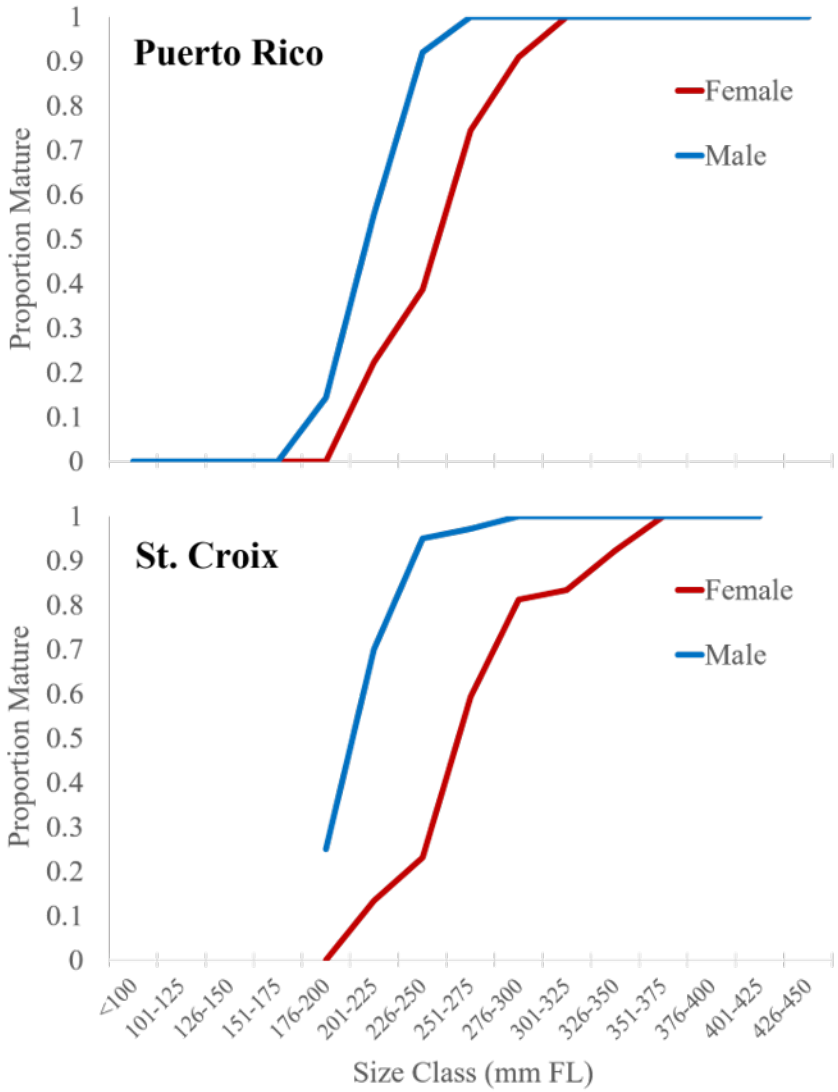
The mean length of fish greater than or equal to 260 mm TL was 330 mm FL.

Maturity data are provided here for reference. The original data are for Puerto Rico and St. Croix and are published in Rivera Hernandez et al. (2019). For details on sample numbers and sources, refer to the original publication.

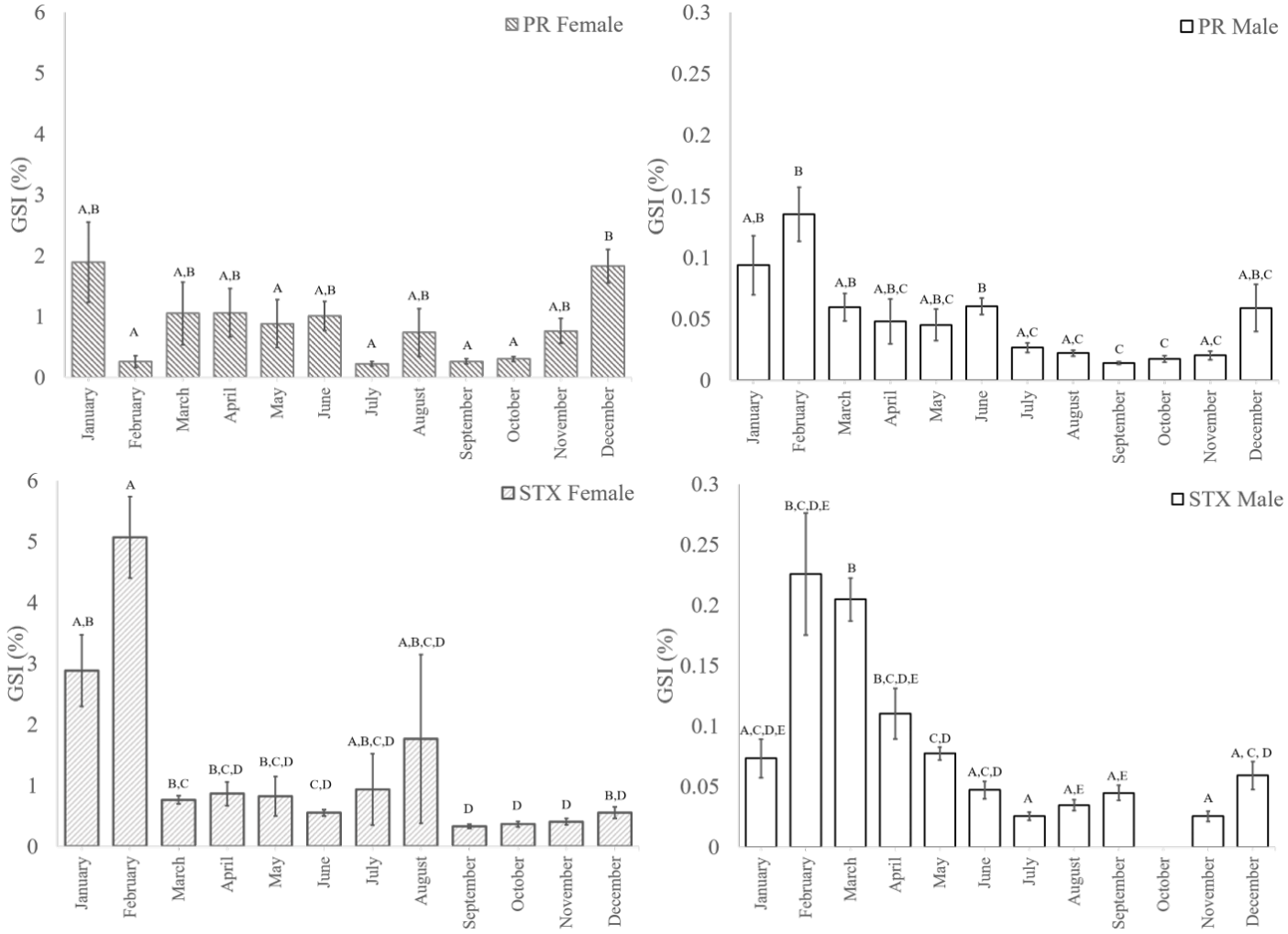
Preliminary data on maturity for St. Thomas, collected as part of a co-occurring investigation under the direction of V. Shervette, are provided here for reference. For details on these findings, refer to Thomas (2018).



