Reproduction, Catch, and Size Structure of Exploited Reef-Fishes at Kamiali Wildlife Management Area, Papua New Guinea

Ken Longenecker, Ross Langston, Holly Bolick, and Utula Kondio

Honolulu, Hawaii
November 2011

COVER

Utula Kondio (left), assisted by Yuninda Utula (foreground), processes fish specimens for rapid reproductive analysis.

Reproduction, Catch, and Size Structure of Exploited Reef-Fishes at Kamiali Wildlife Management Area, Papua New Guinea

Ken Longenecker[1],
Ross Langston[1],
Holly Bolick[1],
and
Utula Kondio[2]

(1) Pacific Biological Survey
Bishop Museum
Honolulu, Hawaii 96817, USA

(2) Kamiali Wildlife Management Area
Lababia, Morobe Province, PNG

Bishop Museum Technical Report 57

Honolulu, Hawaii
November 2011

Bishop Museum Press
1525 Bernice Street
Honolulu, Hawai‘i

Printed in the United States of America

ISSN 1085-455X

Contribution No. 2011-022 to the Pacific Biological Survey

Contents

List of Tables

List of Figures

EXECUTIVE SUMMARY

The Kamiali Initiative is a Bishop-Museum-led project to develop a self-sustaining cycle of environmental conservation, scientific research, and economic development in the coastal community of Kamiali, Papua New Guinea. This area, which includes approximately 120,000 acres of terrestrial and marine habitat, is larger than most of the state parks of California and is globally significant, with numerous endemic plants and animals. The success of the Kamiali Initiative is contingent upon Kamiali residents preserving the natural environment such that biological field researchers are motivated to work in the area. This project is arguably the most successful large-scale terrestrial/marine biodiversity conservation project implemented in Papua New Guinea and it is the only such project that is fully sustainable.

The most challenging conservation issues at Kamiali relate to coral reef fishes. Fish comprise the overwhelming majority of dietary protein for this coastal village, and coral-reef habitats are preferred fishing sites. Thus, fishing practices must balance the conflicting needs of conserving fish populations to attract research against the subsistence needs of Kamiali residents.

Here we describe the status of Kamiali's exploited reef-fish populations to help guide and evaluate conservation efforts. We conducted rapid, histology-based reproductive analysis on five species to generate parameters necessary for life-history-based management of fisheries, decribed catch characteristics of the same five species and evaluate the sustinability of the fishery, used a combination of advanced diving technology and laser videogrammetry to augment our 2009 and 2010 descriptions of the size structure of exploited species (a total 57 species are covered in this report), expanded a literature review of reproductive parameters, estimated (when sufficient information exists) the percentage of reproductive individuals in each population, and estimated the percentage of mature females in populations for which sufficient information exists.

The small grouper, *Cephalopholis cyanostigma*, is a protogynous hermaphrodite. The size at which 50% of individuals are mature (L_{50}) is 23 cm total length (TL) for females and 20 cm for males; however, minimum size at maturity (L_m) is 13 and 19 cm TL for females and males, respectively. This species becomes increasingly male-biased with length, and the sex ratio of mature individuals can be described by the equation: $\% \female = 130.600/(1+e^{-((TL-18.765)/-1.573)})$. Batch fecundity (BF) was not significantly related to female length. Rather, average batch fecundity was 10,652 eggs per spawning event. Total body weight is an approximately cubic function of length and can be described by the equation: $Wt = 0.0062(TL)^{3.3015}$.

The snapper, *Lutjanus semicinctus*, is a gonochore. L_{50} is 21 cm and 18 cm fork length (FL) for females and males, respectively. L_m is 20 cm and 14 cm FL for females and males, respectively. We could not reliably model sex ratios as a function of length, however we observed up to 70% females at 23 cm FL. Batch fecundity is an approximately cubic function of length: $BF = 0.387(FL)^{3.710}$. Total body weight is also an approximately cubic function of length: $Wt = 0.0160(FL)^{3.0341}$.

A second snapper, *Lutjanus timorensis*, is also a gonochore. We could not generate a reliable estimate for female L_{50}, however male L_{50} is 23 cm FL. L_m is 30 cm and 12 cm FL for females and males, respectively. We could not reliably model sex ratios as a function of length, however we observed up to 40% females at 40 cm FL. Batch fecundity is an approximately cubic function of length: $BF = 0.378(FL)^{3.251}$. Total body weight is also an approximately cubic function of length: $Wt = 0.0185(FL)^{2.9669}$.

The goatfish, *Parupeneus barberinus*, is apparently a gonochore. We could not generate a reliable estimate of L_{50} for either sex; however, L_m is 12 cm and 14 cm FL for females and males, respectively. This species becomes increasingly male-biased with length, and is exclusively male above 21 cm FL. Sex ratios of mature individuals of size classes larger than that composed exclusively of females (20 cm FL) can be described by the equation: $\%♀ = 226.5 – 10.8(FL)$. Batch fecundity is an approximately cubic function of length: $BF = 1.198(FL)^{3.323}$. Total body weight is also an approximately cubic function of length: $Wt = 0.0242(FL)^{2.9052}$.

The rabbitfish, *Siganus lineatus*, is a gonochore. Female L_{50} is 24 cm FL, however we could not generate a reliable estimate of L_{50} for males. L_m is 22 cm and 19 cm FL for females and males, respectively. The sex ratio of mature individuals can be described by the equation: $\%♀ = 53.342/(1+e^{-((TL-22.299)/0.527)})$. Batch fecundity is an approximately cubic function of length: $BF = 3.522(FL)^{3.550}$. Total body weight is also an approximately cubic function of length: $Wt = 0.0569(FL)^{2.7103}$.

Life history parameters for coral-reef fishes (which are highly diverse and occur predominantly in developing countries) are commonly considered too time-consuming, difficult, and expensive to generate. This assumption has led to a current emphasis on spatially based fishery conservation and management efforts. The success of these in enhancing fisheries, which must be considered where societies depend on reef fishes for dietary needs, is a subject of intense debate. The information presented above was generated in an open-air “laboratory”, without electricity, during a two-week period when we spent the majority of our available time preparing for and conducting fish surveys. Therefore the methods we describe can help fill an information void that prevents life-history-based management of coral-reef fishes.

A simple comparison of published to estimated size-at-maturity values highlights the need for continued reproductive analyses. The empirically derived equation of Froese & Binohlan (2000) can be used to estimate female L_m. This and other empirically derived equations are being increasingly used when published reproductive information is lacking. The equation overestimates observed values of L_m, and the degree of overestimation increases with size. Contrary to expectations (because L_{50} is expected to be larger than L_m), the same pattern is seen when comparing estimated L_m to published L_{50} values.

Average length in the *Cephalopholis cyanostigma* catch is not significantly different from the average length of the at-large population in the Kamiali Wildlife Management Area (KWMA). A total 44 fish harvested yielded 5.62 kg. A simple modeling exercise, based on suggestions by Froese (2004) that all individuals be reproductively mature and within 10% of optimum length, indicates that an equivalent yield could be obtained by catching 25 fish distributed equally among 23 – 25 cm TL size classes. Under this scenario the at-large population would produce an additional 30,105 eggs per spawning event.

Average length in the *Lutjanus semicinctus* catch is significantly smaller than the length of the at-large population in KWMA. A total 122 fish harvested yielded 12.47 kg. Because we could not generate a reliable description of size-specific sex ratios, we could not model reproductive output for the at-large population if fishing patterns are altered. However, by following Froese's (2004) guidelines, residents can obtain the same yield by catching 61 fish equally distributed among 21 – 24 cm FL size classes.

Because we did not encounter *Lutjanus timorensis* in our laser-videogrammetry surveys, we cannot compare catch to the at-large population. Nor could we model reproductive output of the at-large population. However, a total 120 fish harvested yielded 67.56 kg. Residents can obtain the same yield, following Froese's guidelines, by catching 113 fish equally distributed among 30 – 36 cm FL size classes.

Average length in the *Parupeneus barberinus* catch is significantly larger than the length of the at-large population in KWMA. A total 123 fish harvested yielded 11.08 kg. Residents can obtain an equivalent yield by catching 26 fish distributed equally among 26 – 32 cm FL size classes. Under this scenario the at-large population would produce an additional 543,422 eggs per spawning event.

Average length in the *Siganus lineatus* catch is significantly smaller than the length of the at-large population in KWMA. A total 92 fish harvested yielded 29.32 kg. Residents can obtain an equivalent yield by catching 67 fish distributed equally among 24 – 30 cm FL size classes. Under this scenario the at-large population would initially produce fewer eggs per spawning event; however, if each fish grows 1 cm and fishing patterns remain constant, the suggested scenario would yield an additional 4,448,614 eggs per spawning event in the future.

A total 937 individuals were captured on video during 2011, yielding a combined total 2,646 individuals representing 57 reef-associated species from 15 families (inclusive of 2009 and 2010 data). The mean length of all individuals was 52% of the average maximum length and 84% of average estimated optimum length of all 57 species. That is, an exploited reef fish swimming in Kamiali Wildlife Management Area is likely to be about ½ its potential maximum length, and 16% shorter than the length at which maximum yield can be obtained. Size at maturity is known for only 42% of the species studied. Of these, mean individual length was 135% of female L_m and 91% of female L_{50}. Sex-ratios are known for only seven species. Considering only these species, an average 25% of individuals are mature females.

Based on the apparent ease with which residents are able to catch fish, overfishing does not currently appear to be a threat to the majority of the exploited reef-fish species we examined. We propose that the population characteristics of species we studied at Kamiali Wildlife Management Area (average size ½ of maximum length and equal to female reproductive length), can be used as indicators of robust populations of exploited fishes.

These aspects of exploited fish populations are apparently maintained by several characteristics of the village and its fishery, such as: customary tenure, distance (and relatively high cost of transport) to commercial markets, a subsistence economy, lack of refrigeration, and environmental cycles. Ongoing and anticipated changes related to economic modernization may threaten these aspects of village life. The Kamiali Initiative, by establishing a pathway to economic development that starts with environmental conservation, should help reduce the environmental impact of socioeconomic transformation.

INTRODUCTION

Background

This report presents new marine research conducted at Kamiali, Morobe Province, Papua New Guinea, in 2011, and presents the work in the context of previous years' work (Longenecker *et al*. 2009, 2010). The results presented herein provide crucial information for the success of the Kamiali Initiative, a project to develop a self-sustaining cycle of environmental conservation, economic development, and scientific research. The foundation of this initiative is the residents of Kamiali, who hold traditional tenure over their natural resources. In 1996, they established the Kamiali Wildlife Management Area (KWMA), with 32,000 hectares of terrestrial habitat and 15,000 hectares of adjacent marine habitat.

Kamiali Wildlife Management Area is remote. It is about 65 kilometers south of the port town of Lae, and there are no roads to (or in) the village. Its approximately 600 residents obtain most of life's needs from the surrounding environment.

Gardening and subsistence fishing form the basis of the Kamiali economy and are a focus of village life; however, residents need money for basic supplies and services (*e.g.*, medicine, education, and clothing). These needs, combined with a lack of revenue, make exploitation of natural resources (*e.g.*, logging, mining) a tempting short-term source of income. However, these activities often have disastrous long-term environmental and social impacts in Papua New Guinea. In the interest of conserving their natural resources, and thus preserving their traditional lifestyle, in 2006 Kamiali leaders signed a Memorandum of Understanding with Bishop Museum outlining the development of a world-class remote scientific research station at KWMA. Visiting researchers will pay fees for research permits, field assistance, lodging, and meals. This revenue will subsidize educational costs and community-development projects. The Kamiali Initiative thus establishes a link between economic benefit and environmental conservation, and provides a strong incentive for villagers to protect their land and water in perpetuity (Figure 1).

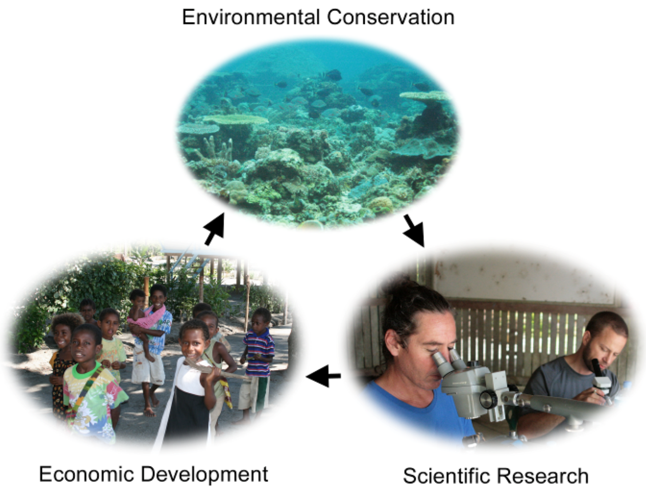

Figure 1. Conceptual model of the Kamiali Initiative: A well-managed environment attracts biological research, providing a means of economic development to pay for school and medicine, thus providing incentive for continued environmental conservation.

For the Kamiali Initiative to succeed, village residents must conserve their natural environment such that it continues to attract biological field researchers. Exploitation of coral reef fishes may represent the biggest challenge to the Kamiali Initiative; the overwhelming majority of dietary protein for this coastal village is fish, and coral reefs are preferred fishing sites. Thus, the village must balance the conflicting needs of marine conservation to attract research revenue against marine exploitation for their dietary requirements.

Fishery Surveys

The most productive starting point to help the village balance fish conservation and exploitation is a baseline description of the size structure of exploited fish populations. This information has intuitive appeal; Kamiali residents understand that shrinking average fish size may be indicative of unsustainable fishing practices. Length-frequency information is also the basis for science-based fishery management and conservation. When combined with life history parameters, an understanding of population size structure enables researchers to formulate predictions about the outcome of various management and conservation actions. Finally, baseline demographic information permits evaluation of any management and conservation efforts enacted.

Reproductive Analysis

Size-at-maturity

Although detailed descriptions of size structure are the foundation of fishery management and conservation, one of the biggest challenges to converting those data into resource management and conservation action is a lack of basic life history information about the majority of exploited fish species. Results from a literature review indicate that remarkably little is known about reproductive parameters for Kamiali's exploited reef fishes. Size at maturity is unknown for nearly 60% of the 41 species examined by Longenecker *et al*. (2010). This problem is not restricted to Papua New Guinea; Longenecker *et al*. (2008a) report that size at maturity is unknown for 38% of the 13 most heavily exploited reef fishes in Hawaii. Worldwide, this information is missing for ~83% of exploited species (Froese & Binohlan 2000). It is impossible to evaluate the reproductive status of a population when this information is missing.

The sheer diversity of coral-reef fishes, and the purported cost associated with the reproductive analysis of each species are often cited as obstacles to obtaining this important information (Roberts & Polunin 1993, Johannes 1998). An additional challenge is the lack of basic infrastructure (*e.g.*, electrical service needed to operate laboratory equipment) in many parts of the developing countries where most of the world's coral reefs are located.

To address the above problems, we developed a method for rapid, low-cost, on-site, histology-based reproductive analysis that does not require electrical service (Longenecker *et al*. 2010). With this method, reproductive parameters can be estimated relatively quickly, and its low cost eliminates one of the arguments against broad-scale reproductive analysis.

We focus on histological examination because gross (macroscopic) examination of gonads may not yield reliable determinations of sex and reproductive status; a comparison of the techniques showed reproductive status and/or sex was misclassified in 47% of specimens examined (Longenecker *et al.* 2010). Interestingly, gross (macroscopic) examinations led to overestimates of the number of mature females and underestimates of the number of mature males. Similar differences have been seen in other studies. Grandcourt *et al.* (2006), based on gross examination of gonads, reported that female *Diagramma pictum* (painted sweetlips) mature at 31.8 cm fork length (FL). However, later histological examination of the same population revealed that females mature at 35.7 cm FL (Grandcourt *et al.* 2011); gross examination of gonads underestimated size-at-maturity by 11%.

Providing accurate reproductive information will allow resource owners in developing countries (*i.e.*, Kamiali residents) to determine how their fishing practices may be impacting the marine environment. For instance, villagers can evaluate whether fish on the dinner table have had the chance to reproduce. Combining reproductive information with descriptions of size structure will allow communities to judge whether there are there enough reproductively active fish to insure an adequate food supply for future generations.

Sex-ratios

A common assumption of fishery management and conservation is that the larger a population's mean length, the higher its reproductive output. For instance, Froese (2004) argues that that old (thus larger) fish play important roles in the long-term survival of a population partially because large females are much more fecund (the number of eggs produced by a given female typically increases exponentially with length). However, this assumption may not be true if the ratio of males to females change with size. For instance, if larger size-classes are male dominated, larger mean-length would not necessarily result in higher egg production. If species reach a length at which individuals are exclusively male, egg production can potentially stop. Longenecker *et al.* (2010) report that in five of seven studies that examined sex ratios of species found at Kamiali, the proportion of males in a population increases with length. The same trend would be expected for protogynous fishes (*e.g.*, Scaridae, Serranidae, and Labridae). Elsewhere in the Pacific the same pattern was found in each of four species examined (Longenecker & Langston 2008, Langston *et al.* 2009) with a fifth species becoming increasingly female-biased with length (Longenecker *et al.* 2008b). Loubens (1980) examined size-specific sex ratios in fishes from New Caledonia. He found that some species reach a size where only males are present. This was true for a triggerfish, a monocle bream, and a wrasse. In seven of 10 groupers, populations become increasingly male-biased with length. The other three species are exclusively male at larger sizes. Patterns are more variable in the emporers and snappers. Of nine emporers, four are exclusively male at larger sizes, two are increasingly male-biased, sexes are approximately equal throughout the size range in one, and one is female-biased though its size range. Of four snappers, two are exclusively male at larger sizes and sexes are approximately equal in the other two. Finally, a lizardfish reaches a size at which only females are present. If the goal of fishery management and conservation is to ensure an adequate number of reproductively active individuals of both sexes, size-specific sex ratios must be known before useful management policies can be formulated. This information will also help evaluate whether conservation and management actions designed to increase average fish length will result in more reproductively active individuals of either sex. Given the results summarized above, increases in average length do not necessarily lead to increases in mature individuals of both sexes.

Batch fecundity

Helping village residents understand the value of various fishery conservation and management measures may be most simply done by generating estimates of reproductive output. One approach is to describe batch fecundity: the number of eggs shed in a single spawning event. Typically, there is an exponential (typically cubic) relationship between fish length and batch fecundity. Thus, it is generally expected that an increase in mean fish size will result in vast increases in reproductive output (and the number of young fish available to replace those harvested). For instance, Longenecker & Langston (2008) suggest that the number of eggs produced by the goatfish, *Parupeneus multifasciatus*, during a single spawning event can be described by the relationship:

$$\#\ \text{Eggs} = 0.0018(\text{FL in mm})^{3.092}$$

Applying this relationship to the average length (14 cm) to the 50 individuals captured on video by Longenecker *et al*. (2010) at KWMA suggests this population produces 389,108 eggs per spawning event. If these same 50 individuals had an average length just 1 cm larger, reproductive output would increase by 92,528 eggs. These numbers can be a powerful motivator for subsistence fishers attempting to balance immediate dietary needs with longer term goals of marine conservation.

The above calculations assume that all individuals are mature females. Estimates of reproductive output change dramatically when size-at-maturity and size-specific sex ratios are considered. Because *Parupeneus multifasciatus* matures at 15 cm and becomes predictably male-biased with increasing size (Longenecker & Langston, 2008), actual reproductive output in the population observed by Longenecker *et al*. (2010) is likely to be closer to 28,235 eggs per spawning event. Remarkably, if every individual in the same population was 1-cm larger, reproductive output would *decrease* by 3,115 eggs. These calculations highlight the need to consider a combination of reproductive parameters so that village residents to not have unreasonable expectations when considering various fishery conservation and management actions.

Catch Characteristics

The estimates of mean length described above are based on at-large individuals. However, choice of fishing gear, time, and location of fishing efforts can result in catches that differ significantly from the characteristics of a general fish population. A detailed description of fish catch can help village residents understand how their fishing practices may impact their marine resources. For instance, Froese (2004) proposed three easily understood indicators to help evaluate the status of fish populations. The two simplest metrics are percent of reproductively mature individuals in the catch and percent of individuals within 10% of optimum length (L_{opt}, the length where, for an unexploited population, the number of fish of a given age multiplied by mean weight at that age is maximized and thus maximum yield can be obtained). Applying Froese's indicators to fish catch at Kamiali will allow residents to evaluate whether fishing practices at KWMA are sustainable.

Purpose

The purpose of this study is to generate more-robust descriptions of the population size-structure of Kamiali's exploited reef fishes by augmenting, with a series of *in situ* surveys, demographic information gathered in 2009 and 2010. Length-frequency information will be examined in light of estimated length at optimum yield and life-history parameters such as maximum length, reproductive size, and sex-ratios. Size-structure surveys will provide important baseline information which will allow Kamiali residents to detect changes in fish populations and, when necessary, take action to improve their fish stocks. To address the scarcity of reproductive information on exploited fishes at KWMA, we will describe size-at-maturity, size-specific sex ratios, and length-fecundity relationships for five species. Finally, we will describe catch characteristics of the same five species to help evaluate whether fishing practices are sustainable. Providing this information in the context of life history parameter will allow Kamiali residents to more-precisely define their conservation goals (*e.g.*, from "we want more fish" to "we will fish in a manner consistent with increasing the number of reproductive females"). Combined, the size-structure and life-history information will also serve as the basis for evaluating the effectiveness of conservation efforts enacted by the Kamiali community.

METHODS

Study Area

Kamiali is one of six Kala-speaking villages in Papua New Guinea and is located on the Huon Coast, approximately 64 km SSE of the port city, Lae. Approximately 600 residents control the distribution and use of land, adjacent marine areas, and the resources contained therein. The northern boundary of the Kamiali Wildlife Management Area (KWMA) is the mouth of the Bitoi River, whereas the Sela River is the southern limit. A third major river, the Alealer, also drains into the management area. Nassau and Saschen Bays are wholly contained within the management area, as are Lababia and Jawani Islands and Capes Dinga and Roon. The northern part of Hessen Bay is also contained within the management area.

The terrestrial portion of the KWMA is remarkably undeveloped and characterized by lush vegetation. Kamiali Village is concentrated along the northern portion, where the shoreline is exclusively sandy beach. The southern shoreline is dominated by fringing reefs on Capes Dinga and Roon. Fringing reefs also surround the islands of Lababia and Jawani. These reefs may abut rocky shoreline or sandy coves. The intertidal zone is dominated by mangroves, mud flats, and seagrass beds. Seaward, the reef flats typically feature carbonate bench or coral beds with occasional patches of sand or rubble. The reef crest features a high abundance and diversity of corals and other marine invertebrates, although occasional beds of rubble composed of coral fragments also occur. The reef face is steep, typically descending 20 to 30 meters, and features corals, consolidated carbonate substrate, and rubble. At the base, fringing reefs give way to sandy sediment that is believed to occupy the majority of the marine area. Some coral outcroppings, patch reefs and pinnacles are interspersed throughout this presumably sedimentary area. These isolated structures are the coral-reef habitat most frequently targeted by local fishers.

Rapid Reproductive Analysis

Study species and specimen collection

We chose five species for rapid reproductive analysis, based on the following criteria: 1) all are an important part of village fish catch; 2) village residents expressed an interest in learning more about each species; 3) published reproductive information was lacking or incomplete; and 4) each species is distinctive enough that the chance of misidentification was low. We analyzed the serranid (or grouper), *Cephalopholis cyanostigma*, two lutjanids (or snappers) *Lutjanus timorensis* and *Lutjanus semicinctus*, a mullid (or goatfish), *Parupeneus barberinus*, and a siganid (or rabbitfish), *Siganus lineatus*.