Percent mature by length of female Queen triggerfish from (A) St. Thomas and (B) St. Croix. Red dotted line denotes 50% mature. (From Thomas (2018), Figure 15.)

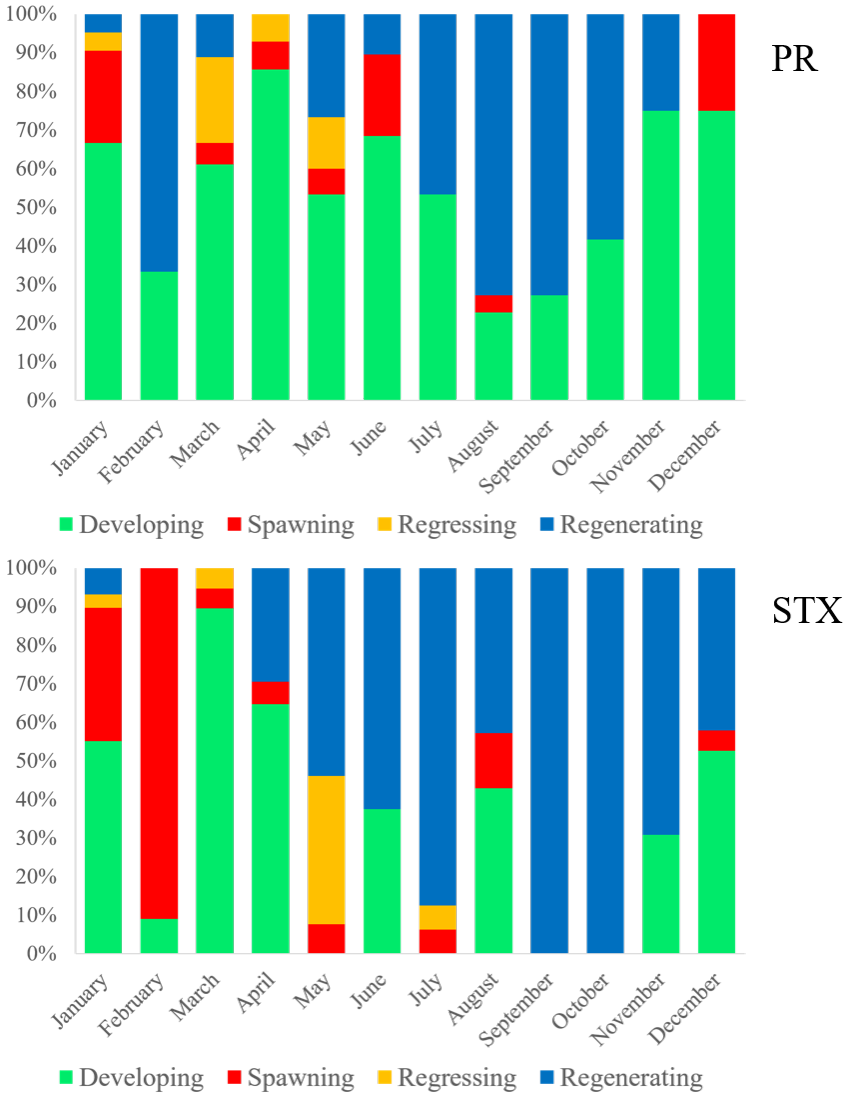


Female and male 50% sexual maturity curves for Queen triggerfish in Puerto Rico and St. Croix. (From V. Shervette, unpublished results).