Cephalopholis cyanostigma ranges throughout the tropical western Pacific, including the Philippines, Thailand, Indonesia, Papua New Guinea, Palau, New Britain, the Solomon Islands, and the north coast of Australia from the Dampier to the Capricorn Islands (Heemstra & Randall 1999). *Lutjanus semicinctus* occurs mainly in southern Oceania from Tahiti to New Guinea, and extends north to the Philippines (Anderson & Allen 2001). *Lutjanus timorensis* is found mainly in the western Pacific Ocean from Fiji to the Malay Peninsula; it has also been recorded from the Andaman Sea off Thailand (Anderson & Allen 2001). *Parupeneus barberinus* occurs throughout most of the Indo-Pacific region but is unknown from the Red Sea, Gulf of Oman, Persian Gulf, and Hawaii (Randall 2001). *Siganus lineatus* has a disjunct distribution. A single population occurs in southern India, and the other is found in the West Pacific, mainly from eastern Indonesia to New Caledonia (Woodland 2001).

All specimens used for reproductive analysis were caught by village residents between March and June 2011. They delivered their fish to our processing station and allowed us to obtain the length and weight, and remove the gonads of each fish. Fishers received a modest bounty (3.00 kina) for each specimen and the fish were returned to them for consumption. Fork length (FL) was measured to the nearest mm. Total whole body weight was determined with the most-appropriate of two hanging spring-scales. These scales had capacities of 1 or 10 kg and had gradations of 10 or 100 g, respectively. We then made a mid-ventral incision from the vent toward the head (through the pelvic girdle) to expose gonads. We estimated the sex and reproductive status (mature vs. immature) based on gross examination, then removed and fixed gonads in a modified Dietrich's solution (30% ethanol, 10% formalin, and 2% acetic acid).

From 26 May - 10 June 2011 we processed gonads for size-at-maturity and batch fecundity analysis. Whole gonads were weighed to 0.001 g on a battery-powered jeweler's scale. An approximately 1-cm thick transverse section was removed from one lobe of each ovary that appeared to be at or nearing maturity. This section was weighed to 0.001 g and transferred to Gilson's fluid for later batch fecundity analysis (below).

Size at maturity and size-specific sex ratios

For size-at-maturity analysis, we cut an approximate 2 mm^3 section from one lobe of each gonad (the unsampled lobe of ovaries used for batch fecundity analysis), placed the sections in a 24-well tissue culture plate, and dehydrated them in a graded alcohol series (30 min in each of 50%, 75%, and two changes – to ensure adequate dehydration - of 95% ethanol. We placed tissues in Beem capsules (size 00), then infiltrated and embedded them in glycol methacrylate resin (JB4, Electron Microscopy Sciences) per kit instructions. Because high humidity in our open-air "laboratory" often prevented tissue blocks from hardening completely, we removed the cured tissue blocks from the Beem capsules and further dehydrated them for 12 hours in a desiccating chamber (an airtight container – in our case, a diver's dry box - containing silica gel packets) placed in full sunlight.

We obtained at least five tissue sections (approximately 7 μm thick), distributed evenly throughout each tissue block, with an MT1 Porter-Blum microtome outfitted with a glass knife. We floated the tissue sections on pre-distributed water drops, and dried the slides on a "warmer" (a cast iron baking dish exposed to direct sunlight). We stained tissue sections (now affixed to slides) in a 0.5% (by weight) solution of Toluidine Blue in water for 15 s. Excess stain was removed with a gentle stream of water and slides were once again dried on the "warmer". Tissue sections were examined at 40 - 100X on a portable, battery-powered, compound microscope for evidence of reproductive maturity. We classified ovaries according to Wallace & Sellman (1981) and testes according to Nagahama (1983). We considered females mature with the onset of vitellogenesis (appearance of yolk protein in the oocytes), and males mature when the testes contained visible spermatozoa. We report size at sexual maturity as the size at which a regression (3-parameter, sigmoidal) of percent mature individuals in each size class versus fork length (the average length of individuals within a size class) indicates 50% of individuals are mature (L_{50}) or, if L_{50} curves could not be constructed, the minimum size at which individuals were mature (L_m).

To determine size-specific sex ratios, we calculated the percent of mature females (of total mature individuals) in each size class (1 cm for *Cephalopholis cyanostigma* and *Parupeneus barberinus*, 2 cm for *Lutjanus semicinctus* and *Siganus lineatus*, 4 cm for *Lutjanus timorensis*). We then plotted % mature females as a function of average length within each size class. We used regression analysis to explore whether sex ratios varied predictably with length.

Batch Fecundity

To estimate batch fecundity (the number of eggs shed by a female during a single spawning event), we used a technique modified from Agger *et al*. (1974). Ovarian samples reserved for batch-fecundity analysis (above) were stored in Gilson's fluid for five months. We analyzed those with oocytes in late vitellogenesis or beyond (stage 3b or greater), based on the histological examination described above. Oocytes were liberated from the stroma by agitation with an ultrasonic cleaner. Samples were diluted with water to a total volume of 75 ml. Samples were stirred to distribute oocytes throughout the liquid, and a Stempel pipette was used to obtain three 1-ml subsamples. We counted the largest size-class of oocytes in each subsample (for most species, oocytes $\geq$ stage 3b were ≥ 400 µm in diameter, thus oocyte size was used as an indicator for oocyte maturity). Batch fecundity was estimated with the following equation:

$$\text{Batch fecundity} = (\text{mean \# oocytes/ml})(75\text{ ml})(\text{total ovary weight/sample weight})$$

Batch fecundity estimates were plotted as a function of fork length. Regression analysis (2-parameter power function) was used to describe relationships between length and fecundity.

Catch Characteristics

We used the specimens obtained for reproductive analysis to describe length-weight relationships and to construct fishery-dependent length-frequency histograms. We used one-sample t (or, if data could not be transformed to meet statistical assumptions, one-sample sign) tests to test for differences between mean catch size and empirically derived estimates of L_{opt} (Froese & Binohlan 2000) and our estimates of L_{50} or L_m for each of five species. We also calculated the percent mature individuals and the percent of individuals within 10% of L_{opt} in each catch.

Fishery Surveys

From 27 May – 9 June 2011, we conducted 14 laser-videogrammetry surveys to describe the size distribution of exploited reef fishes in Kamiali Wildlife Management Area. These surveys were performed at preferred fishing sites, most of which are beyond the depth limits of conventional open-circuit SCUBA. As such, we used closed-circuit rebreathers with 10/50 trimix diluent as life support to reach depths to 91 m. Due to the lengthy decompression obligations incurred while working at these depths (*e.g.*, 3 hours for a 20-minute dive to 91 m), the work was performed in areas with bathymetric profiles that permitted work to continue while ascending. Thus, surveys are concentrated at offshore pinnacles and near fringing reefs (Figure 2, Table 1).

A high-definition video camera fitted with parallel laser pointers was used to capture images of individual fish when they were oriented perpendicular to the laser beam axes (Figure 3). We then reviewed the video with Sony Picture Motion Browser® and captured still frames where both lasers appeared on the fish. Because the beams are parallel, the lasers superimpose a reference scale on the side of the fish, allowing length estimates by solving for equivalent ratios. These size estimates were calculated using ImageJ software (Rasband 2009). Longenecker & Langston (2008) have demonstrated a nearly 1:1 relationship between estimated and actual fish lengths. Further, a prediction interval suggested 95% of estimates will be within 0.5 cm of the actual fish length (Longenecker & Langston 2008).

The fishes included in the fishery survey met the following four criteria: 1) they are reef fishes, 2) exploited by local fishers, 3) common enough to have been captured at least several times on video, and 4) can be reliably identified from still images. A total 56 species representing 15 families (Acanthuridae, Balistidae, Caesionidae, Carangidae, Ephippidae, Haemulidae, Holocentridae, Kyphosidae, Lethrinidae, Lutjanidae, Mullidae, Scaridae, Scombridae, Serranidae, and Siganidae) met these criteria.

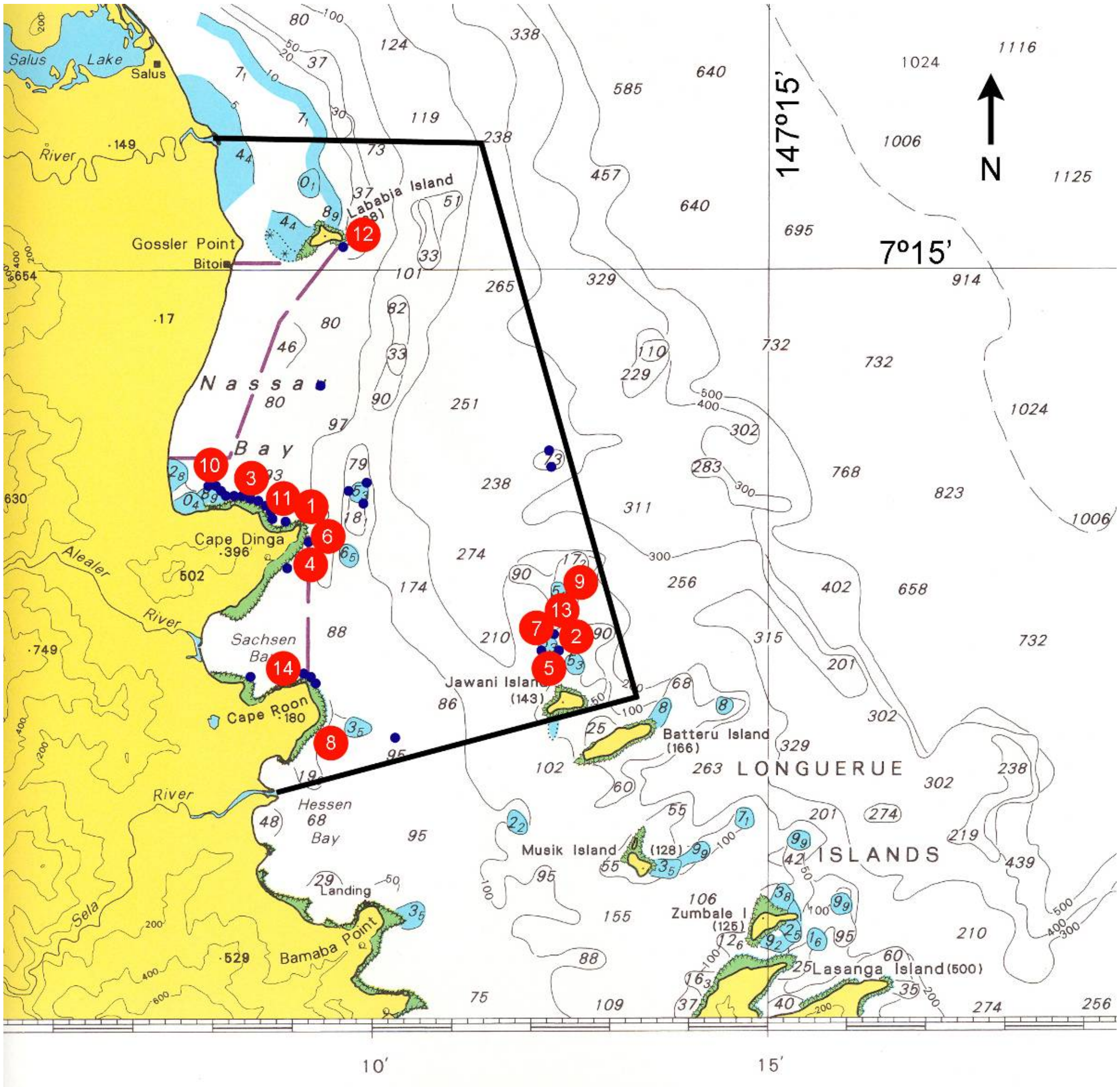

Figure 2. The marine portion of Kamiali Wildlife Management Area (outlined in black). Red circles indicate locations of 2011 survey sites (coordinates are given in Table 1). Smaller blue circles indicate 2009 and 2010 survey sites (coordinates in Longenecker *et al*. 2009, 2010). Adapted from chart Aus 523, published by the Australian Hydrographic Service. Depths are in meters.

Table 1. List of marine sites surveyed at Kamiali Wildlife Management Area during 2011. Latitude and longitude were estimated by GPS using the WGS84 datum. FR = Fringing Reef, OP = Offshore Pinnacle.

Survey	Date	Latitude (ºS)	Longitude (ºE)	Habitat	Max Depth (m)
1	27-May-11	7.30313664	147.1539337	FR	33
2	28-May-11	7.32093922	147.2061619	OP	47
3	29-May-11	7.30044027	147.1345179	FR	16
4	30-May-11	7.31002908	147.1512775	FR	48
5	31-May-11	7.31920618	147.2066462	OP	61
6	1-Jun-11	7.30434439	147.1541959	FR	91
7	2-Jun-11	7.32048718	147.2057845	OP	47
8	3-Jun-11	7.34727256	147.1559625	FR	54
9	4-Jun-11	7.29036715	147.2084690	OP	46
10	5-Jun-11	7.30035829	147.1328309	FR	42
11	6-Jun-11	7.29843766	147.1441638	FR	35
12	7-Jun-11	7.24607340	147.1616607	FR	31
13	8-Jun-11	7.28949124	147.2085205	OP	36
14	9-Jun-11	7.33532801	147.1530331	FR	33

A systematic literature review was conducted using the methods of Longenecker *et al.* (2008a) to obtain estimates of maximum length (L_{max}), size at maturity, size-specific sex ratios, spawning season, and reproductive mode. Briefly, we: 1) searched electronic resources (*e.g.*, Google Scholar, FishBase) using key word combinations of species names plus “reproduction” or “maturity”; 2) upon obtaining these publications, we identified and obtained additional relevant literature listed in their reference section; 3) we then searched these publications and obtained any additional references.

In summarizing life history information, preference was given to studies specific to Papua New Guinea (*e.g.*, maximum length information of Allen & Swainston 1993). Preference was also given to length at 50% maturity (L_{50}) over other estimates of size at maturity (*e.g.*, minimum size at maturity or L_m). Results from studies outside the southern hemisphere were included only when data for southern populations were not available (*e.g.*, reproductive size for *Caranx melampygus*). Conversely, information on spawning seasonality was included only for southern hemisphere populations.

Figure 3. Laser videogrammetry, a non-destructive technique to estimate fish length. A diver operates a video camera fitted with parallel lasers (left); the lasers superimpose a measurement scale on the side of *Parupeneus barberinus* (right).

We applied the empirically derived equations of Froese & Binohlan (2000) to estimate fishery and, when necessary, reproductive parameters. Published maximum lengths (L_{max}, see Results) were used to generate estimates of L_∞. The latter were then used to generate estimates of L_{opt}. If published values of L_{50} were not available, we also used L_∞ estimates to generate ♀L_m estimates.

We constructed length-frequency histograms for each species for which at least 15 specimens were captured on video suitable for length estimation. Mean length was compared to L_{max}, L_{opt}, and female L_m or L_{50}. When size-specific sex ratios were available, we estimated the percentage of reproductive females in each population.

The length information presented below is the distance between the front of the head and the end of the middle caudal ray. These lengths correspond to fork length (FL) for acanthurids, caesionids, carangids, holocentrids, kyphosids, lethrinids, lutjanids, mullids, scarids and scombrids; and total length (TL) for balistids, ephippids, haemulids, and serranids. This length slightly underestimates total length for siganids, which have an emarginate caudal fin, and is called “fork” length in this report.

RESULTS

Reproductive Analysis

Cephalopholis cyanostigma

We histologically examined 44 gonads. Twenty four individuals were immature females (mean TL = 18.3 cm, range 12.7 – 23.8), seven (7) were mature females (mean TL = 20.0 cm, range 16.6 – 24.6), one (1) 19.8 cm individual had an ovotestis, and 12 individuals were mature males (mean TL = 22.5 cm, range 19.4 – 25.0). Examples of each category are presented in Figure 4.

Cephalopholis cyanostigma has classic signs of sex change identified by Sadovy & Shapiro (1987): a t-test detected a significant sex-based bimodal size distribution, with males larger than females (Figure 5), yellow bodies were present in testes, and one individual had an ovotestis consisting of immature oocytes and developing spermatogenic tissue. Testes of several mature males also retained a central lumen. This species is apparently a protogynous hermaphrodite.

Immature females occurred throughout the female size range. With the exception of the single transitional male, all males were mature. When individuals are grouped into 1-cm size classes, our data suggest L_{50} is 22.9 cm TL for females, and 19.6 cm TL for males (Figure 6); however these plots are strongly influenced by a single mature specimen in the largest female size class (23 cm TL), and a single transitional male at 19.8 cm TL. When data are reorganized into larger (2 cm) size classes, females never reach a point at which 50% are mature. Rather about 25% are mature once females reach the minimum size at maturity (L_m) of 16.6 cm TL (Figure 7). Considering only females, the percent mature individuals at a given size (in cm) can be predicted by the equation ($n = 5$, $r^2 = 0.987$):

$$\%\ \text{mature} = 26.674/(1 + e^{-((TL-15.438)/0.767)})$$

Sex ratio becomes increasingly male-biased with size (Figure 8). Regression analysis suggests 100% of mature individuals are female between 16.6 (♀L_m) and 16.9 cm TL. The percentage of females at larger sizes can be predicted by the equation ($n = 8$, $r^2 = 0.625$):

$$\%\ ♀ = 130.600/(1+e^{-((TL-18.765)/-1.573)})$$

We could not construct an adequately descriptive equation for a relationship between size and fecundity. Average batch fecundity was 10,652 eggs for the six mature females (16.6 – 24.6 cm TL) in our sample. Batch fecundity estimates ranged between 2,177 and 28,259 eggs. Remarkably, the highest fecundity estimate was obtained from the smallest mature female (16.6 cm TL).

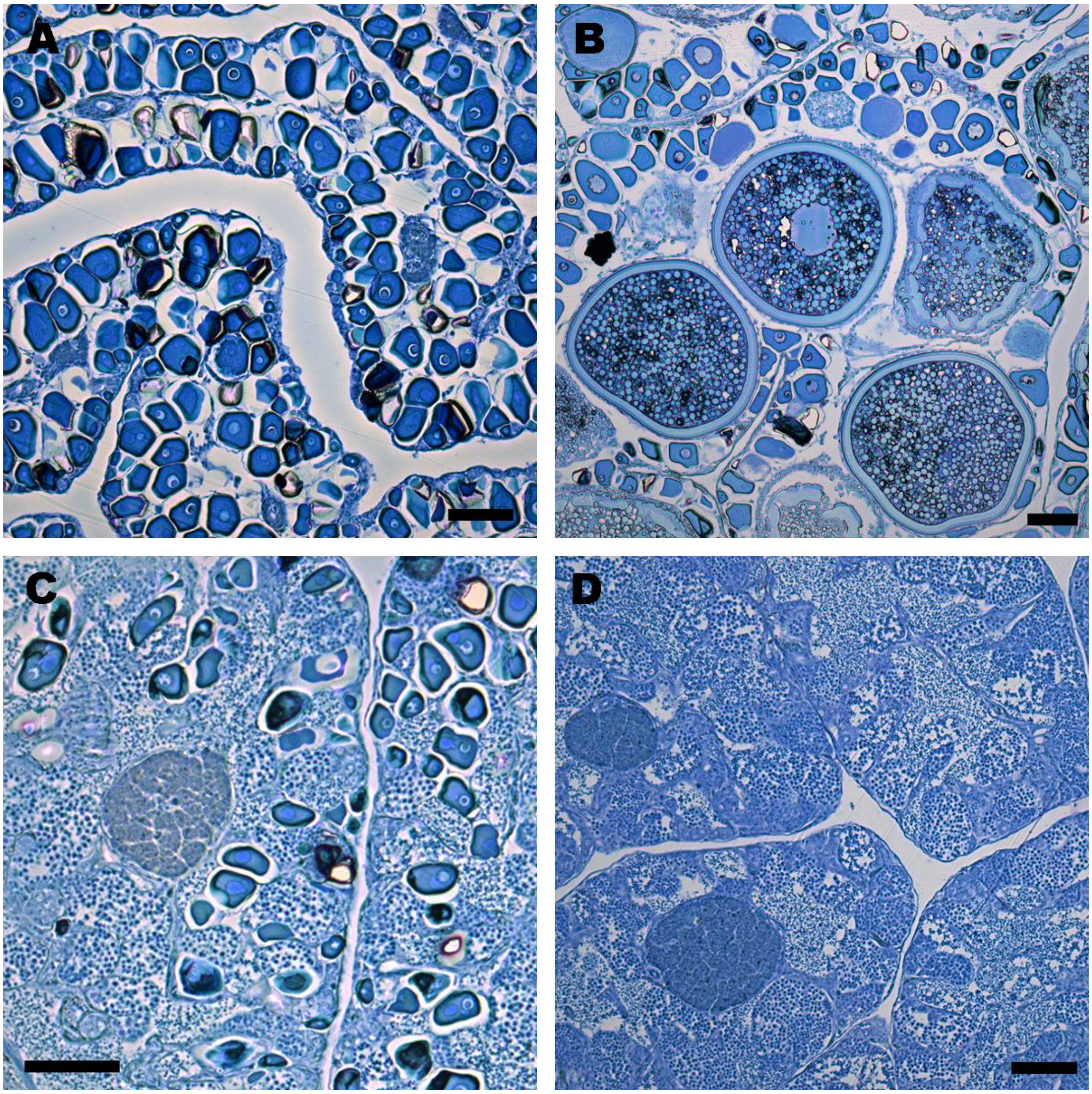

Figure 4. Histological preparations of *Cephalopholis cyanostigma* gonads. (A) immature female, 18.7 cm (B) mature female, 24.6 cm (C) transitional male, 19.8 cm (D) mature male, 21.3 cm. Specimen sizes in TL, all magnifications 100X, scale bars = 100 µm.

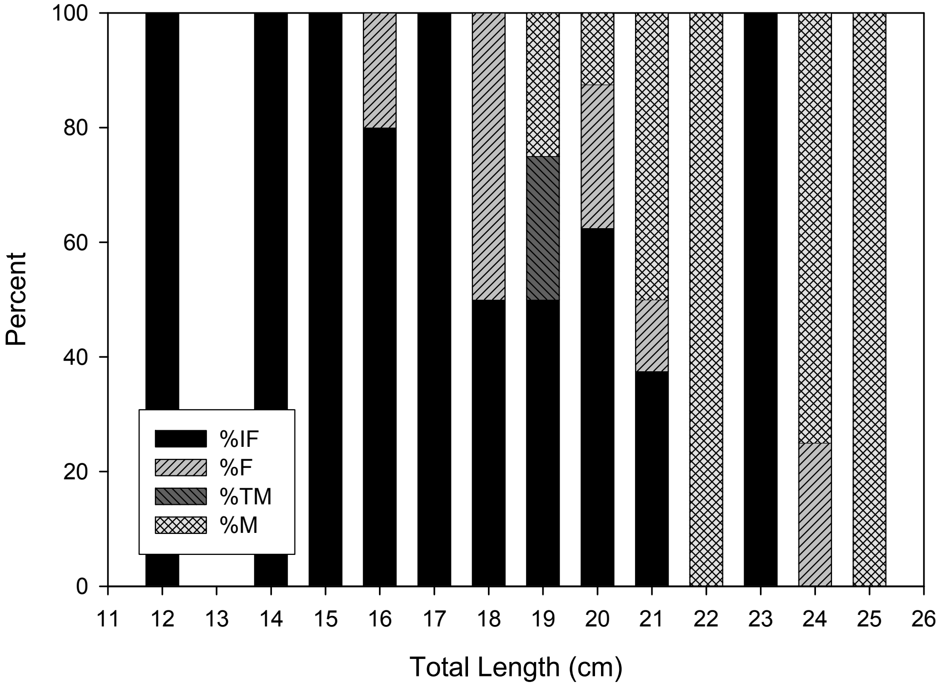

Figure 5. Reproductive status of *Cephalopholis cyanostigma* by size class. IF = immature female, F = mature female, TM = transitional male, M = mature male.