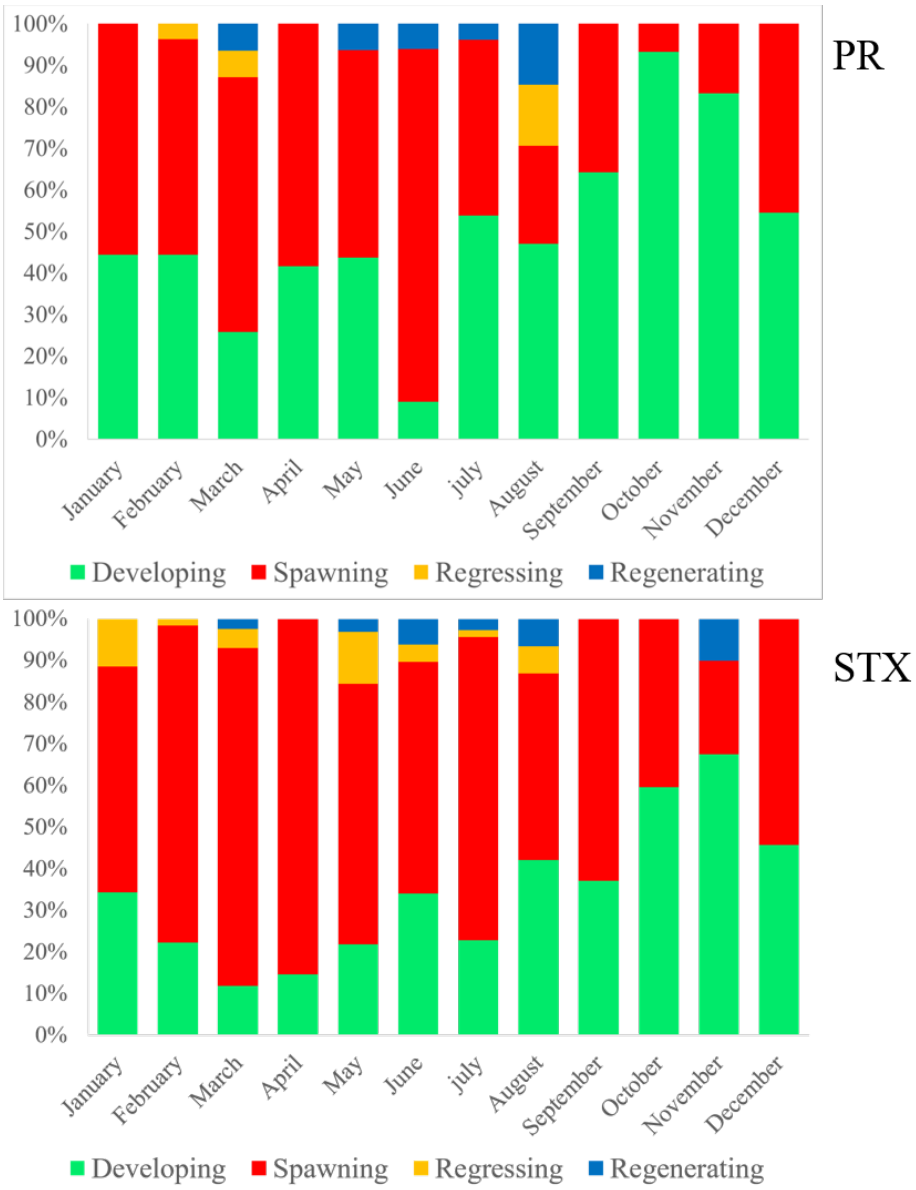


Mean monthly GSI for sexually mature Queen Triggerfish females and males from Puerto Rico and St. Croix. Error bars represent standard error. Letters within each graph indicate significant differences in monthly mean GSI for pairwise comparisons (a = 0.05). Note that no mean value is presented for STX Males; this is because the scale for weighing gonads that measures to the 0.01 g malfunctioned before testes could be weighed.

Female spawning occurs in every month except September, October, November (see figures below). Males, on the other hand, spawn in every month. The mismatch in timing of spawning of males and females may be due to sample sizes. For details concerning these data, refer to Rivera Hernandez et al. (2019) and Thomas (2018).



Female Queen Triggerfish reproductive seasonality. Monthly proportions of individual females in each reproductive phase.



Male Queen Triggerfish reproductive seasonality. Monthly proportions of individual males in each reproductive phase.

Modeling the Implications of the Findings

This section is developed using Queen triggerfish as an example. The commercial catch sampling gave rise to length-frequency distributions which, in theory, can provide estimates of total instantaneous mortality rate, *Z*. Age and growth studies (Thomas 2018; Rivera Hernandez et al. 2019) provide information on longevity which can provide estimates of natural mortality rate, *M* (Then et al. 2015). Subtracting *M* from *Z* gives an estimate of instantaneous fishing mortality rate, *F*. To understand the implications of a given level of fishing mortality, the spawning potential ratio for that level of fishing mortality can be computed. In the case of Queen triggerfish, the age and growth study of Thomas (2018) also provides age composition of the

commercial catch which can be used for a catch curve analysis to estimate total mortality rate. The relevant data and parameters are given in Tables 5 and 6. A caveat is that the age and growth estimates of Thomas (2028) were derived from spines. This structure is not as reliable as otoliths and therefore the computational procedure presented here is illustrative and should be updated when more reliable age data are available. We also considered alternative growth parameter estimates from Albuquerque et al. (2011).

Table 5. Parameters used to model spawning potential ratio.

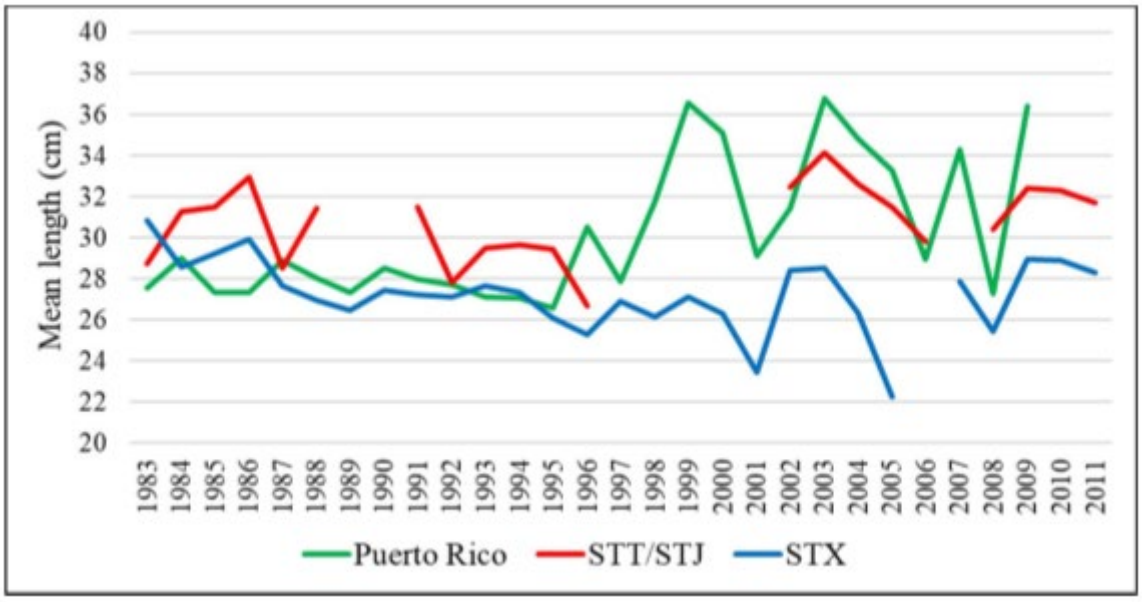
L_c, mm FL	260 (this study)
$\bar{L}$ (> L_c)	330.0 (this study)
K, yr^{-1}	0.33 (Thomas 2018)
L_∞, mm FL	428, females; 426 males (Thomas 2018)
T_o, yr	-0.48 (Thomas 2018)
T_{max}	14 (Thomas 2018), 20 (Rivera Hernandez et al. 2019)
t_c	2 (see text)
t_{mat}	2 or 4 (see text)
b (allometric growth)	2.82 females, 2.89 males (Thomas 2018)

Table 6. Composition of Queen triggerfish landings from the US Virgin Islands. From Table 6, Figure 15, and the von Bertalanffy growth curve (derived by averaging the parameters for males and females) of Thomas (2018). Numbers for % mature were read off a graph and are approximate; first numbers are for St. Croix, second numbers for St. Thomas.