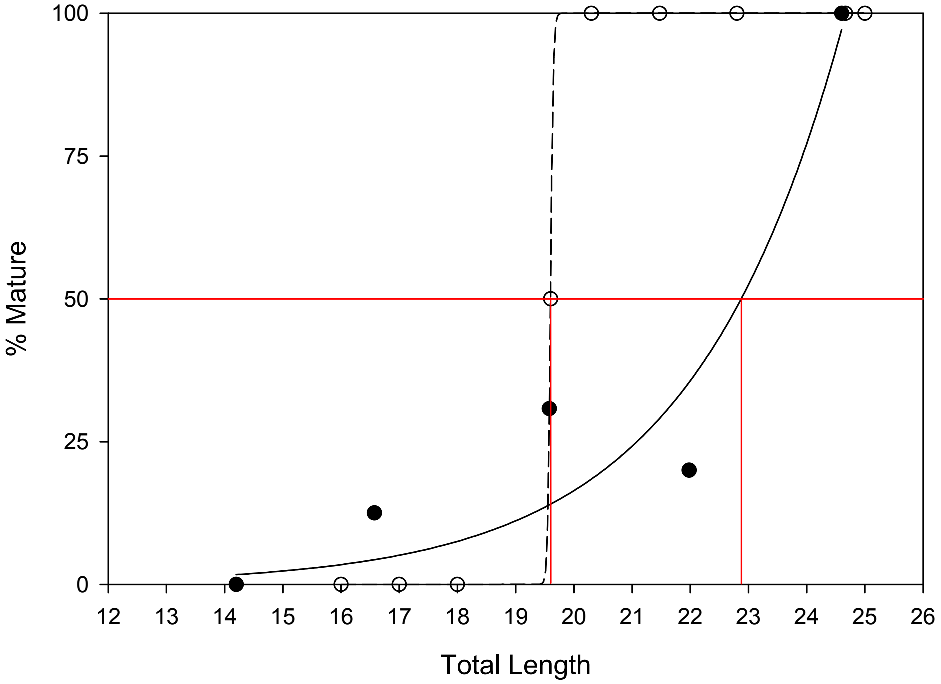

Figure 6. Percent mature individuals of *Cephalopholis cyanostigma* by size class. Females: closed circles, solid line; males: open circles, dashed line.

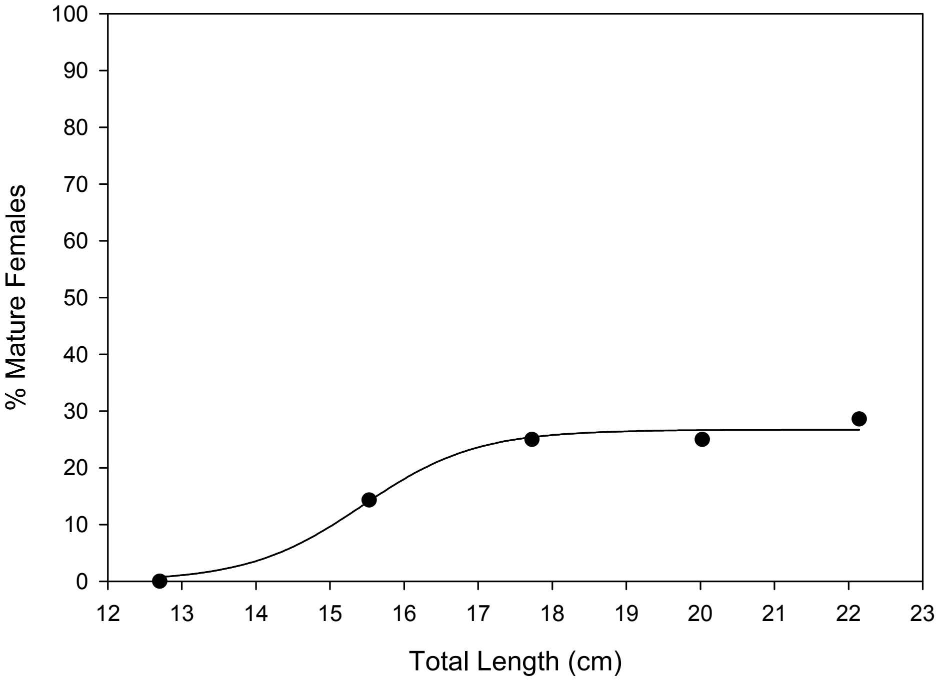

Figure 7. Percent mature females of *Cephalopholis cyanostigma* by size class.

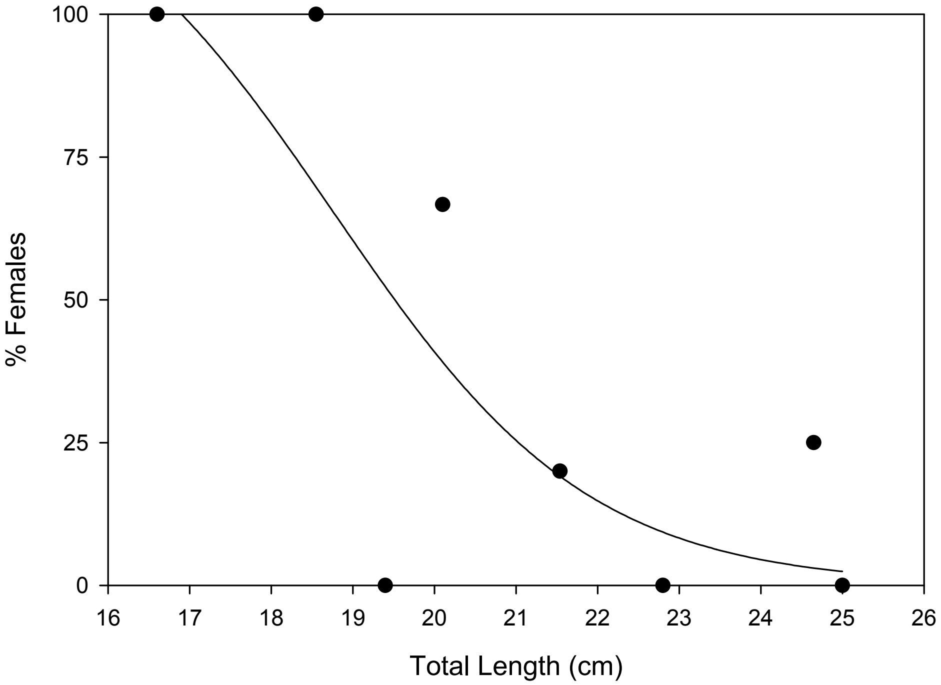

Figure 8. Sex ratio of mature *Cephalopholis cyanostigma* by size class.

Lutjanus semicinctus
We histologically examined 111 gonads. Thirteen individuals had undifferentiated gonads (mean FL = 14.8 cm, range 10.9 – 17.0), and six (6) were in the process of differentiating (mean FL = 15.7 cm, range 12.9 - 17.8). Of the individuals for which sex could be determined, 33 were immature females (mean FL = 16.8 cm, range 12.3 – 18.9), 11 were mature females (mean FL = 22.4 cm, range 20.4 – 23.8), 17 were immature males (mean 16, range 13.8 – 20.2), and 31 were mature males (mean FL = 20.2 cm, range 14.1 – 25.2). Examples of each category are presented in Figure 9.

We found no evidence for sequential hermaphroditism in *L. semicinctus*. A t-test for a sex-based bimodal size distribution was not significant. Nor did we see classic histological signs of sex change (see Sadovy & Shapiro 1987): testes lacked a central lumen or brown bodies, and ovaries did not contain spermatogenic tissue. *Lutjanus semicinctus* is apparently a gonochore.

Data grouped into 2-cm size classes indicate L_{50} is 17.5 cm FL for males and 20.7 cm for females (Figure 10). All males $\geq$ 20.4 cm FL were mature, and all females $\geq$ 22 cm FL were mature.

We could not construct an equation that adequately described size-specific sex ratios of mature individuals. However, after grouping data into 2-cm size classes, we did find a maximum of 70% females at 23.3 cm FL (Figure 11). We could not reliably extend a curve past this point because there were no females in larger size classes, and the extreme right point on the plot is based on a single male.

Figure 12 presents the relationship between length and batch fecundity (BF) for nine (9) *Lutjanus semicinctus*. Regression analysis did not result in a statistically significant relationship; however, we present the equation (with its low descriptive power, $r^2 = 0.208$) below:

$$BF = 0.387(FL)^{3.710}$$

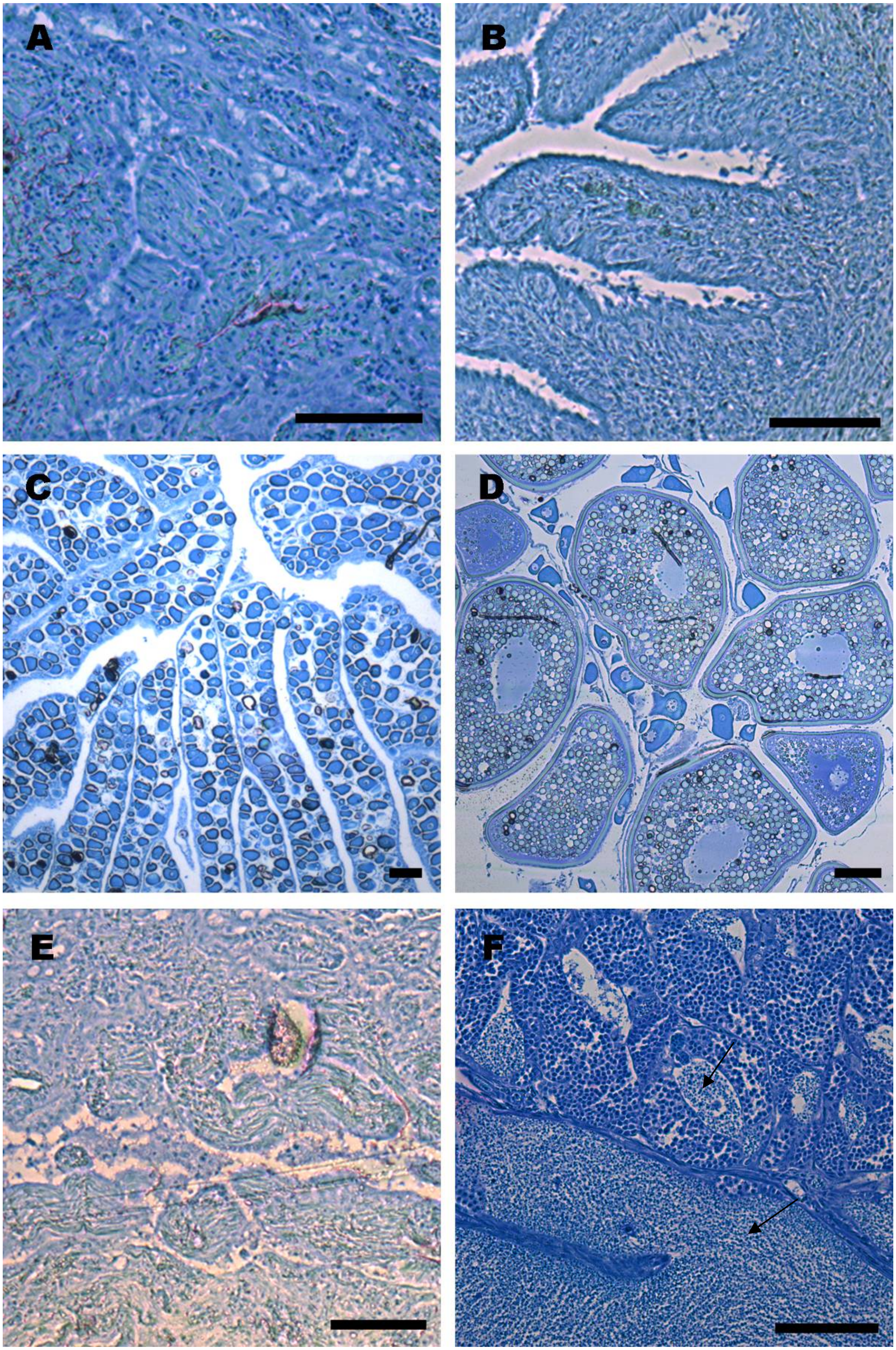
A
B
C
D
E
F

Figure 9 (facing page). Histological preparations of *Lutjanus semicinctus* gonads. (A) undifferentiated, 14.1 cm, 100X (B) differentiating female, 16.5 cm, 100X (C) immature female, 18.0 cm, 40X (D) mature female, 23.0 cm, 100X (E) immature male, 15.5 cm, 100X (F) mature male, 20.4 cm, 200X. Arrows indicate ducts containing mature spermatozoa. Specimen sizes in FL, scale bars = 100 µm.

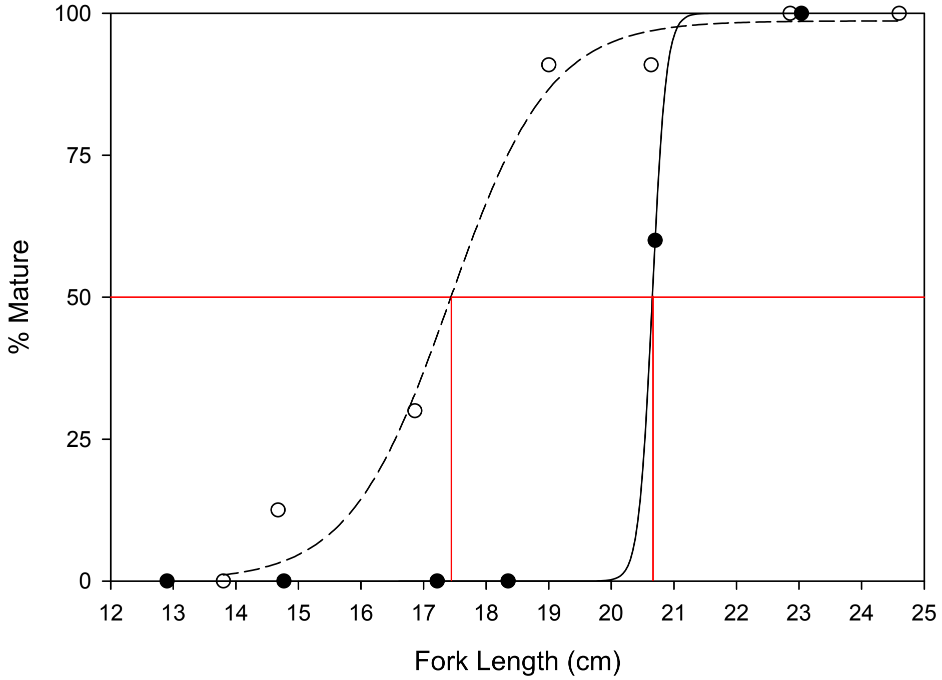

Figure 10. Percent mature individuals of *Lutjanus semicinctus* by size class. Females: closed circles, solid line; males: open circles, dashed line.

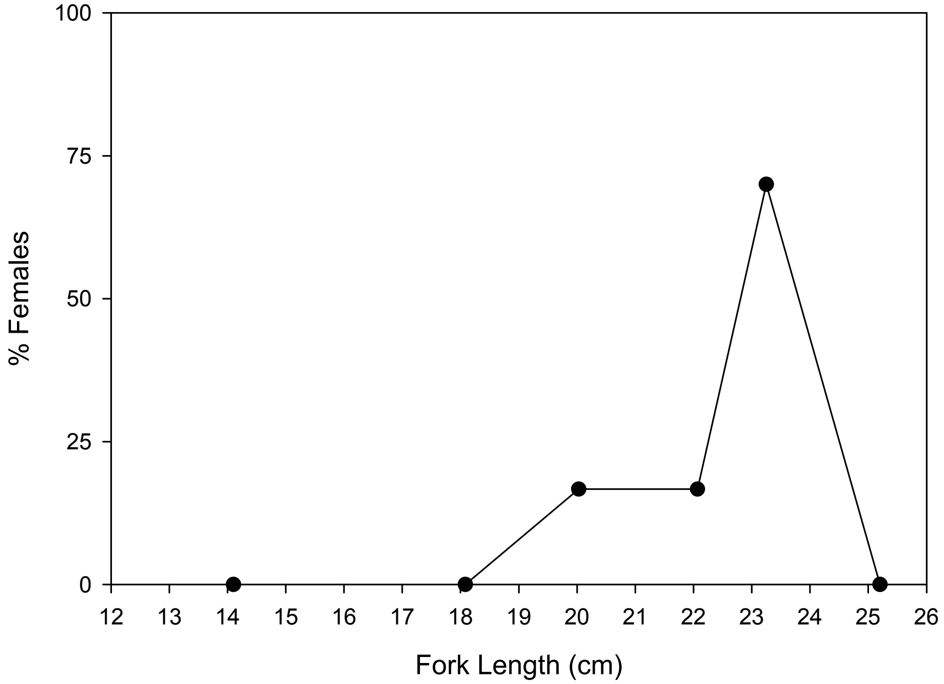

Figure 11. Sex ratio of mature *Lutjanus semicinctus* by size class.

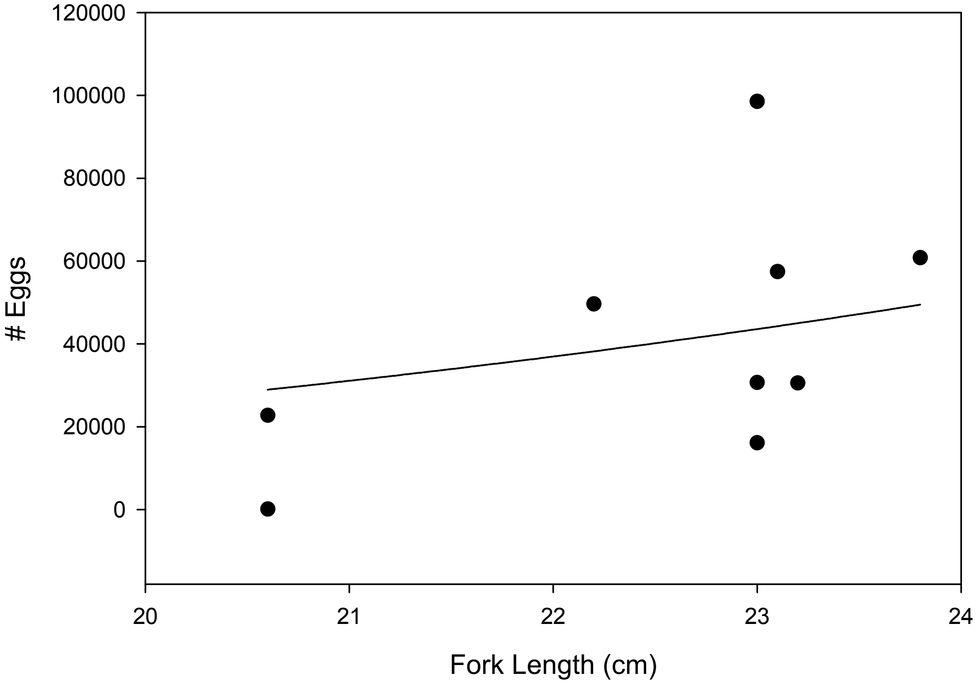

Figure 12. Batch fecundity of *Lutjanus semicinctus* versus size.

Lutjanus timorensis

We histologically examined 120 gonads. One (1) 18 cm FL individual had not differentiated, and one (1) 41.9 cm FL individual appeared to be a differentiating female. Of the remaining individuals for which sex could be determined, 58 were immature females (mean FL = 30.8 cm, range 19.0 – 43.4), five (5) were mature females (mean FL = 35.6 cm, range 30.0 – 39.0), six (6) were immature males (mean FL = 21.2 cm, range 17.0 – 27.2), and 49 were mature males (mean FL = 32.3 cm, range 11.6 – 48.6). Examples of each category are presented in Figure 13.

We found no evidence for sequential hermaphroditism in *L. timorensis*. A t-test for a sex-based bimodal size distribution was not significant. Nor did we see classic histological signs of sex change (see Sadovy & Shapiro 1987): testes lacked a lumen or brown bodies, and ovaries did not contain spermatogenic tissue. *Lutjanus timorensis* is apparently a gonochore.

Immature females occurred throughout female size range, all males ≥ 28 cm FL were mature. Data grouped into 2-cm size classes indicate L_{50} for males is 23 cm FL, no female size class in our collection had more than one-third mature females (*i.e.*, we could not construct a sigmoidal equation for female maturity). For the latter, we used linear regression analysis on size classes from when mature females first appear through size ranges where mature females were present (*i.e.*, excluding two largest size classes with no mature females, but based on only one or two individuals). This suggests female L_{50} may be as high as 48 cm FL (Figure 14).

We could not construct an equation that adequately described size-specific sex ratios of mature individuals. However, we did find a maximum of 40% mature females at 39.5 cm FL. There were no mature females in larger size classes, but these contained a combined total of only six individuals (Figure 15).

Figure 16 presents the relationship between length and batch fecundity for five (5) *Lutjanus timorensis*. Regression analysis did not result in a statistically significant relationship; however, we present the equation (with its low descriptive power, $r^2 = 0.392$) below:

$$BF = 0.378(FL)^{3.251}$$

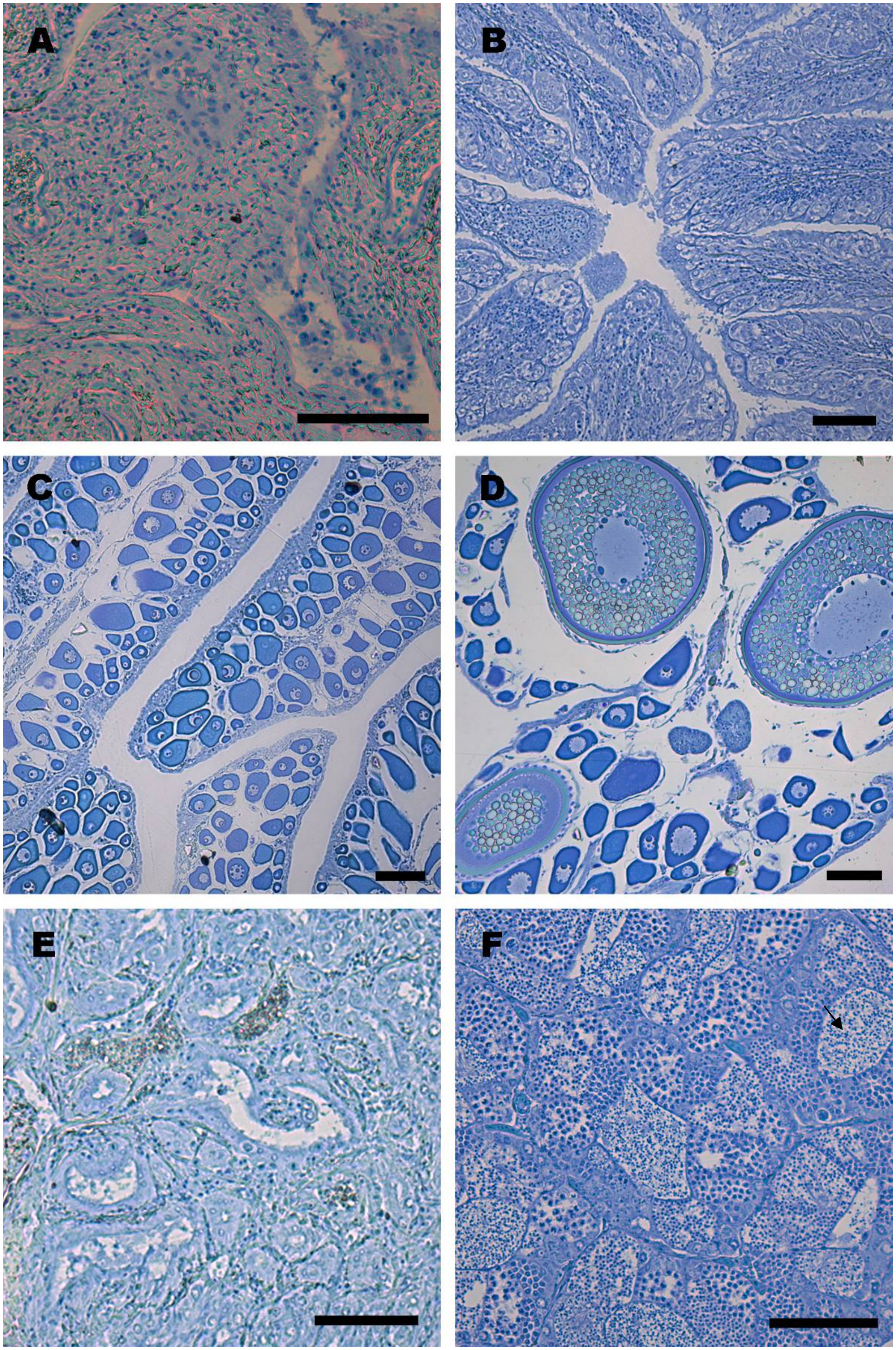
A
B
C
D
E
F

Figure 13 (facing page). Histological preparations of *Lutjanus timorensis* gonads. (A) undifferentiated, 18.0 cm, 200X (B) differentiating female, 41.8 cm, 100X (C) immature female, 29.8 cm, 100X (D) mature female, 30.0 cm, 100X (E) immature male, 18.8 cm, 100X (F) mature male, 47.5 cm, 200X. Arrow indicates a duct containing mature spermatozoa. Specimen sizes in FL, scale bars = 100 µm.