Age	Number	% Mature	Length
2	18	5, 8	239
3	50	80, 75	292
4	82	80, 95	330
5	105	100	358
6	98	100	378
7	68	100	392
8	41	100	402
9	29	100	409
10	19	100	415
11+	37	100	>418

Mortality rates. We can use the Beverton-Holt length-based mortality estimator to estimate Z, with the following inputs: L_c = 260, $\bar{L}$ = 330, and von Bertalanffy growth parameters from Thomas (2018) of K = 0.35, L_∞ = 428. This gives rise to an estimate of Z = 0.49. Thomas (2018), following Bryan (2012), presented time series of mean length data for Puerto Rico, St. Thomas/St. John, and St. Croix (see figure below). These data suggest the mean length went up in Puerto Rico and St. Thomas/St. John in the New Millennium but stayed relatively stable in St. Croix. If the data could be updated to the present, and the mean length calculated for just those

fish larger than L_c, it might be possible to estimate period specific total mortality rates (Gedamke and Hoenig 2006). It should be noted that Albuquerque et al. (2011) provide a different set of von Bertalanffy parameters: $K = 0.14$, $L_\infty = 441$. This gives rise to an estimate of Z of 0.22.

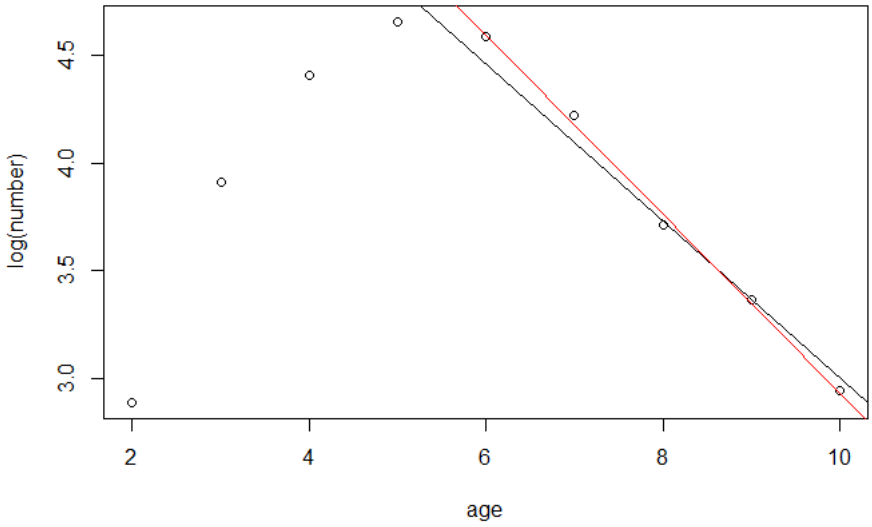


Mean length data for Puerto Rico, St. Thomas/St. John and St. Croix. Figure is from Thomas (2018) who adapted it from Bryan (2012).

Using a maximum age of 14, 16 or 20 years with the empirical estimator of natural mortality rate of Then et al. (2015) gives estimates of $M = 0.44$, 0.39 and 0.32 yr^{-1}, respectively. Subtracting M from the total mortality 0.49 estimated above gives estimates of instantaneous fishing mortality of 0.05, 0.10 and 0.17 yr^{-1}, respectively. The alternative growth parameter estimates of Albuquerque et al. (2011) give rise to a total mortality rate that is considerably lower than the estimate of natural mortality rate which is an impossible condition. As Stevens et al. (2019) note, the best available growth parameter estimates for Queen Triggerfish including those of Albuquerque et al.) did not representatively sample the entire size range of the population based on what is seen in the National Marine Fisheries Service TIP (trip interview program) database (both in Florida and the Caribbean).

For the particular case of Queen triggerfish, we are fortunate to have an estimate of the age composition of the commercial catch (Table 6 above). The overall sex ratio (females/males) is 0.95 in samples from St. Thomas and 0.94 in samples from St. Croix (Thomas 2018). This suggests the male and female mortality rates are similar (Hoenig and Hewitt 2005). Consequently, a combined-sex estimate of total mortality rate is appropriate. Because the data are censored (there is an 11+ "plus group") the estimator of Robson and Chapman (1961) is used to estimate total mortality because this estimator accommodates censoring. We assume fish are fully recruited at age 5 or 6. Then the Robson-Chapman estimator of Z is 0.38 or 0.39, respectively, which compares to the value of 0.49 obtained from the Beverton-Holt estimator using the growth parameter estimates of Thomas (2018). (In contrast, the estimated total mortality rate from the Beverton-Holt estimator using the growth parameter estimates from

Albuquerque et al. (2011) are much lower). In general, in data-limited situations, we would not have an estimate of age composition but, for the present purposes, it is reassuring to have a check that the length-based estimator is not grossly different from a more data-rich estimator. Also, a catch curve constructed from the age data shows a strong linear trend (see figure below). The linearity of the relationship suggests the assumption of constant selectivity with age of the commercial sample is reasonable, and the strength of the linear relationship suggests recruitment variability may be reasonably low. Subtracting natural mortality values of 0.43 and 0.31 from the Robson-Chapman mortality estimate of 0.39 gives estimates of fishing mortality, *F*, of -0.04 (an infeasible estimate) and .08, respectively. These estimates are somewhat lower than those obtained using the length data and the parameter estimates from Thomas (2018).



Cross sectional catch curve for Queen triggerfish showing a strong linear decline on the right. Black line is for case where ages 5-10 were used; red line, ages 6-10.

Spawning potential. The spawning potential ratio is a measure of the reproductive output under an assumed vector of fishing mortality-with-age relative to the reproductive output if fishing mortality is zero. It is assumed that fishing mortality does not affect the proportion mature at age and the fecundity of mature fish at age. The basic equation can be written as:

$$\text{SPR} = X / Y \tag{1a}$$

where X is

$$X = L_t \sum_{t=\min(t_c, t_{mat})}^{\infty} e^{-\sum_{i=\min(t_c,t_{mat})}^{t} Z_i (i - t_c)} \emptyset_t L_t^b \tag{1b}$$

and Y is the same as X except that Z_i is replaced by M; here

t_c is the age at which fish enter the fishery,
t_{mat} is the age of maturity,

Z_i is the total mortality experienced by fish of age i,
M is the natural mortality rate, assumed constant with age,
$\emptyset_t$ is the proportion mature at age t,
L_t is the length at age t, and?
b is the exponent in the length-weight regression (or 3, if an estimate is not available).