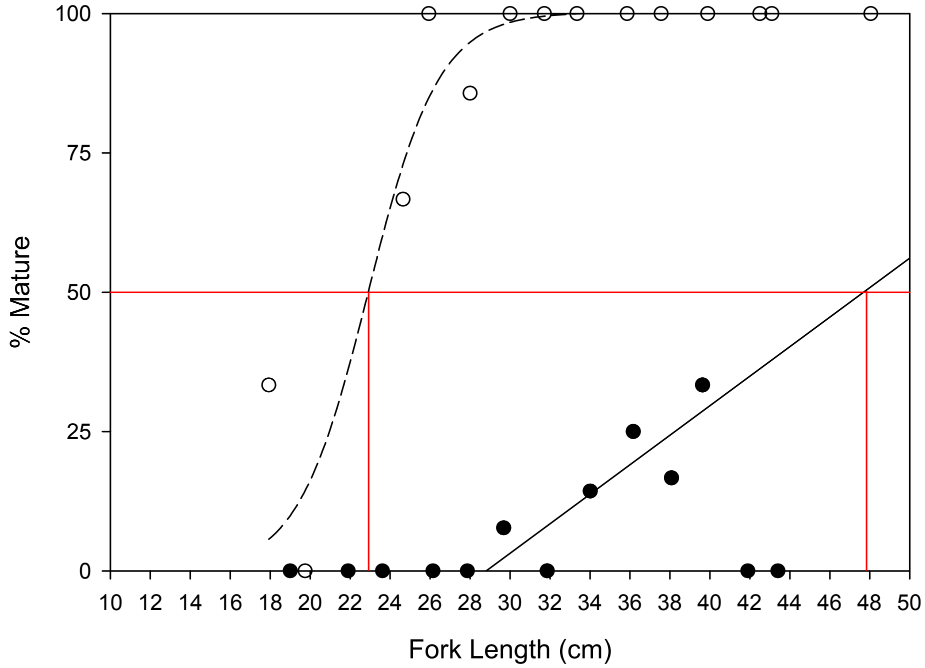

Figure 14. Percent mature individuals of *Lutjanus timorensis* by size class. Females: closed circles, solid line; males: open circles, dashed line.

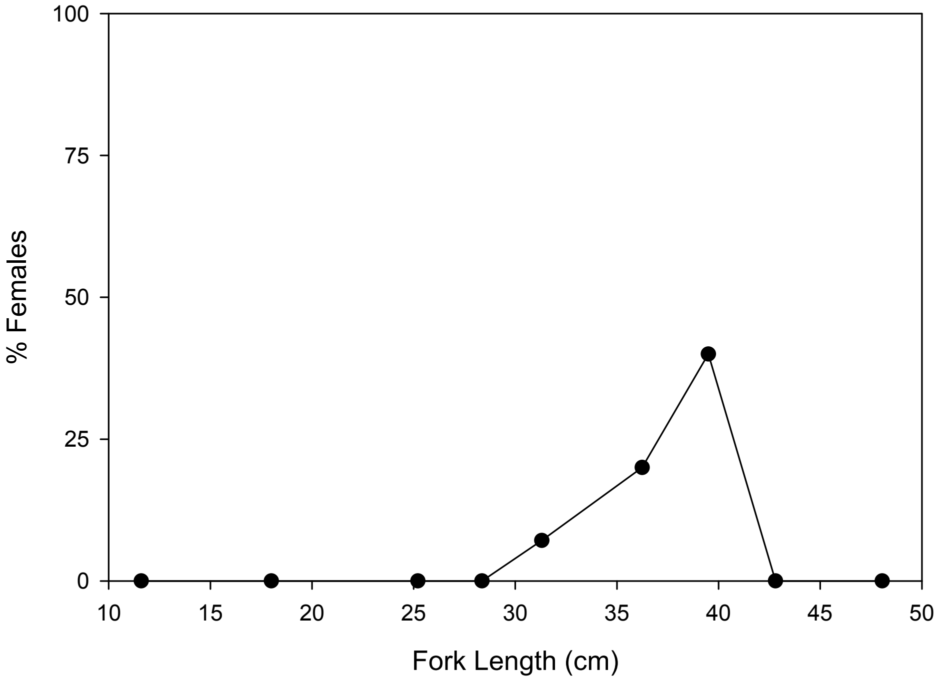

Figure 15. Sex ratio of mature *Lutjanus timorensis* by size class.

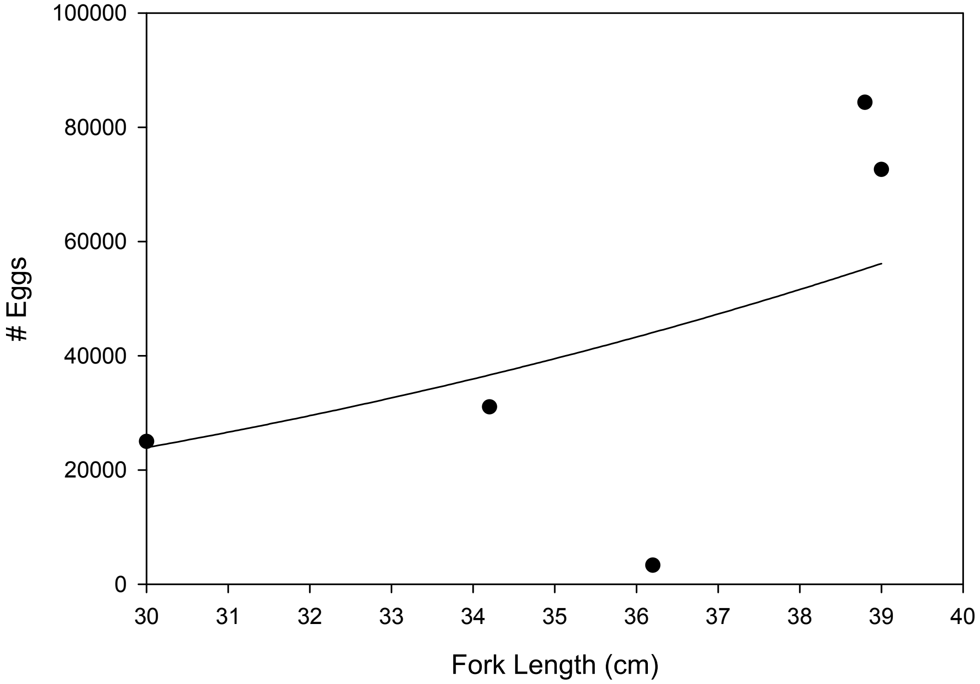

Figure 16. Batch fecundity of *Lutjanus timorensis* versus size.

Parupeneus barberinus

We histologically examined 111 gonads. Fifteen individuals were immature females (mean FL = 16.4 cm, range 12.1 – 20.5), 41 were mature females (mean FL = 15.0 cm, range 11.9 – 19.0), nine (9) were immature males (mean FL = 18.2 cm, range 14.5 – 24.2), and 46 were mature males (mean FL = 17.7 cm, range 14.2 – 25.0). Examples of each category are presented in Figure 17.

Parupeneus barberinus displays two characteristics of sequential hermaphroditism; a t-test of log-transformed data (to meet assumptions of normality) indicates the females in our collection are significantly shorter than males, we also found ovotestis in one 12.9 mm individual (Figure 18). However, we did not see other classic histological signs of sex change (see Sadovy & Shapiro 1987): testes lacked a lumen or brown bodies. Based on these results, we assume *Parupeneus barberinus* is a gonochore.

Immature individuals of both sexes occurred throughout the size range in our collection. We were unable to organize data such that L_{50} could be plotted (Figure 19). Minimum size at maturity (L_m) is 14.2 cm FL for males, but 80% of males were mature in the smallest (14.2 – 14.9) size ranges. Minimum size at maturity (L_m) is 11.9 cm FL for females, but 70% of females were mature in the smallest (11.9 – 12.9) size range. Notably, the percentage of mature females *decreased* with increasing size; only 33% were mature in the 19 – 20.9 cm FL size range.

Of mature individuals, sex ratio becomes increasingly male-biased with size and exclusively male above 21.0 cm FL (Figure 20). Linear regression analysis of 1-cm size classes from the largest average size with 100% females (13.3 cm FL) through the smallest average size with 100% males (20.3 cm FL) indicates the percentage of females can be predicted by the equation ($n = 8$, $r^2 = 0.824$):

$$\%♀ = 226.5 - 10.8(FL)$$

Batch fecundity (Figure 21) of *Parupeneus barberinus* can be predicted by the equation ($n = 19$, $r^2 = 0.393$):

$$BF = 1.198(FL)^{3.323}$$

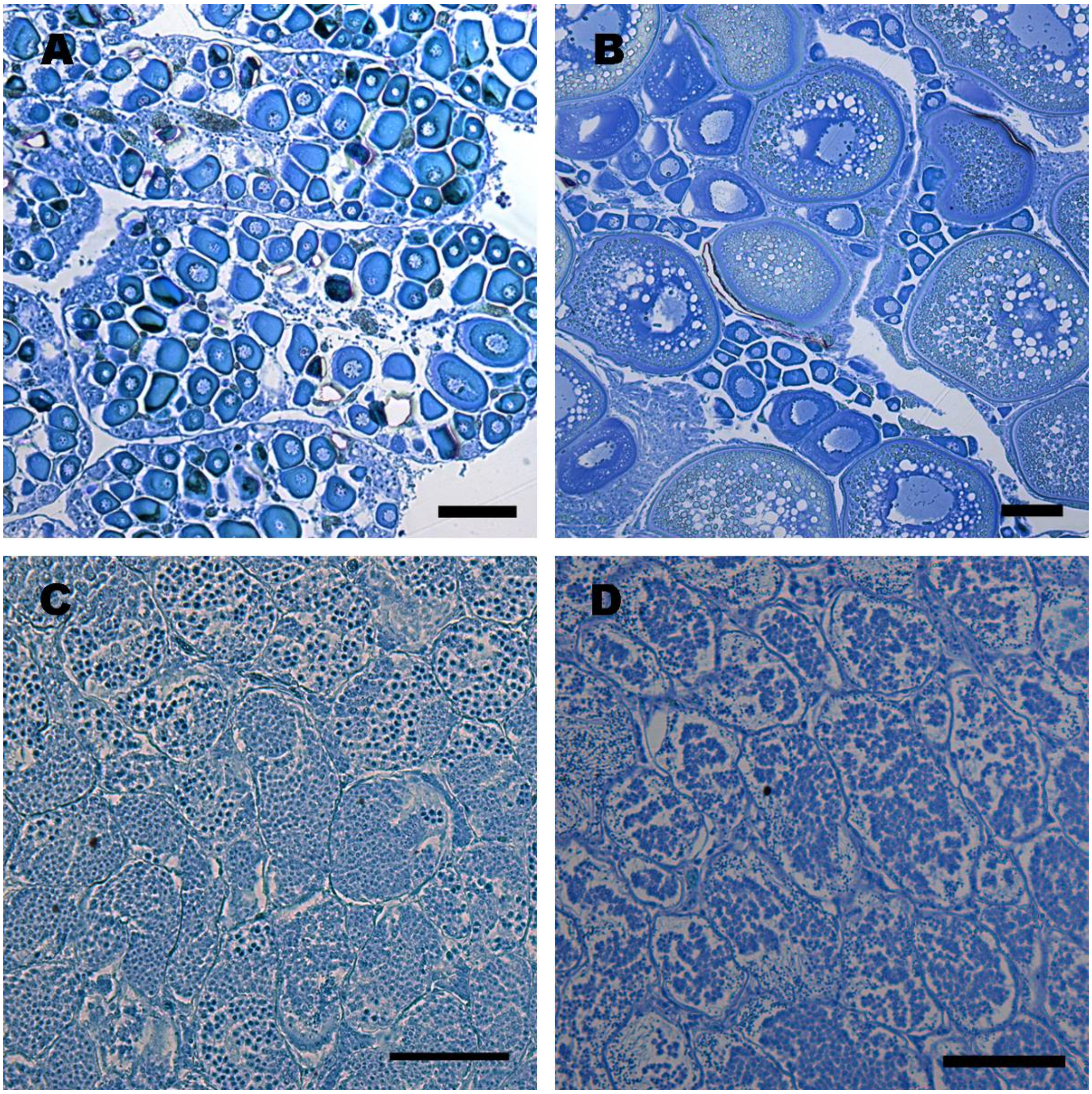

Figure 17. Histological preparations of *Parupeneus barberinus* gonads. (A) immature female, 16.8 cm, 100X (B) mature female, 15.3 cm, 100X (C) immature male, 15.0 cm, 200X (D) mature male, 20.1 cm, 200X. Specimen sizes in FL, scale bars = 100 µm.

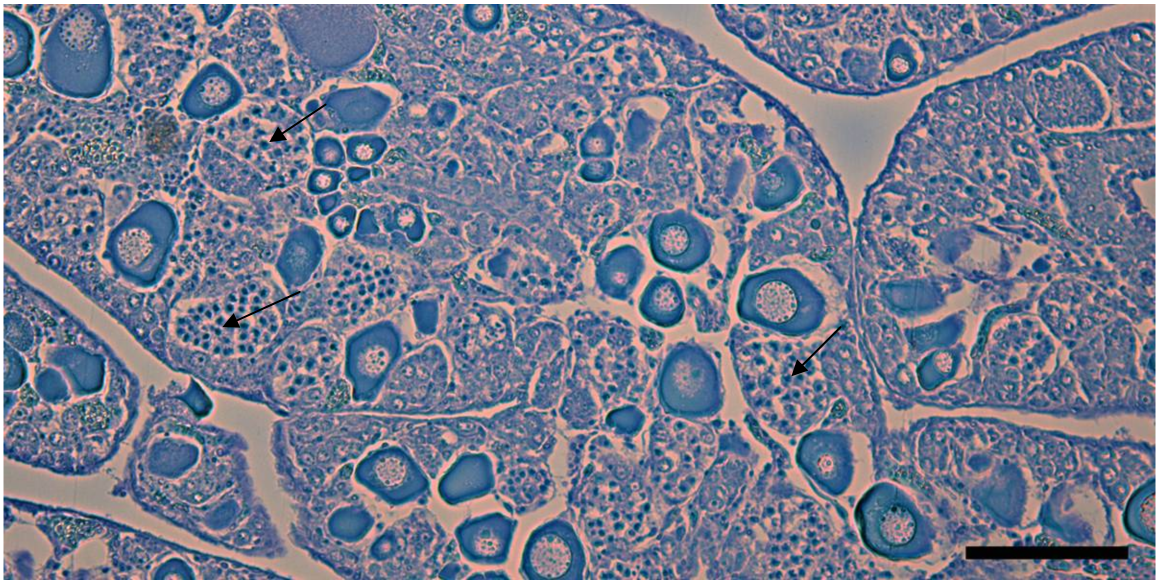

Figure 18. Ovotestis of a 12.9 cm FL *Parupeneus barberinus* (200X). Arrows indicate immature spermatocytes.

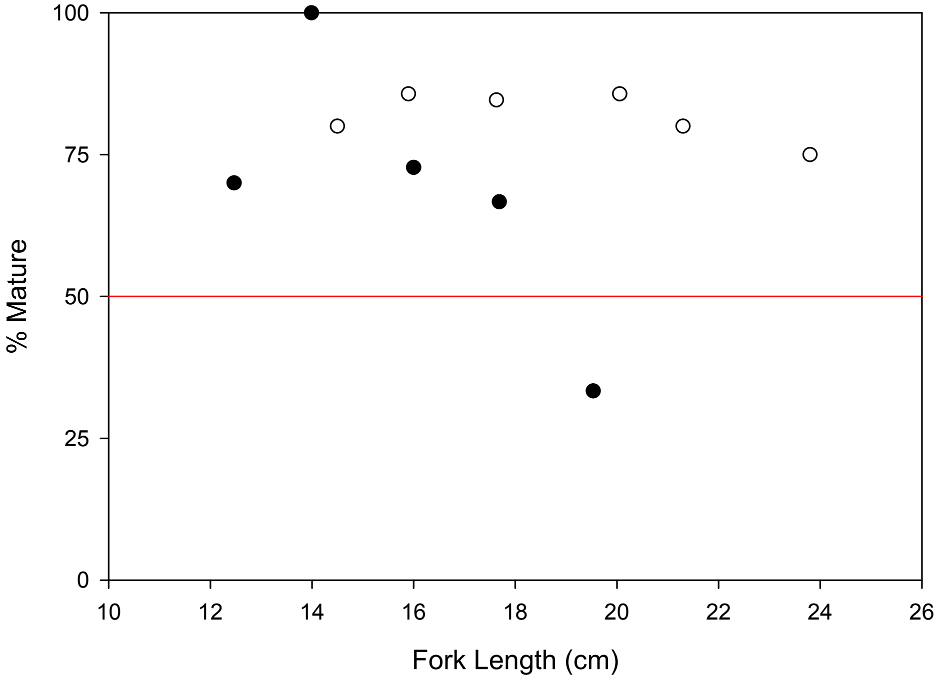

Figure 19. Percent mature individuals of *Parupeneus barberinus* by size class. Females: closed circles, solid line; males: open circles, dashed line.

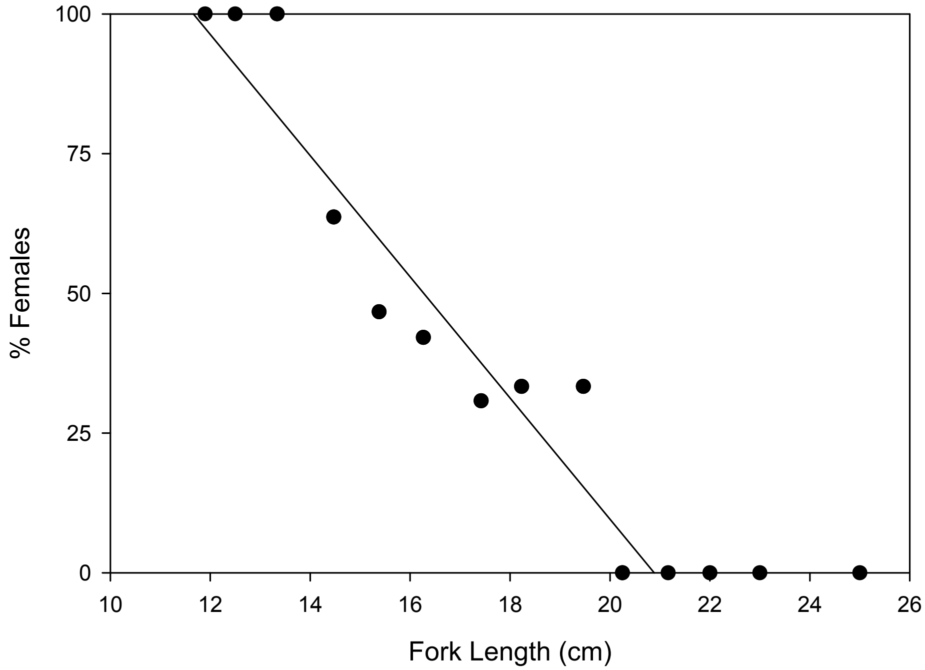

Figure 20. Sex ratio of mature *Parupeneus barberinus* by size class.

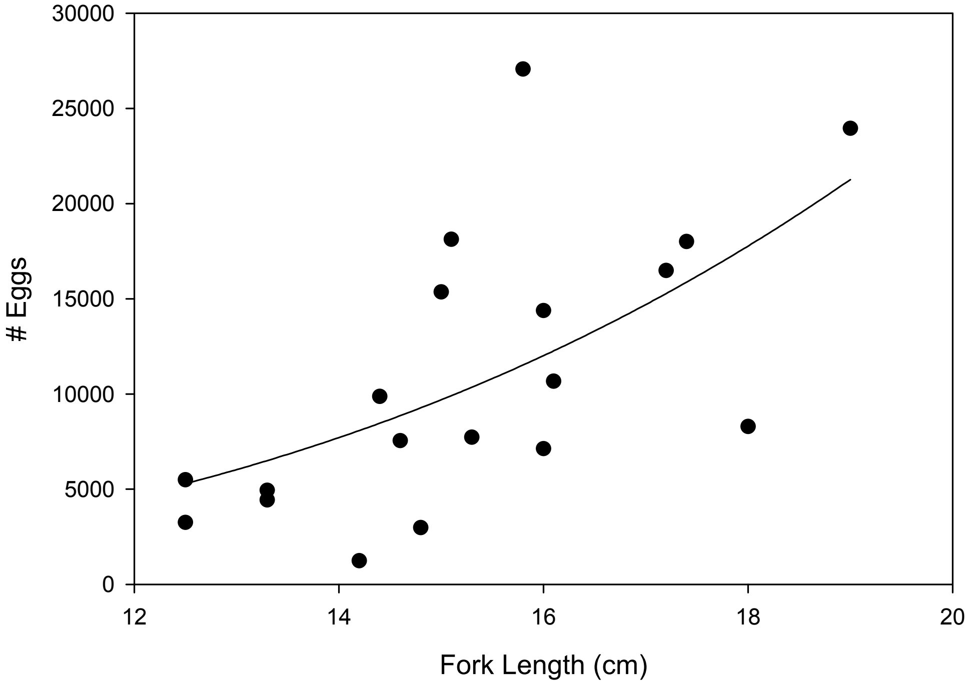

Figure 21. Batch-fecundity relationship for *Parupeneus barberinus* versus size.

Siganus lineatus
We histologically examined 91 gonads. Twenty-six individuals were immature females (mean FL = 22.8 cm, range 20.9 – 28.5), 23 were mature females (mean FL = 25.6 cm, range 21.9 – 29.0), one (1) 22.4 cm FL individual was an immature male, and 41 individuals were mature males (mean FL = 23.6 cm, range 18.6 – 29.5). Examples of each category are presented in Figure 22.

We found no evidence for sequential hermaphroditism in *S. lineatus*. A t-test for a sex-based bimodal size distribution was not significant. Nor did we see classic histological signs of sex change (see Sadovy & Shapiro 1987): testes lacked a lumen or brown bodies, and ovaries did not contain spermatogenic tissue. *Siganus lineatus* is apparently a gonochore.

All but one male in our collection were mature so we could not construct an L_{50} curve for males. Minimum size at maturity (L_m) for males is 18.6 cm FL, and all males ≥ 22.7 cm were mature. Based on 2-cm size classes, female L_{50} is 24.1 cm FL (Figure 23), all five (5) females ≥ 28.6 cm FL were mature.

Of mature individuals, sex ratios were approximately 1:1; however, our collection does not permit examination of sex ratios in sizes above 29 cm FL (Figure 24). Size-specific sex ratios for the specimens in our collection can be predicted by the equation ($n = 6$, $r^2 = 0.873$):

$$\%♀ = 53.342/(1+e^{-((TL-22.299)/0.527)})$$

Batch fecundity (Figure 25) of Siganus lineatus can be predicted by the equation ($n = 16$, $r^2 = 0.552$):

$$BF = 3.522(FL)^{3.550}$$

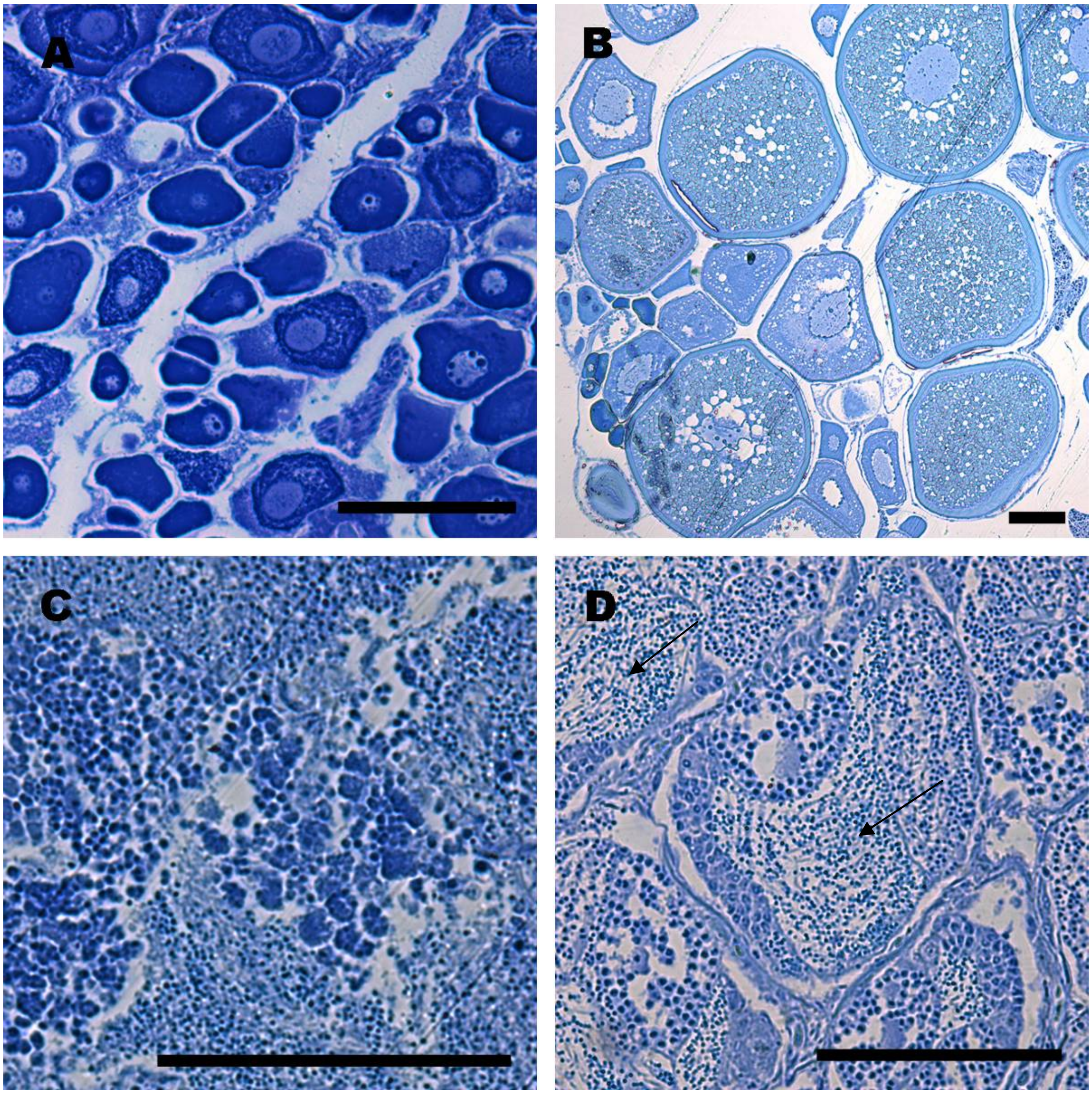

Figure 22. Histological preparations of *Siganus lineatus* gonads. (A) immature female, 21.7 cm, 200X (B) mature female, 24.6 cm, 100X (C) immature male, 22.4 cm, 400X (D) mature male, 22.0 cm, 400X. Arrows indicate ducts containing mature spermatozoa. Specimen sizes in FL, scale bars = 100 µm.

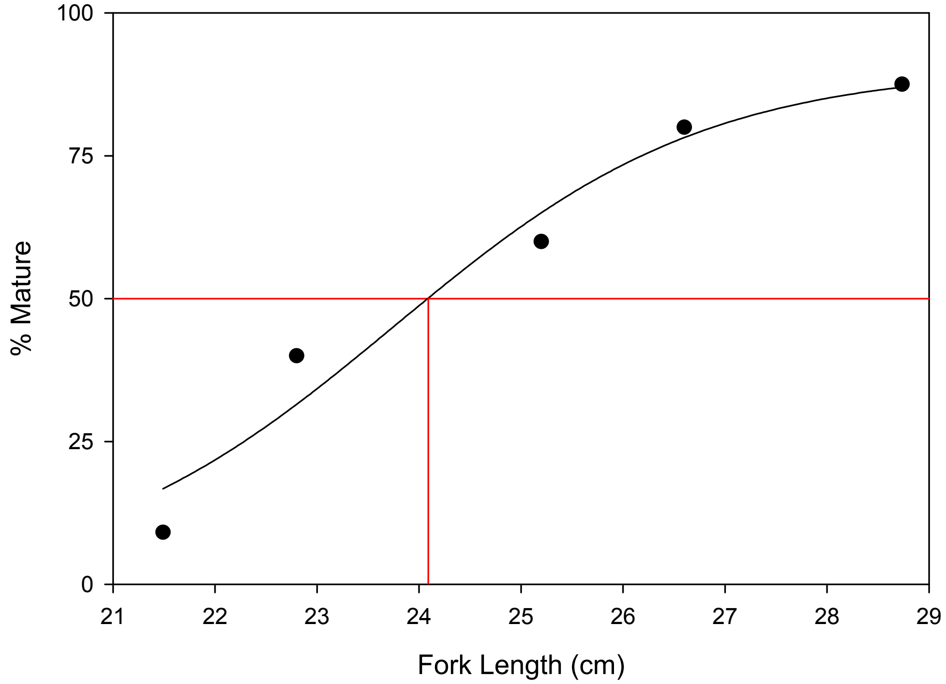

Figure 23. Percent mature females of *Siganus lineatus* by size class.

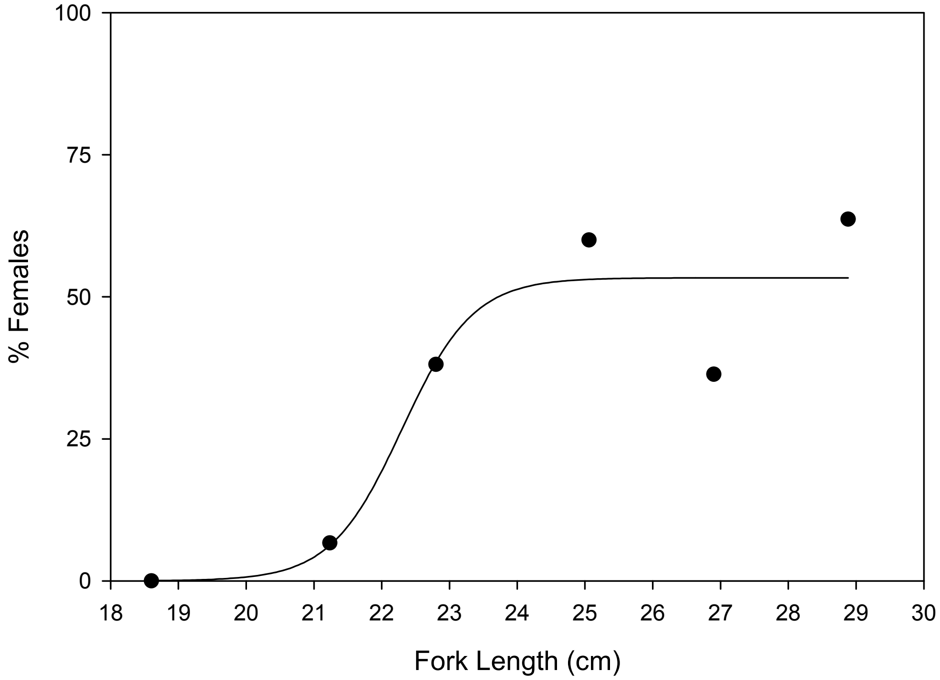

Figure 24. Sex ratio of mature *Siganus lineatus* by size class.

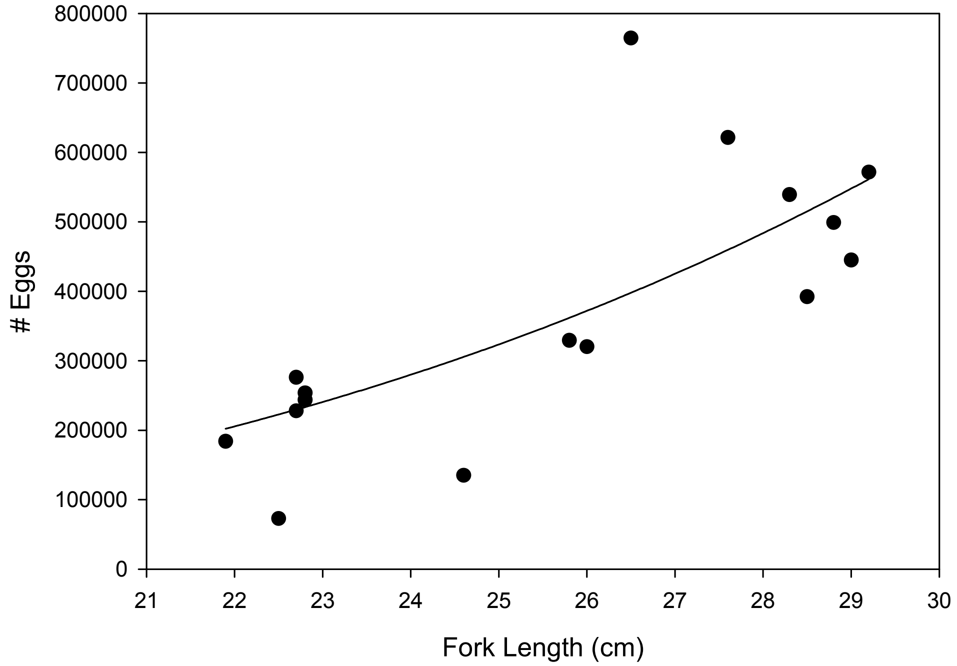

Figure 25. Batch fecundity of *Siganus lineatus* versus size.

Length-Weight Relationships

Length is highly predictive of total body weight for the five species on which we conducted reproductive analyses. For all species, weight is an approximately cubic function of length (Table 2). Plots of length-weight data are presented in Figure 26.

Table 2. Length-weight relationships for five exploited fishes based on fishery catch. Wt = total body weight (g), FL = fork length (cm).

Species	Equation	N	Range (cm)	r^2
Cephalopholis cyanostigma	$Wt = 0.0062(TL)^{3.3015}$	44	12.7 – 25.0	0.942
Lutjanus semicinctus	$Wt = 0.0160(FL)^{3.0341}$	127	10.9 – 25.2	0.978
Lutjanus timorensis	$Wt = 0.0185(FL)^{2.9669}$	123	11.6 – 48.6	0.959
Parupeneus barberinus	$Wt = 0.0242(FL)^{2.9052}$	123	11.2 – 25.0	0.940
Siganus lineatus	$Wt = 0.0569(FL)^{2.7103}$	93	18.6 – 29.5	0.926

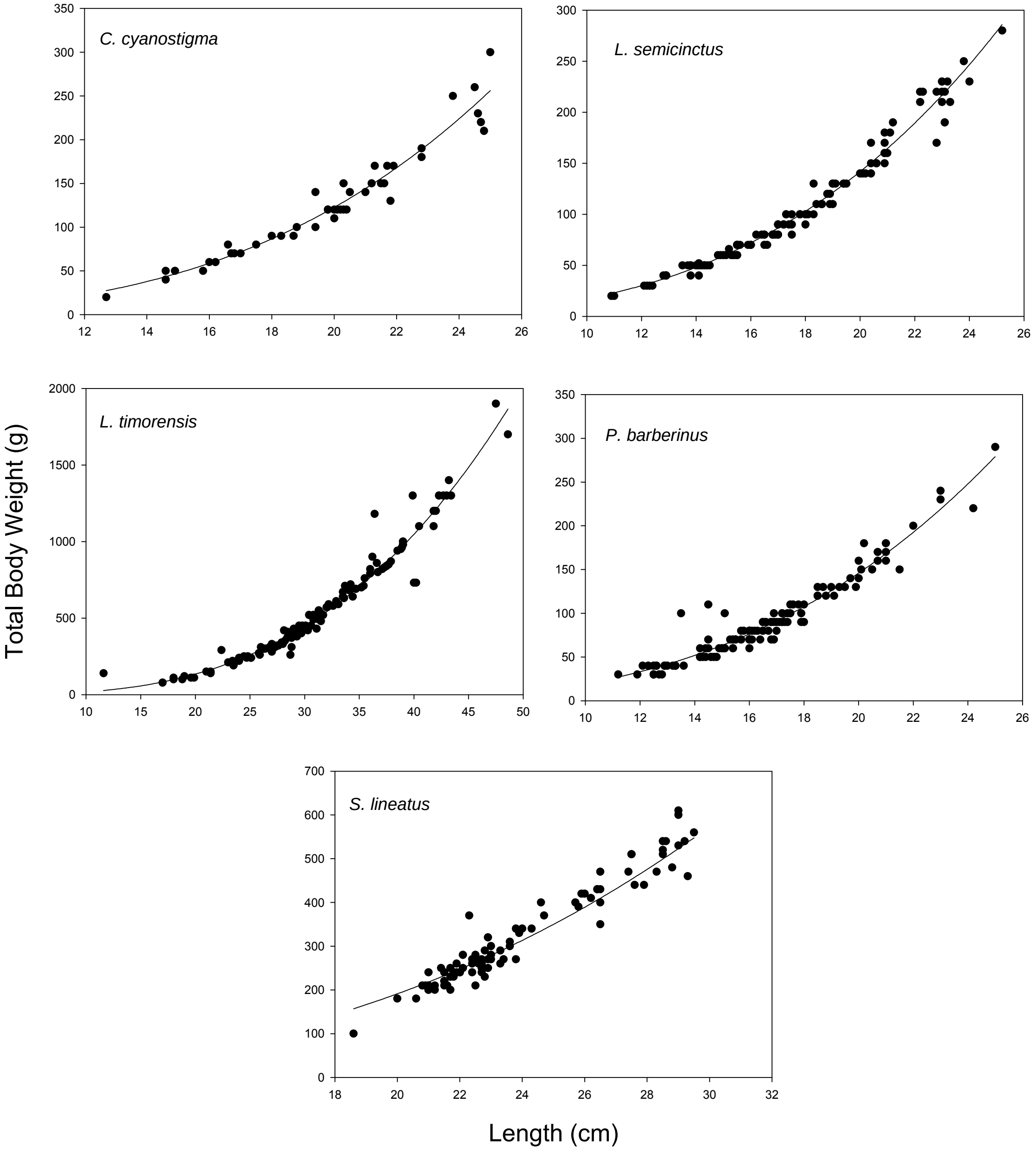

Figure 26. Scatterplots of length versus weight for five exploited species at Kamiali Wildlife Management Area.

Catch Characteristics

Cephalopholis cyanostigma

A size-frequency histogram of *Cephalopholis cyanostigma* caught by village residents participating in our fishing program from March through June 2011 is presented in Figure 27. Average total length is 19.7 cm, which is 13% lower than estimated optimum length (L_{opt}) and observed female L_{50}, both 23 cm TL. A one-sample t-test indicates average size is significantly lower than L_{opt} and female L_{50}. Eighteen percent of individuals had attained female L_{50}, and 86% had attained minimum size at maturity (L_m) for females (16.6 cm TL). Fifty percent of individuals were within 10% of L_{opt}.

When size-specific sex ratios and percent maturity parameters are considered, 65% of the catch was mature individuals. Of these, 5% were females and 60% were males. Thus, current fishing practices are biased toward mature males.

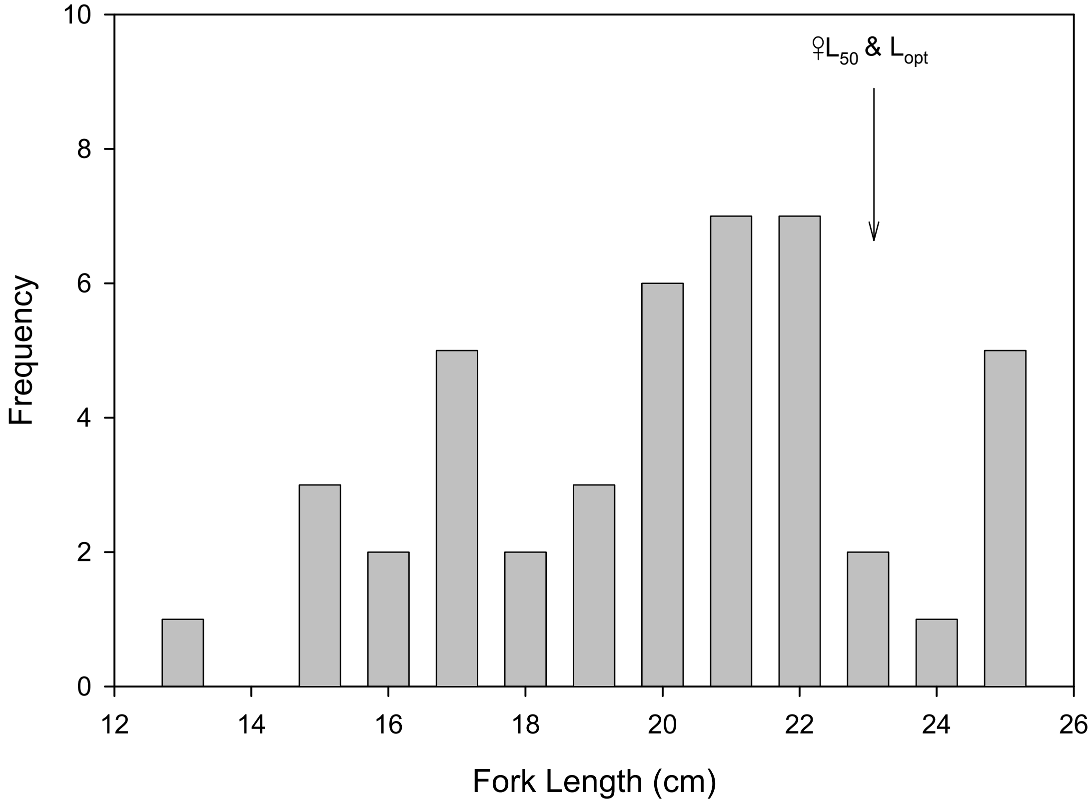

Figure 27. Size structure of *Cephalopholis cyanostigma* catch at KWMA, March – June 2011.

Lutjanus semicinctus

A size-frequency histogram of *Lutjanus semicinctus* caught by village residents participating in our fishing program from March through June 2011 is presented in Figure 28. Average fork length is 17.4 cm, which is 21% lower than the estimated L_{opt} of 22.0 cm FL. A one-sample t-test indicates this difference is significant. Average length is 16% lower than female L_{50} of 21 cm FL. A one-sample t-test indicates this difference is also significant. Twenty-four percent of individuals had attained female L_{50}, and 28% had attained female L_m (20.2 cm FL). Thirty-nine percent of individuals were within 10% of L_{opt}.

When size-specific sex ratios and percent maturity parameters are considered, 57% of the catch was mature individuals. Of these, 7% were females and 50% were males.

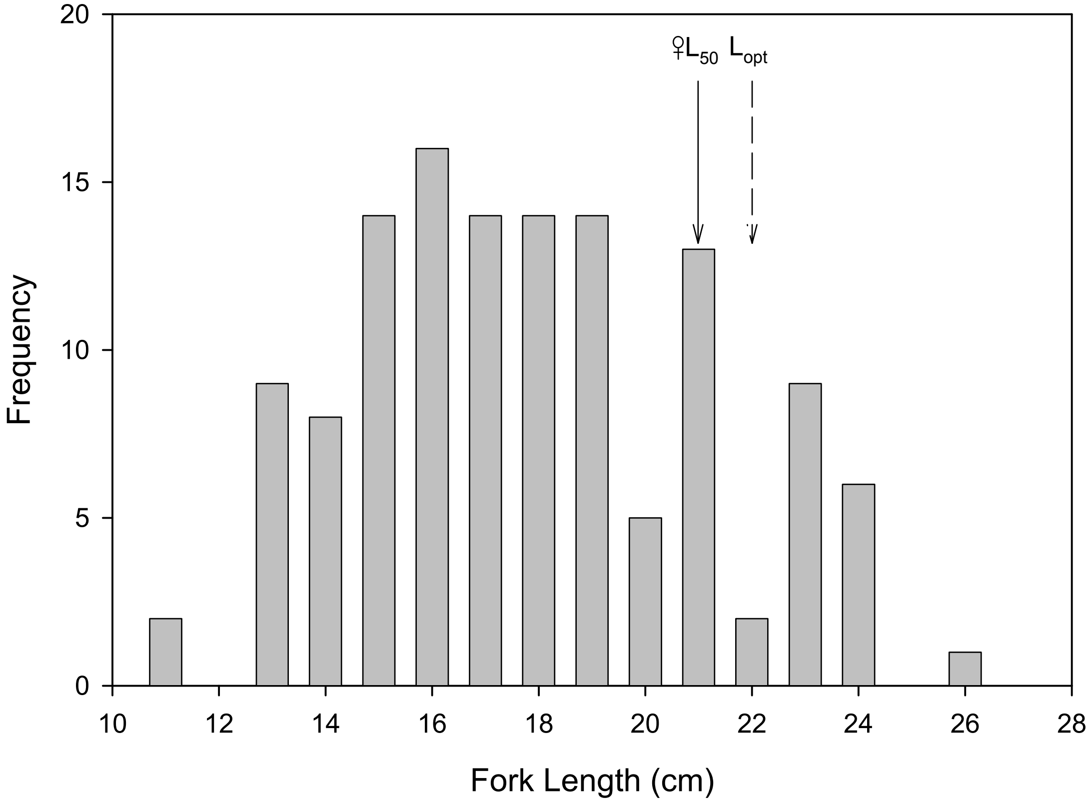

Figure 28. Size structure of *Lutjanus semicinctus* catch at KWMA, March – June 2011.

Lutjanus timorensis

A size-frequency histogram of *Lutjanus timorensis* caught by village residents participating in our fishing program from March through June 2011 is presented in Figure 29. Average fork length is 30.9 cm, which is 6% lower than the estimated L_{opt} of 32.7 cm FL. A one-sample t-test indicates this difference is significant. Average length is 1% higher than the female L_m of 30 cm FL. A one-sample t-test indicates this difference is not significant. Sixty-one percent of individuals had attained female L_m, and 37 % of individuals were within 10% of L_{opt}.