In applying equation (1) it is necessary to specify the mortality at age, the proportion mature at age and weight at age (under the assumption that reproductive output is proportional to weight of the fish).

It appears that Queen triggerfish become vulnerable to the fishing gear around 260 mm which corresponds to an age of 2 (Table 6). Based on Table 6, animals appear to be largely mature around age 3. This provides a fundamental contradiction because most of the animals we observed in the commercial catch (86.4%) are mature but according to the study of Thomas (2018) less than 10% of the age 2 animals – which appear to be close to fully recruited – are mature. The age determinations of Thomas were made on the basis of spines which are not as reliable as otoliths; therefore, we caution against a reliance on the growth curve for determining age at maturity. On the other hand, it is well established by histology that the vast majority of the commercially caught Queen triggerfish are sexually mature. We compute spawning potential ratio for a variety of assumptions on natural mortality rate, age of first capture and age at maturity. However, we think the most likely scenarios are those consistent with the strong information on maturity, i.e., those assuming either a) fish are recruited at age 2 and age 2 fish are mature, or b) fish are recruited at age 3 and age 3 fish are mature. The table below gives calculated values of SPR ranging from a low of 0.62 to 0.88, with the favored scenarios providing values ranging from 0.70 to 0.80.

The low estimates of fishing mortality rate, coupled with the high values for SPR indicate Queen triggerfish is lightly exploited. One might be tempted to conclude that the fishery could reasonably be exploited more heavily except for two important caveats: first, the growth estimates are uncertain and should be replaced with estimates based on otoliths; second, although the stock or stocks appear to be lightly exploited at present, the absence reliable catch statistics make it imprudent to relax regulations until a way to see the effects on landings can be implemented.

Calculated values of spawning potential ratio (SPR) for three assumptions on longevity (and hence derived natural mortality rate, M), three assumptions on age of first capture, t_c, and three assumptions on age at maturity, t_{mat} (assuming knife-edge maturity). Growth parameter estimates are from Thomas (2018). Underlined scenarios are discussed in the text. The lowest value obtained (0.62) is shown in bold typeface.

Longevity	M	t_c	t_{mat}	SPR
14	0.44 yr^{-1}	2	2	0.77
14	0.44	2	3	0.72
14	0.44	2	4	0.67
14	0.44	3	2	0.83
14	0.44	3	3	0.80
14	0.44	3	4	0.74
14	0.44	4	2	0.88
14	0.44	4	3	0.86
14	0.44	4	4	0.82
16	0.39	2	2	0.74
16	0.39	2	3	0.70
16	0.39	2	4	0.65
16	0.39	3	2	0.81
16	0.39	3	3	0.77
16	0.39	3	4	0.72
16	0.39	4	2	0.86
16	0.39	4	3	0.84
16	0.39	4	4	0.79
20	0.32	2	2	0.70
20	0.32	2	3	0.66
20	0.32	2	4	**0.62**
20	0.32	3	2	0.76
20	0.32	3	3	0.73
20	0.32	3	4	0.68
20	0.32	4	2	0.81
20	0.32	4	3	0.79
20	0.32	4	4	0.75

Modeling – other species

Life history parameters for other species. Derived M is computed from maximum age using the relationship in Then et al. (2015). Values for L_c and $\bar{L}$ are derived in the text. Von Bertalanffy growth parameters are from Stevens et al. (2019) except where indicated otherwise. For parrotfish, lengths are in mm standard length (SL); for Yellowtail snapper, lengths are in mm total length (TL);and for other species, fork lengths are used.

species	maximum age	derived M	L_c	$\bar{L}$	L_∞	K	t_o
Princess parrotfish	12[a]	0.50	220	253	---	---	---
Queen parrotfish	20[a]	0.32	250	326	---	---	---
Redband parrotfish	11[a], 7[f]	0.54	160	184	178	0.67	0
Redtail parrotfish	14[a], 5[f]	0.44	220	246	258	0.63	0
Yellowtail/redfin parrotfish	16[a], 7[f]	0.39	210	245	238	0.81	-.05
Stoplight parrotfish	17[b], 9[f]	0.37	210	254	357	0.45	-.06
Mutton snapper	22[b], 40[f]	0.29	350	480	799[h]	0.17	-1.23
Blackfin snapper	44[b], 27[f]	0.15	220	264	579	0.16	-1.60
Yellowtail snapper	13-17[d]	0.37-0.47	300	381	545[e]	0.10[e]	-1.83[e]
" "	23[f]	0.28	same	same	618[f]	0.13[f]	-3.13[f]
Coney	19[f]	0.33	220	257	377	.20	-3.53
Red hind	27[b], 18[f]	0.24	250	337	571	0.11	-3.10
Queen triggerfish	14[b], 16[c]	0.44, 0.39	260	330	428[g]	0.33[g]	-0.48[g]
" "	14[f]	same	same	same	441[f]	0.14[f]	-1.80[f]

[a] preliminary, based on reading ~100 otoliths (V. Shervette, unpublished data). [b] Validated by $\delta^{14}C$ (V. Shervette, unpublished data). [c] otolith reading (V. Shervette, unpublished data). [d] range of values given in compilation by Adams and Rios (2015). [e] SEDAR (2005) cited in Adams and Rios (2015). [f] Stevens et al. (2020) provide citations as follows: Redband, Redtail and Yellowtail parrotfishes, Choat and Robertson (2002); Stoplight parrotfish, Choat, Robertson, Ackerman, and Posada (2003); Mutton snapper, O'Hop et al. (2015); Blackfin snapper, Burton, Potts, and Carr (2016); Yellowtail snapper, O'Hop, Murphy, and Chagaris (2012); Coney, Burton et al. (2015); Red hind, Potts and Manooch (1995); Queen triggerfish, Albuquerque et al. (2011).. [g] Thomas (2018). [h] Stevens et al. (2019) gave L_∞ in total length; we converted to fork length using their regression formula (their Table 7).

Natural mortality rates derived from maximum age using the method of Then et al. (2015) and estimates of total mortality rates derived from the mean length of fish greater than or equal in size to L_c using the method of Beverton-Holt. Fishing mortality is obtained by subtraction. --- indicates estimate could not be computed, as follows: Princess parrotfish and Queen parrotfish, lack of growth parameter estimates; Redband parrotfish and Yellowtail/Redfin parrotfish, L_∞ is less than $\bar{L}$; Redtail parrotfish and Yellowtail snapper, $Z < M$.

species	derived *M*	Z	F
Princess parrotfish	0.50	---	---
Queen parrotfish	0.32	---	---
Redband parrotfish	0.54, 0.82	---	---
Redtail parrotfish	0.44, 1.12	0.29	---
Yellowtail/redfin parrotfish	0.39, 0.82	---	---
Stoplight parrotfish	0.37, 0.65	0.45	0.08, ---
Mutton snapper	0.29, 0.17	0.42	0.13, 0.25
Blackfin snapper	0.15, 0.24	1.15	0.91, 1.00
Yellowtail snapper	0.37-0.47	0.20	---
" "	0.28	same	---
Coney	0.33	0.65	0.32
Red hind	0.24. 0.35	0.30	0.06, ---
Queen triggerfish	0.44, 0.39	0.49	0.05, 0.10

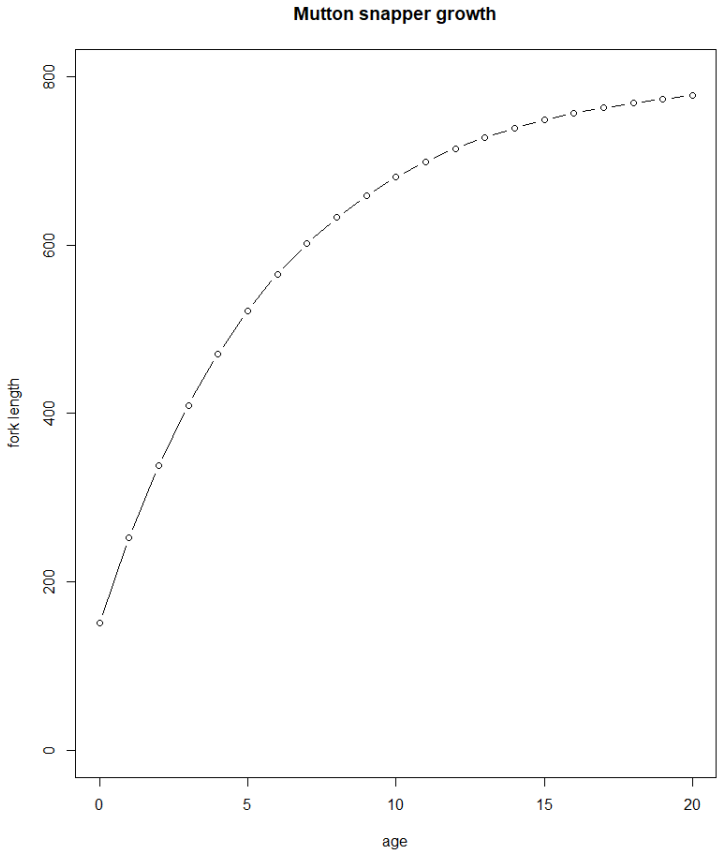
The tables above immediately show problems with applying mortality estimators to Caribbean reef fish data for which life history parameters may not be well established. First, a recent review of the literature on growth and longevity for reef fishes in Florida and the Caribbean (Stevens et al. 2019) gives estimates of longevity that are in many cases substantially lower than unpublished estimates by one of us, Shervette. Five of Shervette's estimates of longevity are verified by isotopic analysis; three are based on readings of otoliths, - the preferred aging structure, but are based on preliminary studies with relatively small samples (~100) and may thus be underestimates. In two cases above, Redband and Yellowtail/Redfin parrotfish, the reported values for L_∞ are lower than the mean length of fully recruited animals in our study. Stevens et al. (2019) state explicitly that one of their goals was to point out the need for further research on longevity and growth, and the findings presented in the current study amplifies this conclusion. As Hoenig (2017) and Stevens et al. (2019) note, the maximum age known for a species or a stock increases over time. This is partly because of the adoption of better techniques over time for processing hard parts. This points to a clear need for modern growth studies based on sectioned otoliths and to the need for validation by isotopic analysis. Another reason for increasing estimates of longevity over time is that the chances of detecting rare, old individuals increases as more and more animals are examined. However, maximum age known for a species increases as the logarithm of the sample size (so it increases rapidly with increasing sample size when sample size is small but increases slowly with sample size when sample size becomes what is typical in an age and growth study). Thus, with the adoption of modern aging techniques and large sample sizes the estimates of growth parameters and maximum age should become reliable and thus afford the opportunity to use the assessment procedure used here.

Mutton snapper

For mutton snapper, we used $b = 3.03$ for the length-weight exponent (SEDAR (2008) cited in Stevens et al. 2019), $M = 0.17$ and 0.29 for natural mortality with corresponding estimates of F of 0.25 and 013. Fish recruit to the fishery at around 350 mm which corresponds to an approximate age of 2 (based on the growth parameters in O'Hop et al. (2015) cited in Stevens et al. (2019)). Most fish caught in the commercial fishery are mature so we assume maturity occurs at age 1 or 2.

Longevity	M	t_c	t_{mat}	SPR
22	0.29 yr^{-1}	2	1	0.45
22	0.29	2	2	0.43
40	0.17	2	1	0.31
40	0.17	2	2	0.30

The results suggest SPR is reasonably high. This is conditional on the growth curve being accurate. The large (negative) value of t_o (corresponding to a large y-axis intercept – see below) suggests that young fish may not have been available to estimate size at age for the left part of the curve, which can make the growth parameter estimates uncertain.



Growth curve based on parameters in O'Hop et al. (2015) cited in *Stevens et al. (2019). Not the large size of the fish at age 0.*

Blackfin snapper

For Blackfin snapper, we used $b = 3.11$ for the length-weight exponent (Burton et al. (2016) cited in Stevens et al. (2019)), $M = 0.15$ or 0.24 for natural mortality and corresponding values of $F = 1.00$ and 0.91. Fish recruit to the fishery at around 220 mm which corresponds to an approximate age of 1 (based on the growth parameters in Burton et al. (2016) cited in Stevens et al. (2019)). Virtually all fish caught in the commercial fishery are mature so we assume maturity occurs at age 0 or 1.