When size-specific sex ratios and percent maturity parameters are considered, 77% of the catch was mature individuals. Of these, 5% were females and 72% were males.

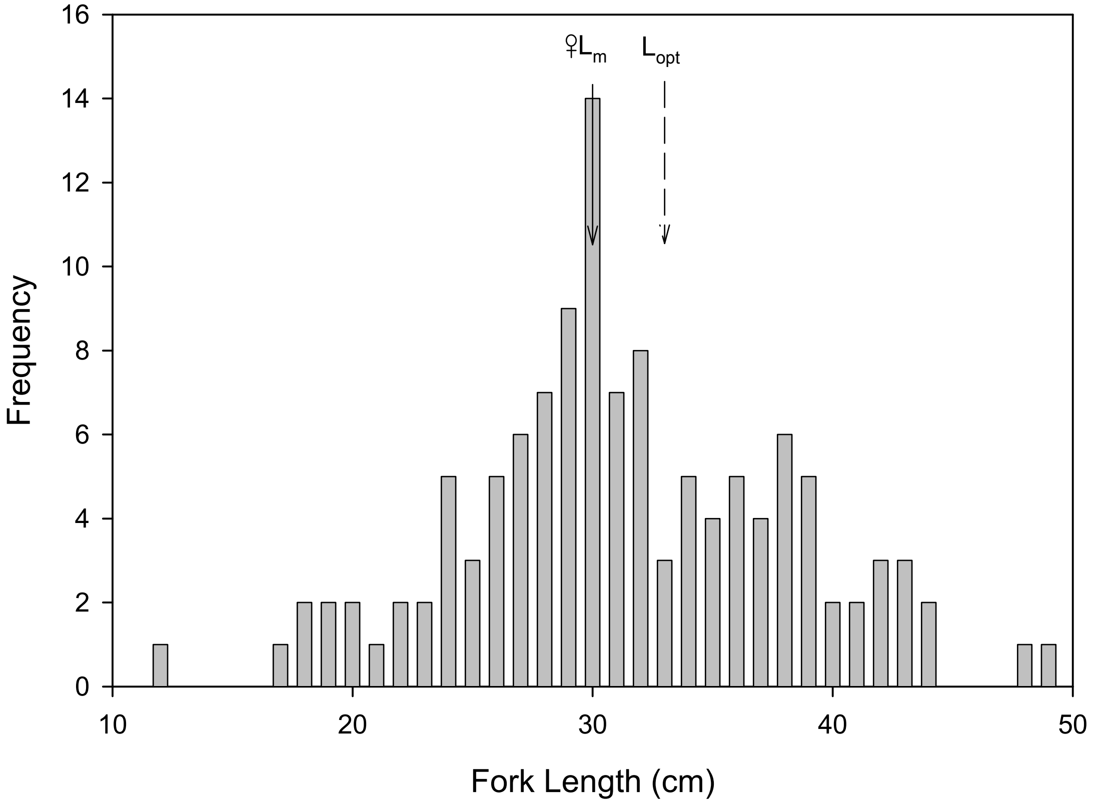

Figure 29. Size structure of *Lutjanus timorensis* catch at KWMA, March – June 2011.

Parupeneus barberinus

A size-frequency histogram of *Parupeneus barberinus* caught by village residents participating in our fishing program from March through June 2011 is presented in Figure 30. Average fork length is 16.5 cm, which is 42% lower than the estimated L_{opt} of 28.5 cm FL. A one-sample t-test on log-transformed data (to meet assumptions of normality) indicates this difference is significant. Average length is 39% higher than the female L_m of 12 cm FL. A one-sample t-test on log-transformed data indicates this difference is significant. One hundred percent of individuals had attained female L_m; however, none of these (0%) individuals were within 10% of L_{opt} estimated from the empirical equation of Froese & Binohlan (2000).

When size-specific sex ratios and percent maturity parameters are considered, 86% of the catch was mature individuals. Of these, 24% were females and 62% were males. Thus, current fishing practices are biased toward mature males.

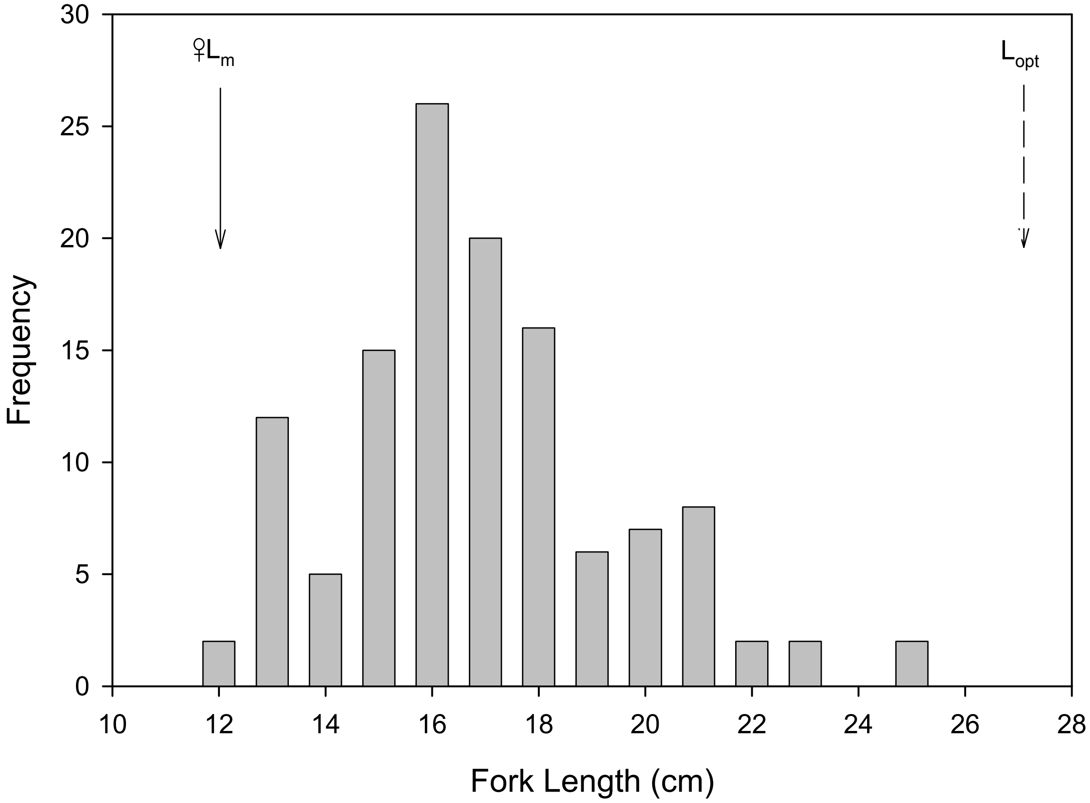

Figure 30. Size structure of *Parupeneus barberinus* catch at KWMA, March – June 2011.

Siganus lineatus

A size-frequency histogram of *Siganus lineatus* caught by village residents participating in our fishing program from March through June 2011 is presented in Figure 31. Average fork length is 23.9 cm, which is 10% lower than the estimated L_{opt} of 26.7 cm FL. A one-sample sign-test (data could not be transformed to meet assumptions of normality) indicates the median length of 22.8 cm is significantly lower than L_{opt}. Average fork length is 1% lower than female L_{50} of 24 cm. A one-sample sign-test indicates the median is also significantly different from L_{50}. Forty-three percent of individuals had attained female L_{50}, 89% had attained female L_m (21.9 cm FL), and 43% were within 10% of L_{opt}.

When size-specific sex ratios and percent maturity parameters are considered, 95% of the catch was mature individuals. Of these, 23% were females and 72% were males. Thus, current fishing practices are biased toward mature males.

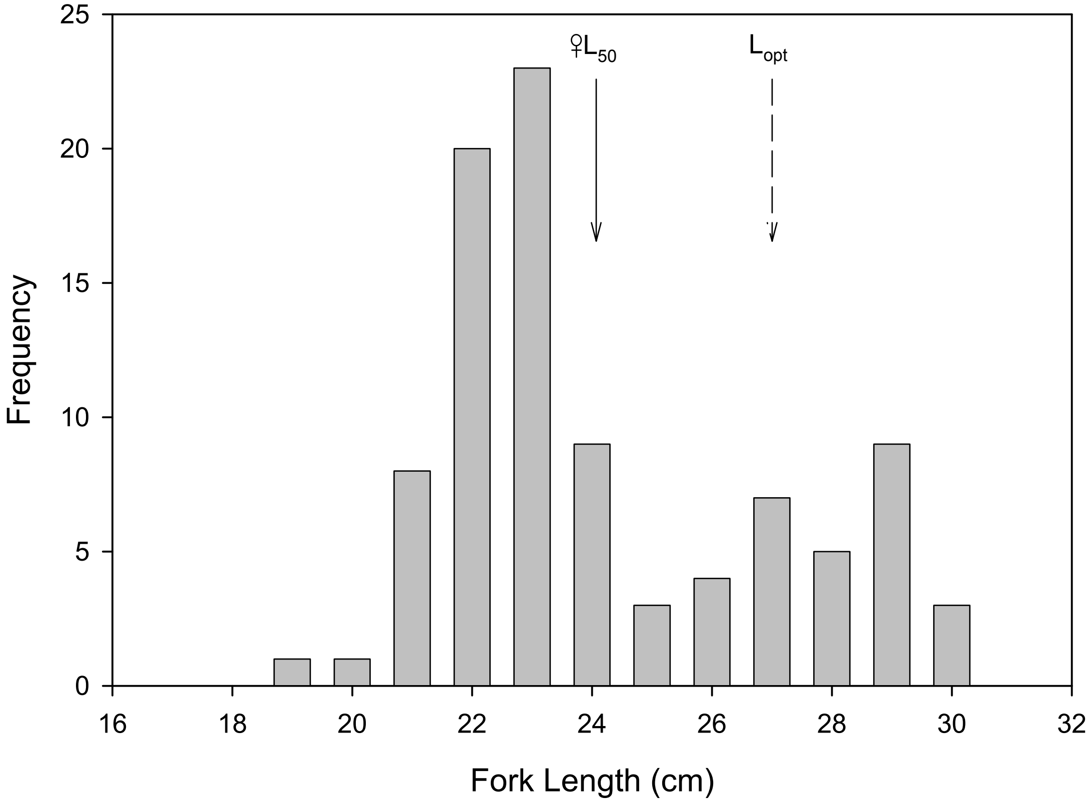

Figure 31. Size structure of *Siganus lineatus* catch at KWMA, March – June 2011.

Fishery Surveys

In 2011, we captured an additional 937 specimens on video suitable for length estimation, yielding a combined total 2,646 individuals analyzed from 2009 to 2011. These specimens include 16 species not analyzed in the 2009 and 2010 surveys (Longenecker *et al*. 2010). Mean length, along with known information on maximum length, size at maturity, size-specific sex ratios, spawning season, and reproductive mode is presented for each of 57 species in Table 3. A tilde (~) preceding values in Table 3 indicates uncertainty. These typically occur before maximum length and size-at-maturity values. For maximum length, a lack of published total length to fork length equations prevented accurate determination of fork length. For size-at-maturity values, only minimum size at maturity (L_m) values were available. These would be expected to be smaller than the preferred size at 50% maturity (L_{50}).

Weighted percent maximum length of all individuals captured on video was 52%. That is, an exploited reef fish swimming in Kamiali Wildlife Management Area is likely to be about ½ its potential maximum length.

Weighted percent estimated optimum length of all individuals captured on video was 84%. In other words, an exploited fish is likely to be about 16% shorter than the length at which the empirical equation of Froese & Binohlan (2000) suggests maximum yield per recruit can be obtained.

Information about reproduction in these species is remarkably scant. Size at maturity is known for only 42% of the species studied. Of this subset, an individual *Naso hexacanthus, Caranx melampygus, Diagramma pictum, Neoniphon sammara*, *Lutjanus carponotatu*s, *Lutjanus gibbus, Lutjanus kasmira*, *Mulloidichthys vanicolensis*, *Parupeneus barberinus, Parupeneus trifasciatus, Scomberomorus commerson*, *Cephalopholis boenak*, *Plectropomus leopardus*, or *Siganus lineatus* in Kamiali Wildlife Management Area was more likely than not to be reproductively mature. These represent 58% of the species for which reproductive information is available. On the other hand, an individual *Lutjanus argentimaculatus*, *Lutjanus biguttatus*, *Lutjanus russelli*, *Lutjanus semicinctus*, *Lutjanus vitta*, *Parupeneus multifasciatus*, *Gymnosarda unicolor*, *Cephalopholis cyanostigma*, or *Cephalopholis sexmaculata* were more likely to be immature. Further, no individual *Plectropomus areolatus* had reached maturity. The latter group represents 42% of the species for which reproductive information is available.

Given the scarcity of reproductive information, we made several comparisons of average length relative to estimates of minimum size at female maturity (♀L_m, using the empirical equation of Froese & Binohlan 2000), observed ♀L_m, and observed size at which 50% of females are mature (♀L_{50}). For all ♀L_m values combined (observed and estimated), an exploited fish was 85% of minimum size at maturity (n = 43). However, results varied depending on whether estimated or observed values were used. When only estimated ♀L_m was available (from Froese & Binohlan 2000), average length was 79% of minimum size at maturity (n = 34); however, average length was 135% of observed (published) ♀L_m values (n = 9). Regression analysis of observed versus estimated values indicates that Froese & Binohlan's empirical equation tends to increasingly overestimate ♀L_m as length increases (Figure 32).

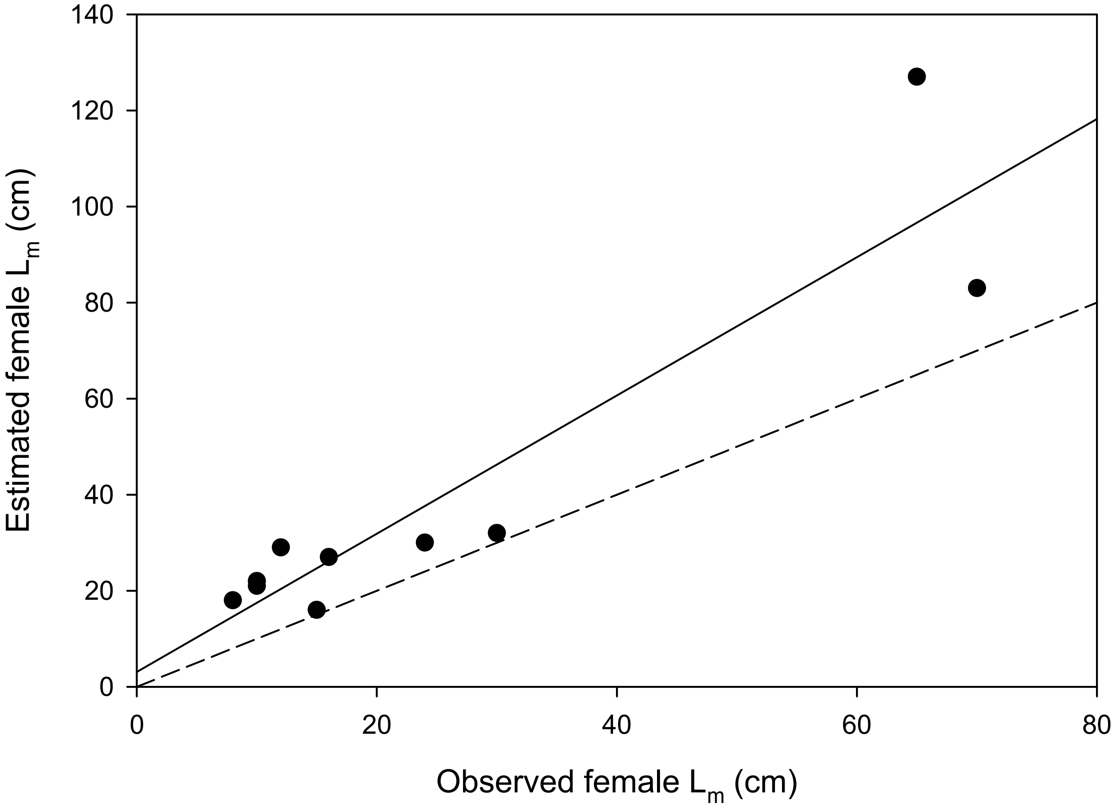

Figure 32. Observed versus estimated female minimum size at maturity. Estimated L_m = 3.072 + 1.440(Observed L_m), n = 10, $r^2 = 0.844$. Dashed line is a 1:1 reference.

Published ♀L_{50} values were available for 14 species. For these, average length was 91% of female L_{50}. Remarkably, the empirically derived ♀L_m estimates from Froese & Binohlan (2000) also increasingly overestimate size at female maturity as length increases (Figure 33).

For six of the 12 species for which adequate information on sex ratios has been published (*Lutjanus gibbus, Lutjanus vitta, Parupeneus barberinus*, *Parupeneus multifasciatus*, *Cephalopholis cyanostigma*, *Plectropomus leopardus)*, larger size classes are increasingly male dominated. For a seventh species, *Lutjanus carponotatus*, the possibility of size-specific sex ratios was not examined (Kritzer 2004). However, sex-specific growth curves indicate males attain a larger size than females, thus sex ratios

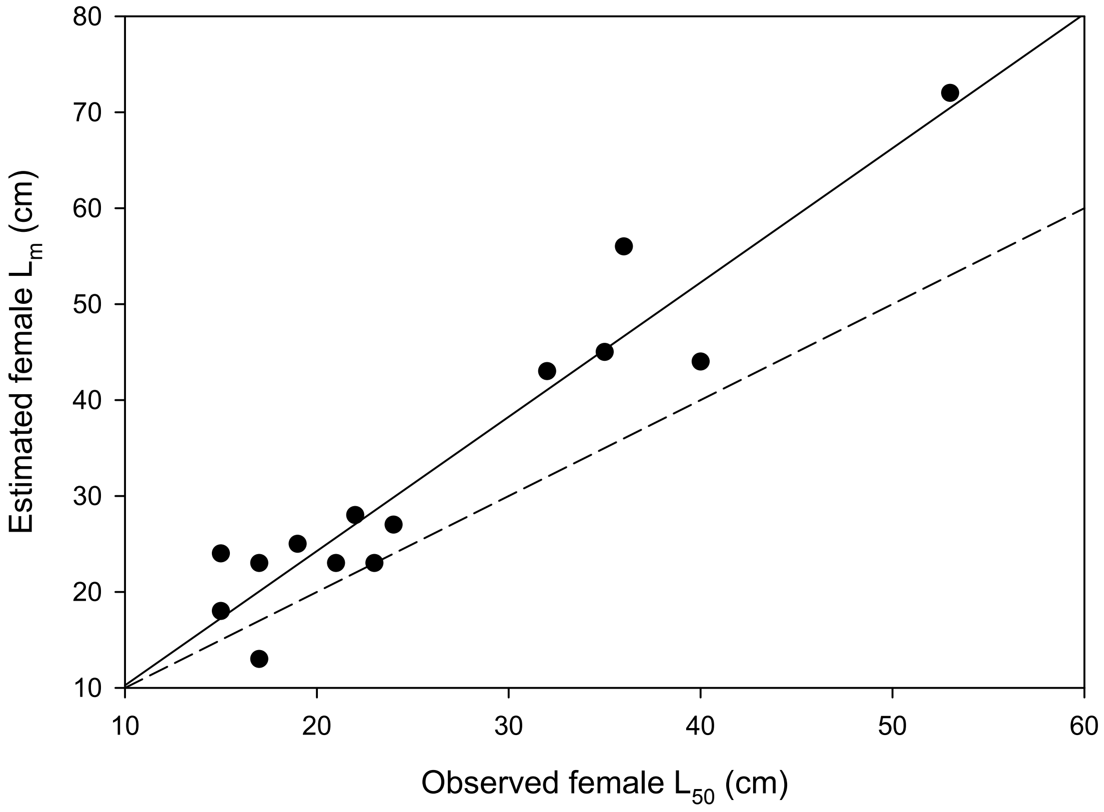

Figure 33. Observed L_{50} versus estimated L_m. Estimated $L_m = -3.760 + 1.400(\text{Observed } L_{50})$, $n = 14$, $r^2 = 0.911$. Dashed line is a 1:1 reference.

would become increasingly male biased as length approaches maximum size. Although sex ratios were not examined in the majority of serranid studies, they are all classified as protogynous hermaphrodites (Heemstra & Randall 1993). Because individuals typically mature as females, then change sex with further growth, these species should also be expected to have male-biased sex ratios with increasing size (this assertion is true for *Cephalopholis cyanostigma* and *Plectropomus leopardus*). Of the remaining five species for which adequate information is available, four species (*Diagramma pictum*, *Lutjanus biguttatus*, *Lutjanus argentimaculatus*, and *Siganus lineatus*) occur in an approximately 1:1 sex ratio, whereas *Scomberomerus commerson* is female-biased at larger sizes. Applying known size-specific sex ratios to the size structure information generated from laser-videogrammetry surveys study suggests, on average, 25% of the exploited reef fish population is composed of mature females.

Demographic information for each of 57 species is presented below. Each species account, with the exception of *Cephalopholis boenak*, includes an *in situ* image from Kamiali Wildlife Management Area. When at least 15 individuals were captured on video suitable for length estimates, these accounts also include size-frequency histograms, with arrows indicating maximum length (L_{max}), optimum length (L_{opt}) and female reproductive length. The reader is cautioned that, depending on information available, reproductive length may be minimum size at maturity (L_m) or size at 50% maturity (L_{50}). Also, note that arrows may be solid for published values, or dashed for estimated values.

Table 3. Size and reproductive information for common, exploited fishes in Kamiali Wildlife Management Area (updated from Longenecker *et al*. 2010). Values bridging female and male L_{50} columns (*Naso hexacanthus, Lutjanus monostigma*, *Gymnosarda unicolor*, and *Scomberomorus commerson*) indicate no sex-specific size-at-maturity values were provided.