Longevity	M	t_c	t_{mat}	SPR
44	0.15 yr^{-1}	1	0	0.04
44	0.15	1	1	0.04
27	0.24	1	0	0.08
27	0.24	1	1	0.08

The results suggest that spawning potential has been reduced to perilous levels, a conclusion that does not seem reasonable given that all but 2 fish examined from the commercial catch were sexually mature. The SPR results arise from extremely high estimates of total mortality.

Then et al. (2018) suggested calculating Z for various levels of L_c to judge the stability of the estimates. This would be worth pursuing to see if a particular local feature of the length-frequency distribution is giving rise to an anomalous estimate of Z.

Yellowtail snapper

Using the parameters in the above table, the Beverton-Holt mean length mortality estimator gives an estimate of Z of 0.20 which is half as high as the estimated natural mortality. This could be because the longevity is severely underestimated (giving rise to an overestimate of natural mortality), or the growth parameters (which are from Puerto Rico) are not well estimated, or the choice of L_c is not appropriate. Another possibility is that the fishers are not catching the largest animals (selectivity/availability is dome-shaped for the hook and line fishery) and the Beverton-Holt model interprets the lack of large animals in the catch as lack of large animals in the population, i.e., large animals have died out. This approach for this species could be reconsidered when more growth information is available. However, if the fishery is indeed selecting against the large animals, better growth information will not solve the problem.

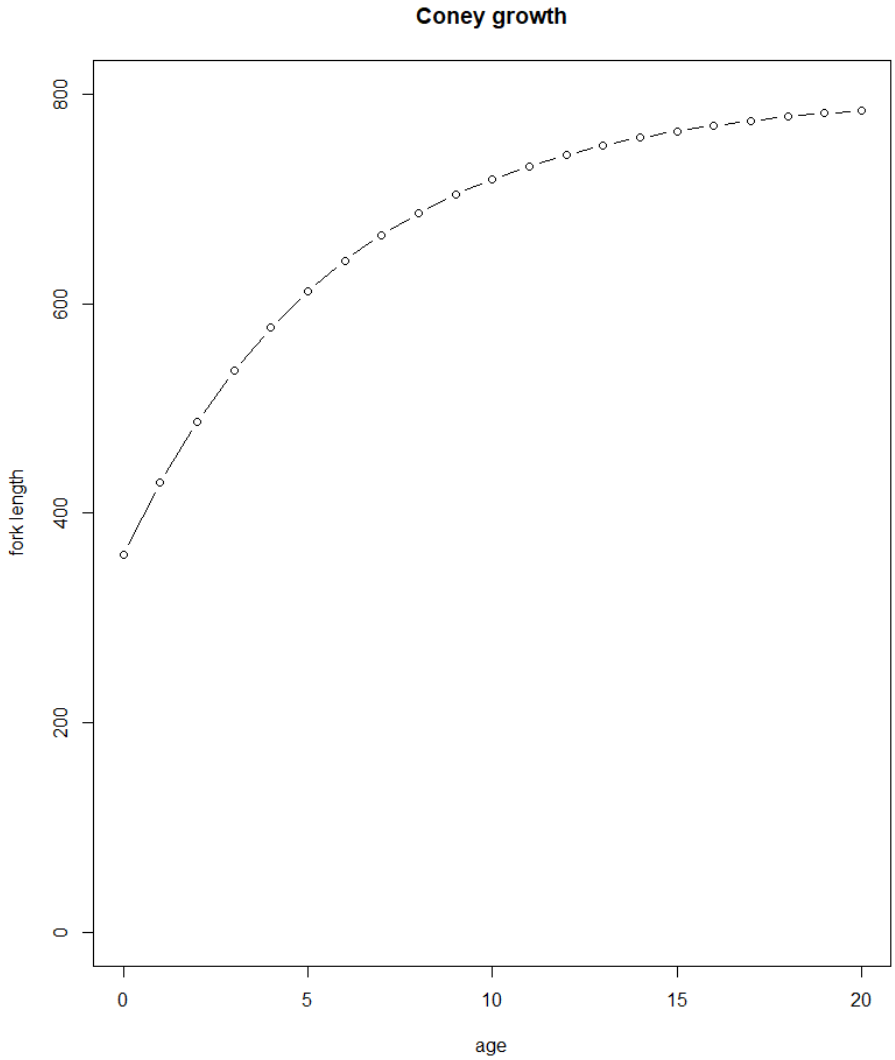
The fact that 97% of the catch is mature animals suggests it is highly unlikely that the population has been fished down to the point that reproduction has been jeopardized.

Coney

For coney, we used $b = 3.03$ for the length-weight exponent (Burton et al. (2015) cited in Stevens et al. (2019)), $M = 0.33$ for natural mortality and $F = 0.32$. Fish recruit to the fishery at around 220 mm which corresponds to an approximate age of 0 (based on the growth parameters in Burton et al. (2015) cited in Stevens et al. (2019)). Most fish caught in the commercial fishery are mature so we assume maturity occurs at age 0.

Longevity	M	t_c	t_{mat}	SPR
19	0.33 yr^{-1}	0	0	0.34

The results suggest SPR is reasonably high. But, as for Mutton snapper, this is conditional on the growth curve being accurate. The large (negative) value of t_o (corresponding to a large y-axis intercept – see below) suggests that young fish may not have been available to estimate size at age for the left part of the curve, which can make the growth parameter estimates uncertain.



Red hind

For Red hind, the estimate of Z was between the two estimates of natural mortality rate, M:

$$M = 0.24 < Z = 0.30 < M = 0.35.$$

This suggests that fishing mortality is very low, or that the estimate of total mortality rate is too low. The low estimate of M is derived from longevity = 27 while the high estimate is derived from longevity = 18. If we accept the premise that more recent data reflect more accurate aging techniques and larger sample sizes, then one could proceed with SPR calculations on the assumption that fishing mortality is low.

Outreach and capacity building work

At the start of this project in 2015, John Hoenig and Jeffrey Shields visited the University of the Virgin Islands (UVI) in St. Thomas and presented seminars on the purposes of this research. The title was: "Why do we care about fish maturity?" In subsequent field work on St. Thomas, they involved graduate students at UVI in the processing of fish specimens, including measuring, weighing, dissecting fish to remove gonads, and removing spines and otoliths.

Virginia Shervette presented three workshops in the Virgin Islands as follows:

May 2016: St. Thomas workshop on fish reproduction and proper methods for preserving gonads for reproductive histology; Workshop participants received certificates upon completion of the activities.