Taxon	N	Mean length (cm)	L_{max} (cm)	Female L_{50} (cm)	Male L_{50} (cm)	Sex ratio	Spawning season	Reproductive mode
ACANTHURIDAE								
Naso hexacanthus	74	44	~71[a,b]	~50[b,c]				Gonochore[d]
Naso lopezi	3	59	~48[a,b]					Gonochore[d]
Naso vlamingii	10	36	~51[a,b]					Gonochore[d]
BALISTIDAE								
Canthidermis maculata	13	33	35[a]					Gonochore[d]
CAESIONIDAE								
Caesio cuning	795	16	~42[a,b]					Gonochore[e]
CARANGIDAE								
Carangoides bajad	34	26	~51[a,b]					

Carangoides plagiotaenia	26	26	~38[a,b]					
Caranx melampygus	32	26	~72[a,f]	31[f]				Gonochore[f]
Caranx papuensis	13	62	~66[b,g]					
EPHIPPIDAE								
Platax pinnatus	9	26	30[a]					
Platax teira	3	36	60[a]					
HAEMULIDAE								
Diagramma pictum	8	25	90[a]	36[h]	27[h]	~1:1[h]	Apr - May & Nov[h]	Gonochore[h]
Plectorhinchus lineatus	19	36	50[a]					
HOLOCENTRIDAE								
Myripristis adusta	13	18	28[a,i]					Gonochore[d]
Myripristis kuntee	58	12	16[a,j]					Gonochore[d]

Taxon	N	Mean length (cm)	L_{max} (cm)	Female L_{50} (cm)	Male L_{50} (cm)	Sex ratio	Spawning season	Reproductive mode
Myripristis violacea	52	13	17[a,k]					Gonochore[d]
Myripristis vittata	20	11	17[a,i]					Gonochore[d]
Neoniphon sammara	14	14	~27[a,i]	~8[l]			Nov – May[l]	Gonochore[d]
Sargocentron caudimaculatum	5	15	~19[a,b]					Gonochore[d]
KYPHOSIDAE								
Kyphosus cinerascens	66	30	~41[b,g]					
Kyphosus vaigiensis	5	21	~56[b,g]					
LETHRINIDAE								
Lethrinus erythropterus	5	22	~48[a,b]					
Monotaxis grandoculis	61	25	~56[a,i]					

LUTJANIDAE								
Lutjanus argentimaculatus	4	48	~118^{a,b}	53^{m}	47^{m}	1♂:1.18♀^{m}	Oct – Nov^{n}, Dec^{m}	Gonochore^{o}
Lutjanus biguttatus	347	14	19^{a,i}	17^{i}	13^{i}	1:1^{i}		Gonochore^{i}
Lutjanus boutton	159	14	~28^{a,b}					Gonochore^{0}
Lutjanus carponotatus	28	20	~38^{a,b}	19^{p}		~1:1^{p}	Oct – Dec^{p}	Gonochore^{q}
Lutjanus fulvus	39	18	~39^{a,b}					Gonochore^{o}
Lutjanus gibbus	20	21	~42^{a,b}	~16^{l}-23^{r}		Increasingly male-biased with length^{s}	Jan – Apr^{l}	Gonochore^{o}
Lutjanus kasmira	3	15	33^{a,t}	~10^{l}	~12^{l}		Year round^{o}	Gonochore^{o}
Lutjanus monostigma	4	21	~48^{a,b}	~32^{u}			Feb & Nov^{o}	Gonochore^{o}
Lutjanus rivulatus	4	31	~63^{a,b}					Gonochore^{o}
Lutjanus russellii	75	22	~43^{a,b}	22^{v}			Aug – Feb^{w}	Gonochore^{o}

Taxon	N	Mean length (cm)	L_{max} (cm)	Female L_{50} (cm)	Male L_{50} (cm)	Sex ratio	Spawning season	Reproductive mode
Lutjanus semicinctus	42	20	~34[a,b]	21[x]	18[x]	Varies unpredictably with length[x]		Gonochore[X]
Lutjanus vitta	19	14	~37[a,b]	15[y]		Increasingly male-biased > 29 cm[z]	Sep – Apr[z,aa]	Gonochore[o]
Macolor niger	5	28	60[a,bb] (TL)					
Macolor macularis	17	31	~55[a,b]					
MULLIDAE								
Mulloidichthys vanicolensis	7	21	~34[a,b]	17[cc]			Oct – Nov[dd]	
Parupeneus barberinus	121	15	44[a,i]	~12[x]	~14[x]	Increasingly male-biased with length[x]	Oct – May[l]	Gonochore[x]
Parupeneus cyclostomus	13	18	44[a,ee]					
Parupeneus multifasciatus	69	14	26[a,i]	15[ff]	15[ff]	Increasingly male-biased with length[ff]		Gonochore[ff]

Parupeneus trifasciatus	28	20	31[a,i]	~10[l]			Sep – Apr[l]	
SCARIDAE								
Scarus flavipectoralis	13	20	~29[a,b]					
SCOMBRIDAE								
Gymnosarda unicolor	17	59	~137[a,b]	~70[gg]			Dec – Feb[hh]	Gonochore[hh]
Scomberomorus commerson	4	95	218[a,ii]	~65[jj]		Female biased >90 cm[jj]	Jul – Dec[hh]	Gonochore[hh]
SERRANIDAE								
Anyperodon leucogrammicus	11	26	52[a]					Protogynous[kk]
Cephalopholis boenak	10	17	24[a]	15[ll]	16[ll]		Apr – Oct[ll]	Protogynous[ll]
Cephalopholis cyanostigma	62	19	35[a]	23[x]	20[x]	Increasingly male-biased with length[x]		Protogynous[x]
Cephalopholis microprion	20	13	23[a]					Protogynous[kk]
Cephalopholis sexmaculata	3	21	47[a]	~24[mm]			Mar-May[mm]	Protogynous[kk]

Taxon	N	Mean length (cm)	L_{max} (cm)	Female L_{50} (cm)	Male L_{50} (cm)	Sex ratio	Spawning season	Reproductive mode
Cephalopholis urodeta	6	18	27[a]					Protogynous[kk]
Plectropomus areolatus	10	18	70[a]	40[b,nn]	48[b,nn]		Jan – May[nn]	Protogynous[kk]
Plectropomus leopardus	6	34	~68[a,b]	32[oo]	37[ll]	Increasingly male-biased > 44 cm[oo]	Sep – Dec[pp]	Protogynous[pp]
Plectropomus oligacanthus	41	32	65[a]					Protogynous[kk]
SIGANIDAE								
Siganus javus	33	25	~53[g,bb] (TL)					
Siganus lineatus	65	26	~41[a,b]	24[x]	~19[x]	~1:1[x]	Year round[qq]	Gonochore[x]
Siganus puellus	3	22	~38[a,bb] (TL)					

(a) Allen & Swainston 1993; (b) using length-length relationship from Froese & Pauly 2009; (c) Choat & Robertson 2002 (authors do not describe how estimate was obtained); (d) Thresher 1984; (e) Carpenter 1998; (f) Sudekum *et al*. 1991; (g) Randall *et al*. 1990; (h) Grandcourt *et al*. 2011; (i) Longenecker *et al*. 2010; (j) FL estimated from Hawaiian specimens (Longenecker 2008 and C.J. Bradley, unpublished data) FL = 0.4314 + 0.8288(FL), $r^2 = 0.993$, n = 13; (k) FL estimated from a general *Myripristis* length relationship (C.J. Bradley, unpublished data) based on Hawaiian specimens of at least three species: *M. berndti*, *M. chryseres*, *M. kuntee*: FL = -0.4139 + 0.8919(TL); $r^2 = 0.993$; n = 50; (l) Anand & Pillai 2002 (authors report minimum size at maturity based on a combination of gross and histological examination of individuals in variable size classes, above lengths are the mean of minimum and maximum class limits); (m) Russell & McDougall 2008; (n) Pakoa 1998; (o)

Allen 1985; (p) Kritzer 2004; (q) Evans *et al*. 2008; (r) Heupel *et al*. 2009 (all females > 23 cm FL were mature); (s) results from Heupel *et al*. 2009 suggest the proportion of females is inversely related to size; (t) Friedlander *et al*. 2002; (u) Munro & Williams 1985 (length at first maturity); (v) Kritzer in Williams *et al*. 2002; (w) authors' interpretation of GSI and developmental stages in Sheaves 1995; (x) Present study, see Results – Reproductive Analysis; (y) Davis & West 1993; (z) authors' interpretation of data in Davis & West 1992: sex ratio is 1:1 to 29 cm, then %♀ = 1.986 – 0.00534(FL); (aa) Loubens 1980; (bb) no length-length relationship available; (cc) Cole 2008; (dd) Jehangeer 2003; (ee) FL estimated from Hawaiian specimens (Longenecker 2008): FL = 0.3132 + 0.8657(TL), $r^2 = 0.998$, n = 14; (ff) Longenecker & Langston 2008, %♀ = 141.3 – 0.6167(FL in mm) with all individuals male above 225 mm; (gg) Sivadas & Anasukoya 2005 report that all individuals < 70 cm were immature; (hh) Collette & Nauen 1983; (ii) Mackie *et al.* 2003; (jj) Lewis *et al*. 1974 (length at first maturity, sex ratio was ~1:1 in specimens <90 cm, but larger size classes were female biased, 4♂:38♀); (kk) Heemstra & Randall 1993; (ll) Chan & Sadovy 2002; (mm) Shakeel & Ahmed 1996 report the smallest mature female was 24 cm; (nn) Rhodes & Tupper 2007; (oo) authors' interpretation of data in Ferreira 1995: sex ratio is ~1♂:4♀ to 44 cm, then %♀ = 333 – 5.6(FL), maximum female size is 56 cm; (pp) Ferreira 1995; (qq) Hamilton *et al*. 2004 report year-round spawning aggregations during the first quarter of the moon phase.

Species Accounts

Acanthuridae

Naso hexacanthus (Bleeker, 1855). Figure 34.

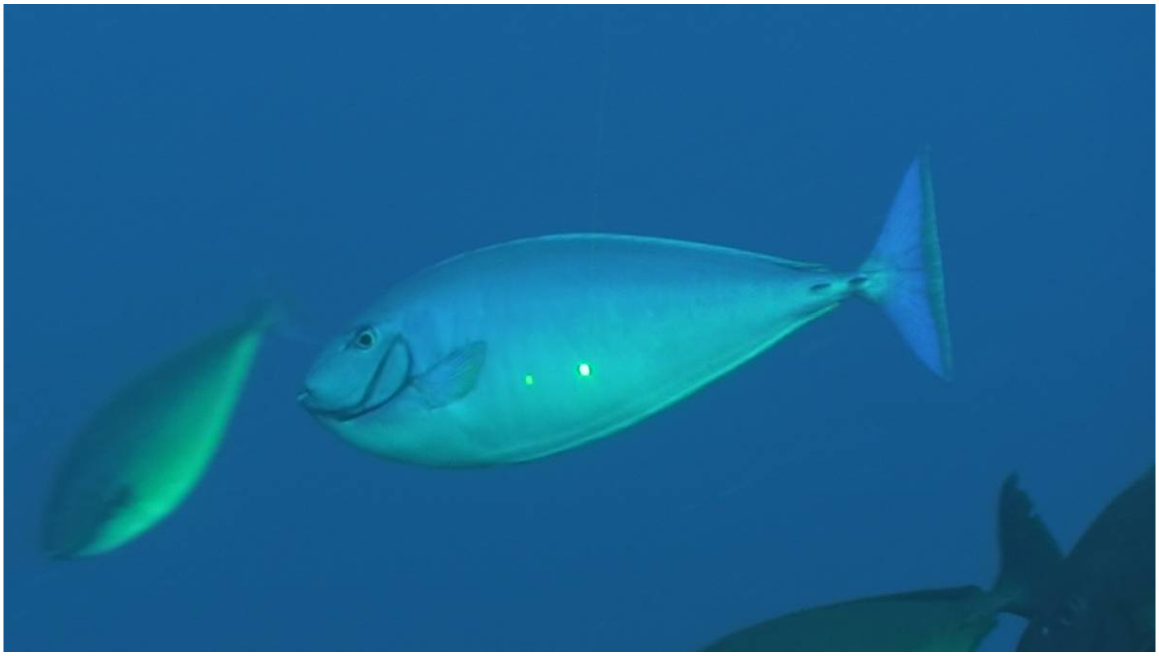

Figure 34. *Naso hexacanthus*. Laser dots are separated by 36 mm.

An additional 14 specimens were added to our data set in 2011, yielding a combined total 74 individuals captured on video suitable for length estimation. The additional data shifted the mean fork length estimate to 44 cm from our 2010 estimate of 43 cm. The updated mean length is 62% of the estimated maximum length of 71 cm, 93% of estimated optimum length of 47 cm, and 89% of the estimated female L_{50} of 50 cm (Figure 35). Results suggest approximately 12% of the individuals had attained female reproductive size, however we were not able to evaluate the reliability of the size-at-maturity estimate.

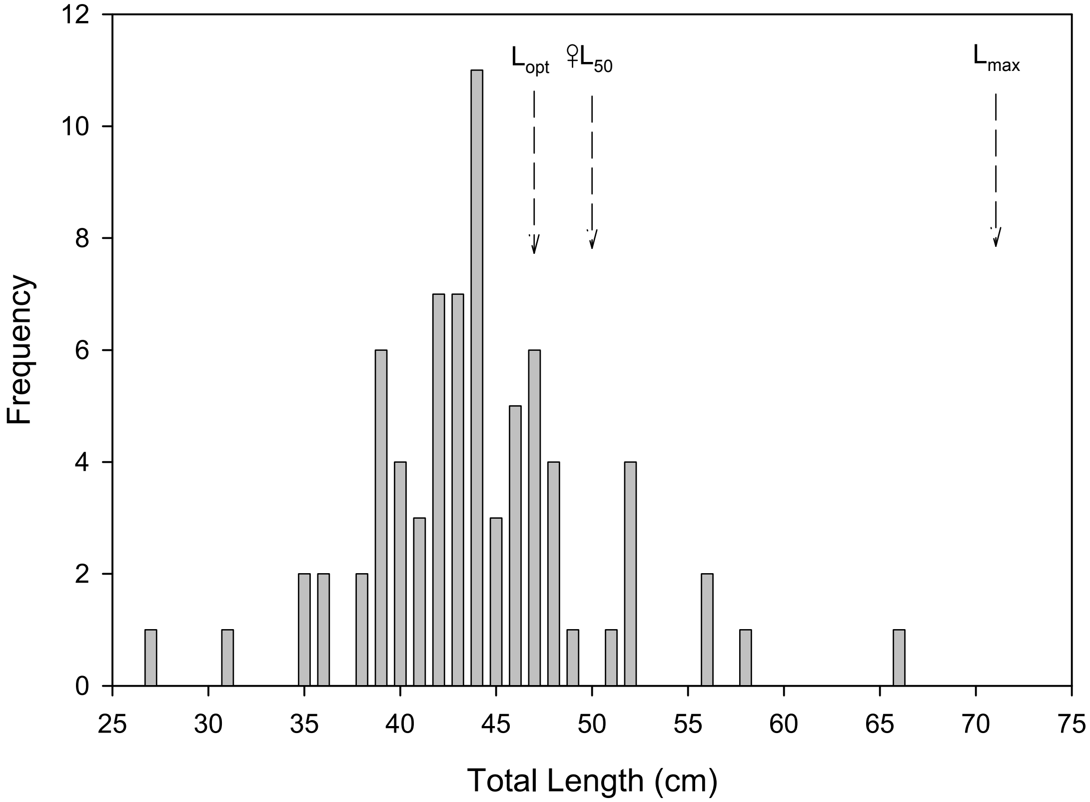

Figure 35. Size structure of *Naso hexacanthus*.

Naso lopezi Herre, 1927. Figure 36.

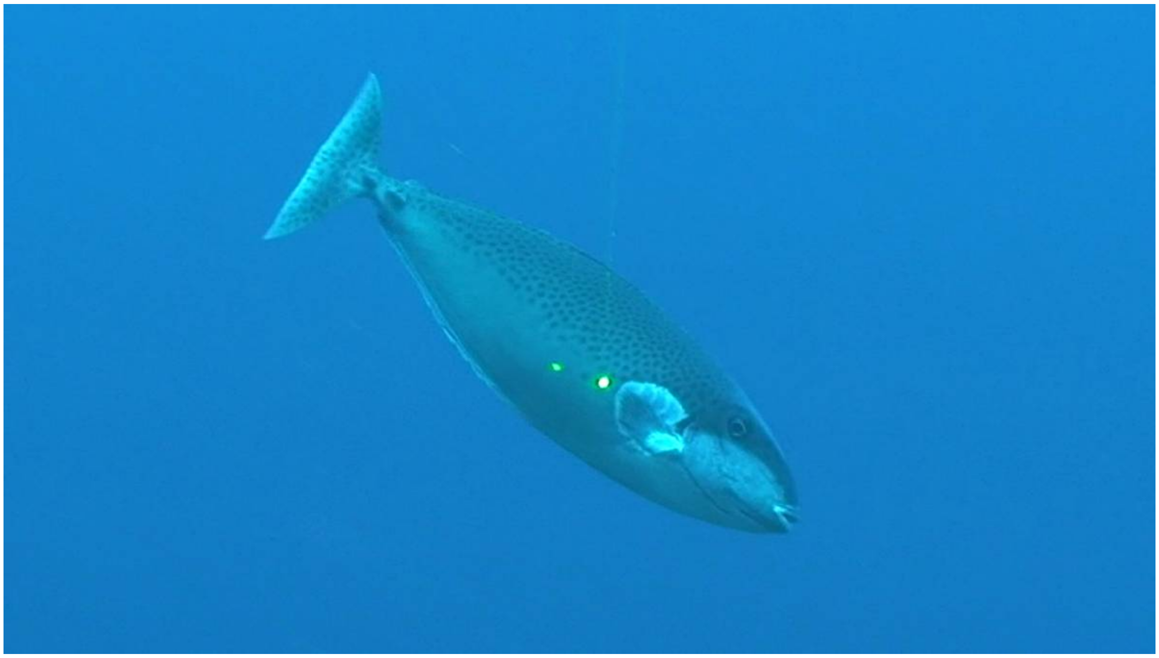

Figure 36. *Naso lopezi*. Laser dots are separated by 36 mm.

A total three (3) individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean fork length was 59 cm, which is 122% of the estimated maximum length of 48 cm, and 189% of estimates of optimum length and female L_m, both 31 cm. The largest specimen captured on video was 85 cm, or 177% of estimated maximum length.

Naso vlamingii (Valenciennes, 1835). Figure 37.

Figure 37. ***Naso vlamingii*****.**

One (1) additional specimen was added to our data set in 2011, yielding a total 10 individuals captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, the additional datum shifted mean fork length to 36 cm from our 2010 estimate of 35 cm. The updated mean size is 71% of the estimated maximum length of 51 cm, and 109% of estimates of optimum length and female L_m, both 33 cm.

Balistidae

Canthidermis maculata (Bloch, 1786). Figure 38.

Figure 38. *Canthidermis maculata.* Laser dots are separated by 36 mm.

No new specimens were added to our data set in 2011, leaving a total 13 individuals captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, the mean total length was 33 cm, which is 95% of the maximum reported length of 35 cm, and 144% of estimates of optimum length and female L_m, both 23 cm.

Caesionidae

Caesio cuning (Bloch, 1791). Figure 39.

Figure 39. *Caesio cuning*.

An additional 370 specimens were added to our data set in 2011, yielding a combined total 795 individuals captured on video suitable for length estimation. The additional data did not change the mean fork length estimate of 16 cm, which is 39% of the estimated maximum length of 42 cm, and 67% of estimates optimum length and female L_m, both 27 cm (Figure 40).

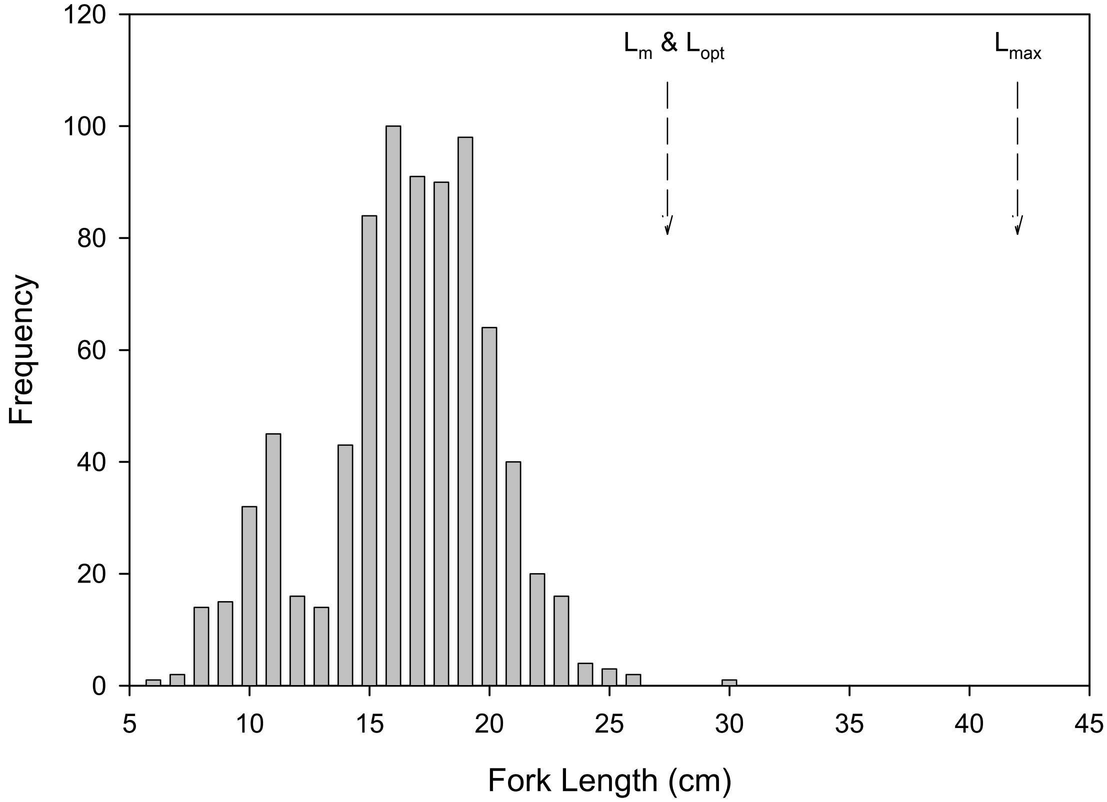

Figure 40. Size structure of *Caesio cuning*.

Carangidae

Carangoides bajad (Forsskål, 1775). Figure 41.

Figure 41. *Carangoides bajad*. Laser dots are separated by 39 mm.

No new specimens were added to our data set in 2011, leaving a total 34 individuals captured on video suitable for length estimation. Mean fork length remains 26 cm, which is 51% of the estimated maximum length of 51 cm, and 78% of estimates of optimum length and female L_m, both 33 cm (Figure 42).

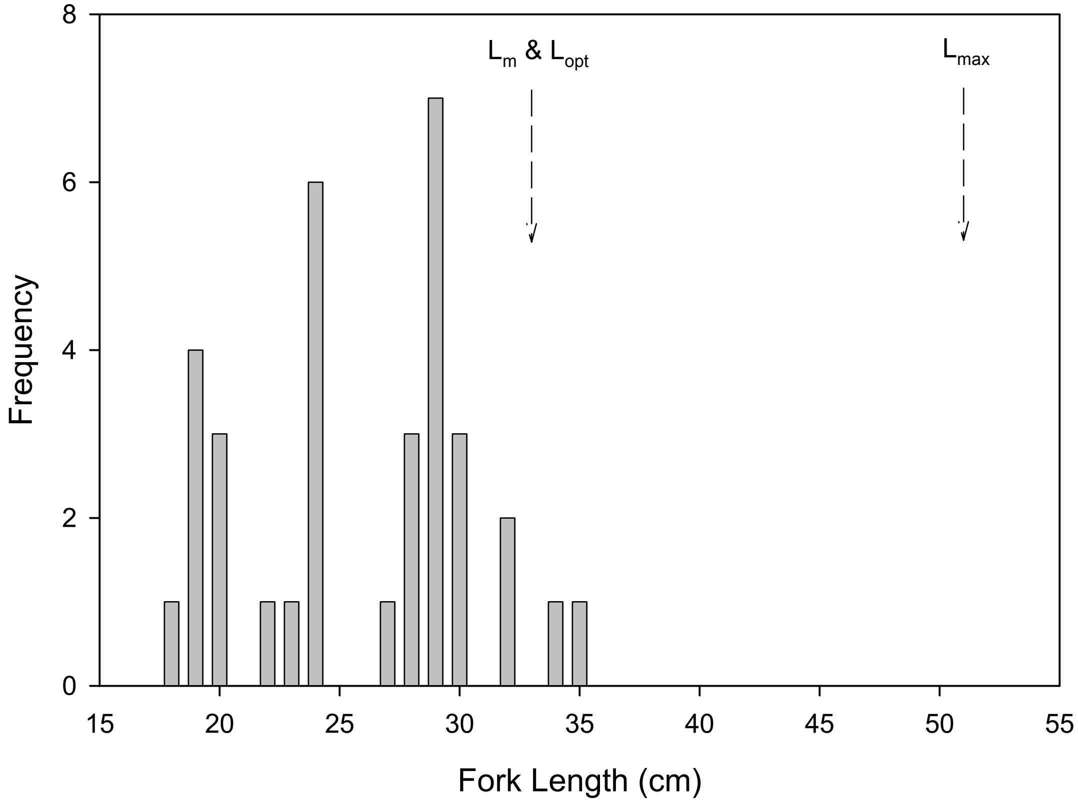

Figure 42. Size structure of *Carangoides bajad*.