July 2016: St. Thomas workshop with VI Department of Parks and Natural Resources on fish age and growth with a focus on extracting otoliths from parrotfish species; Workshop participants received certificates upon completion of the activities.

November 2016: St. Croix workshop with VI Department of Parks and Natural Resources and STX Fishers on otolith extraction and age/growth in fishes; Workshop participants received certificates upon completion of the activities.

John Hoenig had planned to present a workshop on analytical methods for maturity studies as well as age and growth studies in the Virgin Islands during the winter or spring of 2020. However, the corona virus pandemic disrupted those plans and the workshops will have to be given after the completion of this grant.

We provided a graduate student at the University of the Virgin Islands, Sara Thomas, with gonads and hard parts that she used for her Master's thesis at the University of the Virgin Islands (see Thomas 2018). Shervette worked with her closely and served on her committee.

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Literature Cited

Adams, M.S. and A.B. Rios. 2015. Caribbean fisheries life history compilation. Unpublished manuscript, University of Miami RSMAS, NOAA Southeast Fisheries Science Center, Miami.

Albuquerque, C.Q., A.S. Martins, N. Leite Junior, J.N. Araujo, and A.M. Ribeiro. 2011. Age and growth of the queen triggerfish *Balistes vetula* (Tetraodontiformes, Balistidae) of the Central Coast of Brazil. Brazilian Journal of Oceanography 59(3):231-239.

Bryan, M.D. 2012. Evaluation of the available length-frequency information in the US Caribbean Trip Interview Program (TIP) data. SEDAR30-AW-02. SEDAR, North Charleston, SC. 35 pp.

Burton, M., Potts, J., & Carr, D. (2015). Age, growth, and natural mortality of coney (*Cephalopholis fulva*) from the southeastern United States. *PeerJ*, *3*, e825. https://doi.org/10.7717/peerj.825

Burton, M., Potts, J., & Carr, D. (2016). Age, growth, and natural mortality of blackfin snapper (*Lutjanus buccanella*) from the southeastern United States and U.S. Caribbean. *Gulf and Caribbean Research*, *27*, 66–73. https ://doi.org/10.18785/ gcr.2701.10

Choat, J., & Robertson, D. (2002). Age-based studies on coral reef fishes. In P. Sale (Ed.), *Coral reef fishes: dynamics and diversity in a complex system* (pp. 57–80). Boston, MA: Academic Press.

Choat, J., Robertson, D., Ackerman, J., & Posada, J. (2003). An age-based demographic analysis of the Caribbean stoplight parrotfish *Sparisoma viride*. *Marine Ecology Progress Series*, *246*, 265–277. https ://doi.org/10.3354/meps2 46265.

Gedamke, T., and J.M. Hoenig. 2006. Estimating Mortality from Mean Length Data in Non-equilibrium Situations, with Application to the Assessment of Goosefish. Trans. Amer. Fish. Soc. 135:476-487.

Hoenig, J. M. 2017. Should natural mortality estimators based on maximum age also consider sample size? Transactions of the American Fisheries Society 146:136-146.

Hoenig, J.M. and D.A. Hewitt. 2005. What can we learn about mortality from sex ratio data? A look at lumpfish in Newfoundland. Trans. Amer. Fish. Soc. 134:754-761.

Jones D.D. 2020. Addressing life history information gaps in a data-deficient Caribbean reef fish, the princess parrotfish *Scarus taeniopterus*. MS thesis, Marine Biology, College of Charleston. 150 pp.

O'Hop, J., Muller, R., & Addis, D. (2015). *SEDAR 15A Update: Stock Assessment of Mutton Snapper (Lutjanus analis) of the U.S. South Atlantic and Gulf of Mexico through 2013, SEDAR Update Assessment*. Technical Report 15 Florida Fish and Wildlife Conservation Commission St. Petersburg, FL.

O'Hop, J., Murphy, M., & Chagaris, D. (2012). *The 2012 Stock Assessment Report for Yellowtail Snapper in the South Atlantic and Gulf of Mexico, SouthEast Data, Assessment, and Review (SEDAR) 27A*. Technical Report Florida Fish and Wildlife Conservation Commission St. Petersburg, FL, 341 pp.

Potts, J., & Manooch, C. (1995). Age and growth of red hind and rock hind collected from North Carolina through the Dry Tortugas, Florida. *Bulletin of Marine Science*, *56*, 784–794.

Rivera Hernandez, J.M., N. Pena Alvarado, K. Correa Velez, R. Nemeth, R. Appeldoorn and V. Shervette. 2019. Queen triggerfish reproductive biology in U.S. Caribbean waters. Trans. Am. Fish. Soc. 148: 134-147.

Robson, D.S. and D.G. Chapman. 1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90(2):181 – 189.c(18, 59, 82, 105, 98, 68, 41, 29, 19)

SEDAR. 2005. Stock Assessment Report. Caribbean Yellowtail Snapper. Tech. rept. 8. Southeast Data, Assesment, and Review, Charleston, SC. 179pp.

SEDAR. 2008. 15A, Stock Assessment Report 3 (SAR3), South Atlantic and Gulf of Mexico Mutton Snapper. Technical Report 15 Southeast Data, Assessment, and Review North Charleston, SC.

Smith, M.W., A. Then, C. Wor, G. Ralph, J.M. Hoenig and K.H. Pollock. 2012. Recommendations for catch curve analysis. North Amer. J. Fish. Manage. 32:956-967.

Stevens, M.H., S.G. Smith and J.S. Ault. 2019. Life history demographic parameter synthesis for exploited Florida and Caribbean coral reef fishes. Fish and Fisheries 20:1196-1217.

Then, A.Y., J.M. Hoenig, N.G. Hall and D.A. Hewitt. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. ICES J. Mar. Sci. 72:82-92.

Then, A.Y-H., J.M. Hoenig and Q.C. Huynh. 2018. Estimating fishing and natural mortality rates, and catchability coefficient, from a series of observations on mean length and fishing effort. ICES J. Mar. Sci. 75:610-620.

Thomas, S. 2018. Age, growth and reproduction of the Queen triggerfish, *Balistes vetula*, from the U.S. Virgin Islands. M.S. thesis, Univ. Virgin Islands.

Wagner, G.A. 2019. Age, growth, and reproductive biology of a data-deficient parrotfish species (*Sparisoma viride*) in the US Caribbean. M.S. Thesis, College of Charleston, South Carolina.