Carangoides plagiotaenia Bleeker, 1857. Figure 43.

Figure 43. *Carangoides plagiotaenia*. Laser dots are separated by 36 mm.

An additional 11 specimens were added to our data set in 2011, yielding a combined total 26 individuals captured on video suitable for length estimation. The mean additional data shifted mean length to 26 cm from our 2010 mean fork length estimate of 25cm. The updated mean length is 69% of the estimated maximum length of 38 cm, and 104% of estimated optimum and female L_m, both 25 cm (Figure 44).

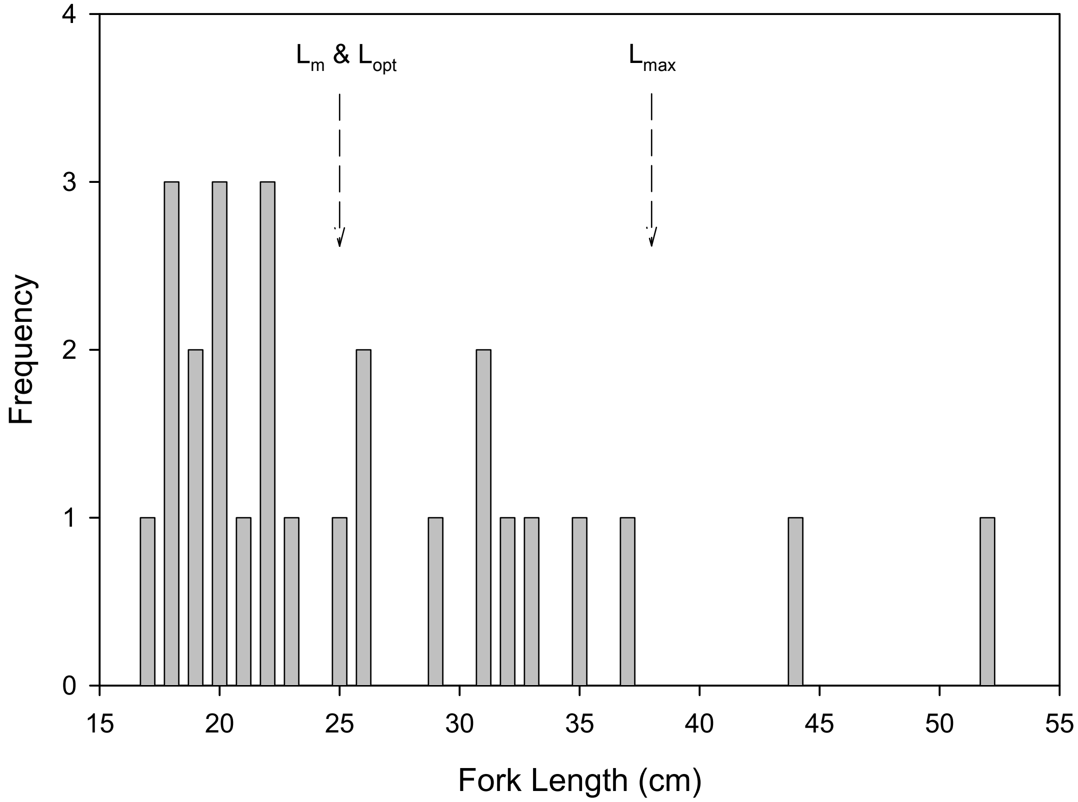

Figure 44. Size structure of *Carangoides plagiotaenia*.

Caranx melampygus Cuvier, 1833. Figure 45.

Figure 45. *Caranx melampygus*.

An additional four (4) specimens were added to our data set in 2011, yielding a combined total 32 individuals captured on video suitable for length estimation. The additional data did not change our 2010 mean fork length of 26 cm, which is 35% of the reported maximum length of 72 cm, 54 % of estimated optimum length of 47 cm and 82% of the published female L_{50} of 35 cm (Figure 46). Three (or 11%) of these individuals had attained the reported female reproductive size (however, size-specific sex ratios are not known).

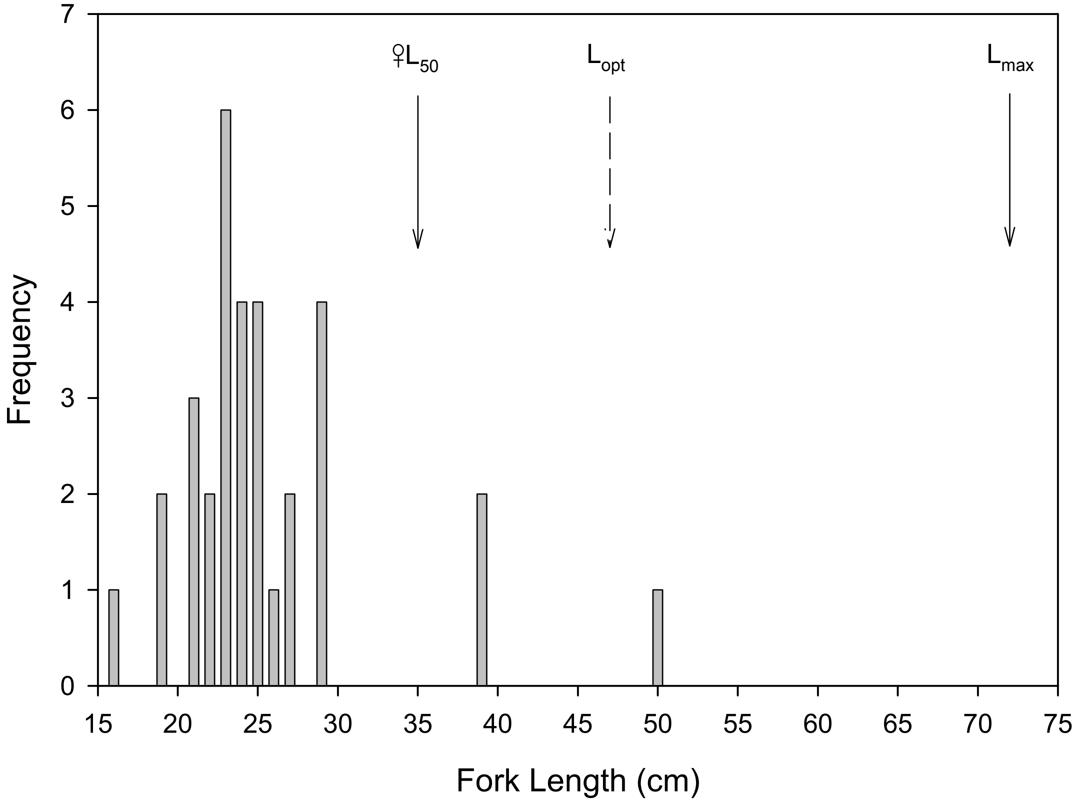

Figure 46. Size structure of *Caranx melampygus*.

Caranx papuensis Alleyne & MacLeay, 1877. Figure 47.

Figure 47. *Caranx papuensis* (with a remora attached near the origin of the first dorsal fin). Laser dots are separated by 39 mm.

An additional seven (7) specimens were added to our data set in 2011, yielding a combined total 13 individuals captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, the additional data shifted the mean fork length to 62 cm from our 2010 estimate of 47 cm. The updated mean fork length is 94% of the estimated maximum length of 66 cm, 144% of the estimated optimum length of 43 cm, and 144 % of the estimated female L_m of 42 cm.

Ephippidae

Platax pinnatus (Linneaus, 1758). Figure 48.

Figure 48. *Platax pinnatus*. Laser dots are separated by 36 mm.

A total four (4) specimens were added to our data set in 2011, yielding a total nine (9) individuals captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, the additional data shifted mean total length to 26 cm from our 2010 estimate of 24 cm. The updated mean length is 87% of the maximum reported length of 30 cm, 138% of the estimated optimum length of 19 cm, and 131% of the estimated female L_m of 20 cm.

Platax teira (Forsskål, 1775). Figure 49.

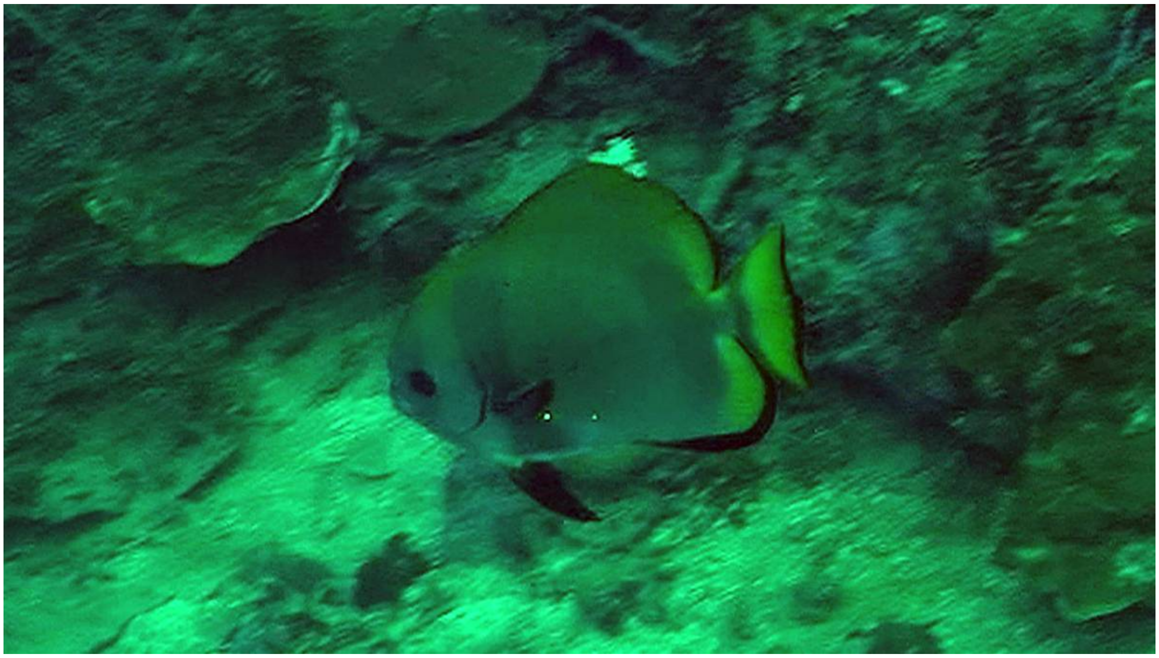

Figure 49. *Platax teira*. Laser dots are separated by 39 mm.

A total three (3) individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean total length was 36 cm, which is 60% of the maximum reported length of 60 cm, 92% of the estimated optimum length of 39 cm, and 95% of the estimated female L_m of 38 cm.

Haemulidae

Diagramma pictum (Thunberg, 1792). Figure 50.

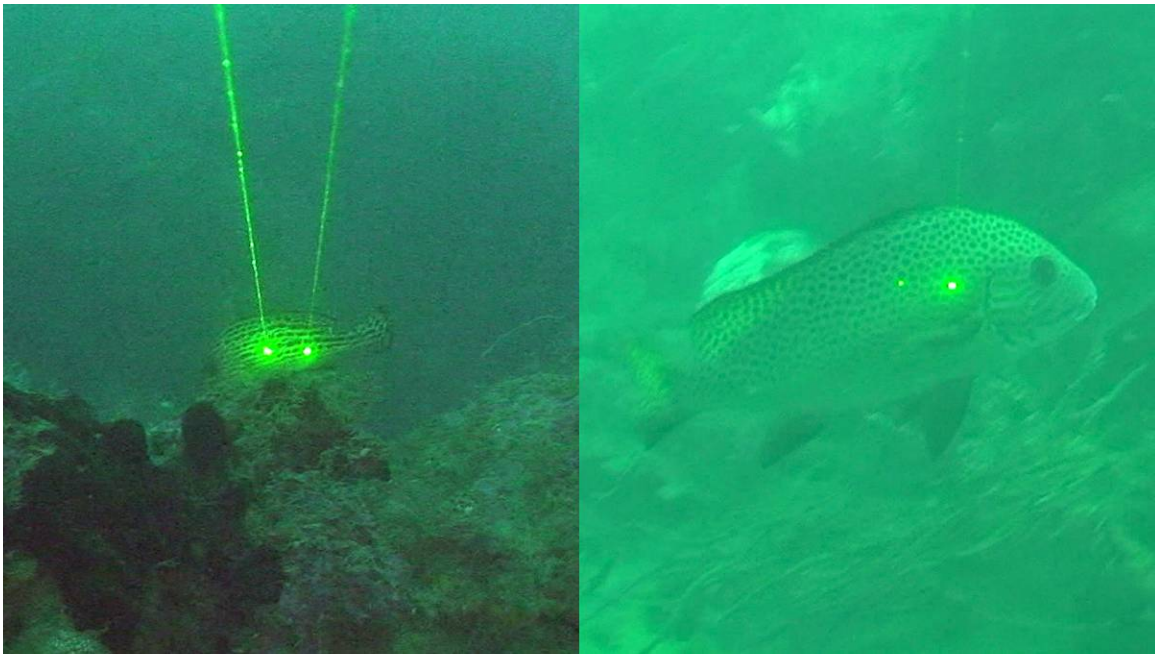

Figure 50. *Diagramma pictum* juvenile (left) and adult (right). Laser dots are separated by 31 and 36 mm, respectively.

A total eight (8) individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, the mean total length was 25 cm, which is 28% of the maximum reported length of 90 cm, 57% of the published optimum length of 44 cm, and 68% of the published female L_{50} of 36 cm. None of the individuals captured on video had reached female L_{50}.

Plectorhinchus lineatus (Linnaeus, 1758). Figure 51.

Figure 51. *Plectorhinchus lineatus*. Laser dots are separated by 39 mm.

An additional four (4) specimens were added to out data set in 2011, yielding a combined total 19 individuals captured on video suitable for length estimation. The additional data did not change our 2010 mean total length estimate of 36 cm. Mean size is 71% of the maximum reported length of 50 cm, 108% of the estimated optimum length of 33 cm and 112% of the estimated female L_m of 32 cm (Figure 52).

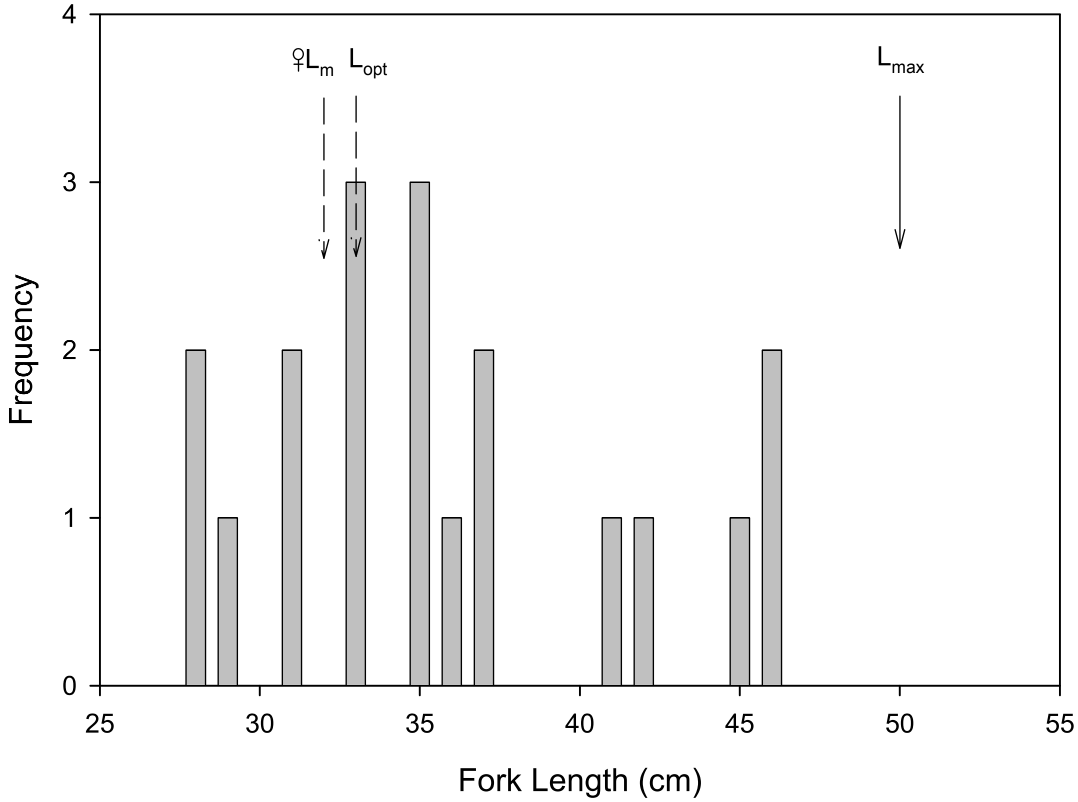

Figure 52. Size structure of *Plectorhinchus lineatus*.

Holocentridae

Myripristis adusta Bleeker, 1853. Figure 53.

Figure 13. *Myripristis adusta*.

An additional two (2) specimens were added to our data set in 2011, yielding a combined total 15 individuals captured on video suitable for length estimation. The additional data did not change the mean fork length estimate of 18 cm, which is 65% of the maximum reported length of 28 cm, 101% of the estimated optimum length of 18 cm, and 96% of the estimated female L_m of 19 cm (Figure 54).

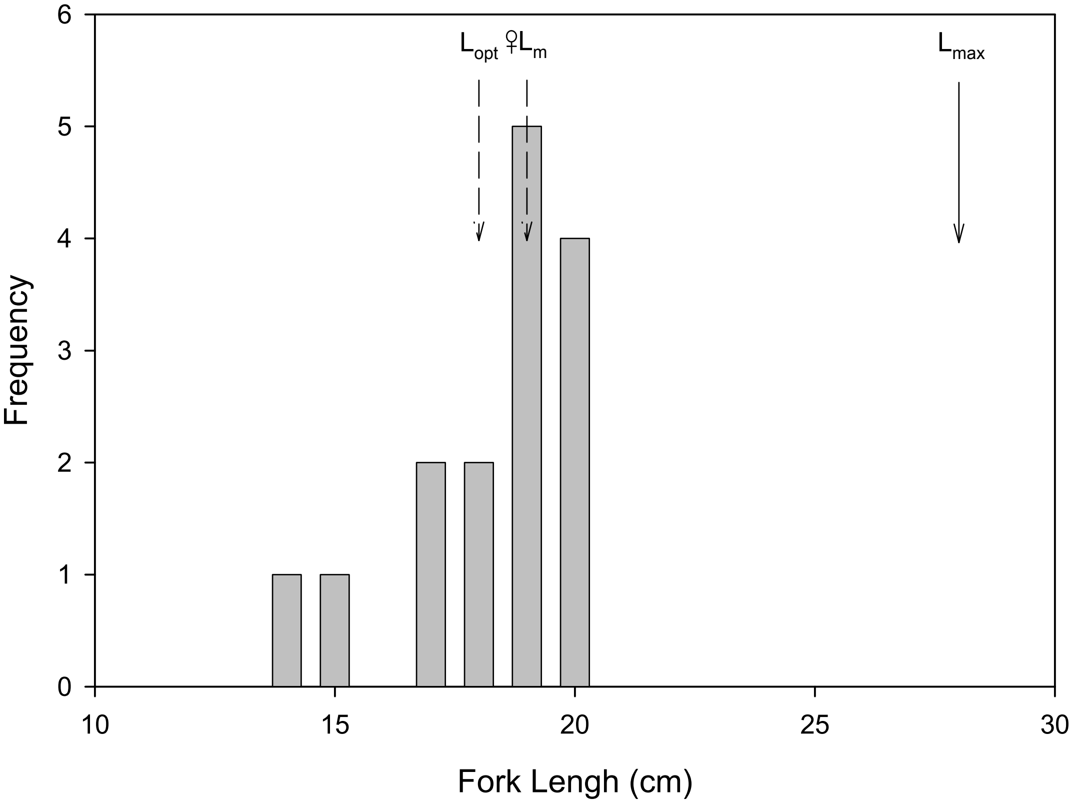

Figure 54. Size structure of *Myripristis adusta*.

Myripristis kuntee Valenciennes, 1831. Figure 55.

Figure 55. *Myripristis kuntee*. Laser dots are separated by 39 mm.

An additional 12 specimens were added to our data set in 2011, yielding a combined total 58 individuals captured on video suitable for length estimation. The additional data did not change the mean fork length estimate of 12 cm. Mean size is75% of the maximum reported length of 16 cm (two individuals were larger than 16 cm), 109% of the estimated optimum length of 11 cm, and 100% of the estimated female L_m of 12 cm (Figure 56).

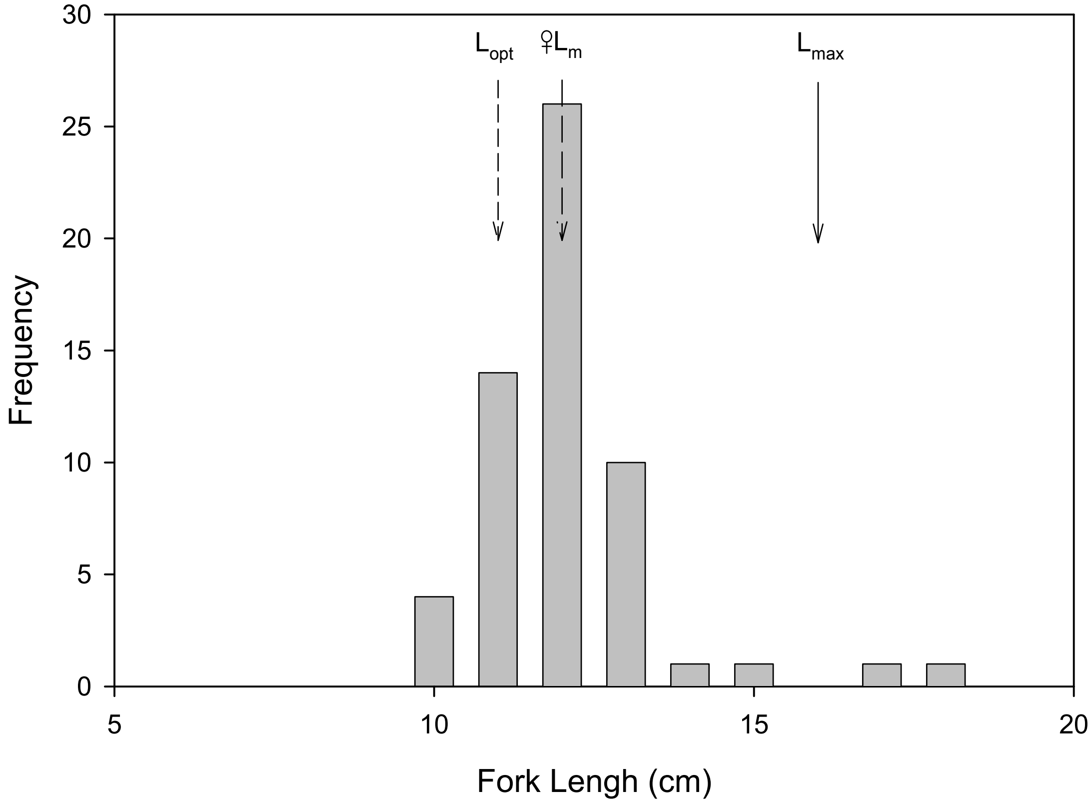

Figure 56. Size structure of *Myripristis kuntee*.

Myripristis violacea Bleeker, 1851. Figure 57.

Figure 57. *Myripristis violacea*.

An additional 12 specimens were added to our data set in 2011, yielding a combined total 52 individuals captured on video suitable for length estimation. The additional data did not change the mean fork length estimate of 13 cm. Mean size is 79% of the estimated maximum length of 17 cm, 122% of the estimated optimum length of 11 cm, and 112% of the estimated female L_m of 12 cm (Figure 58).

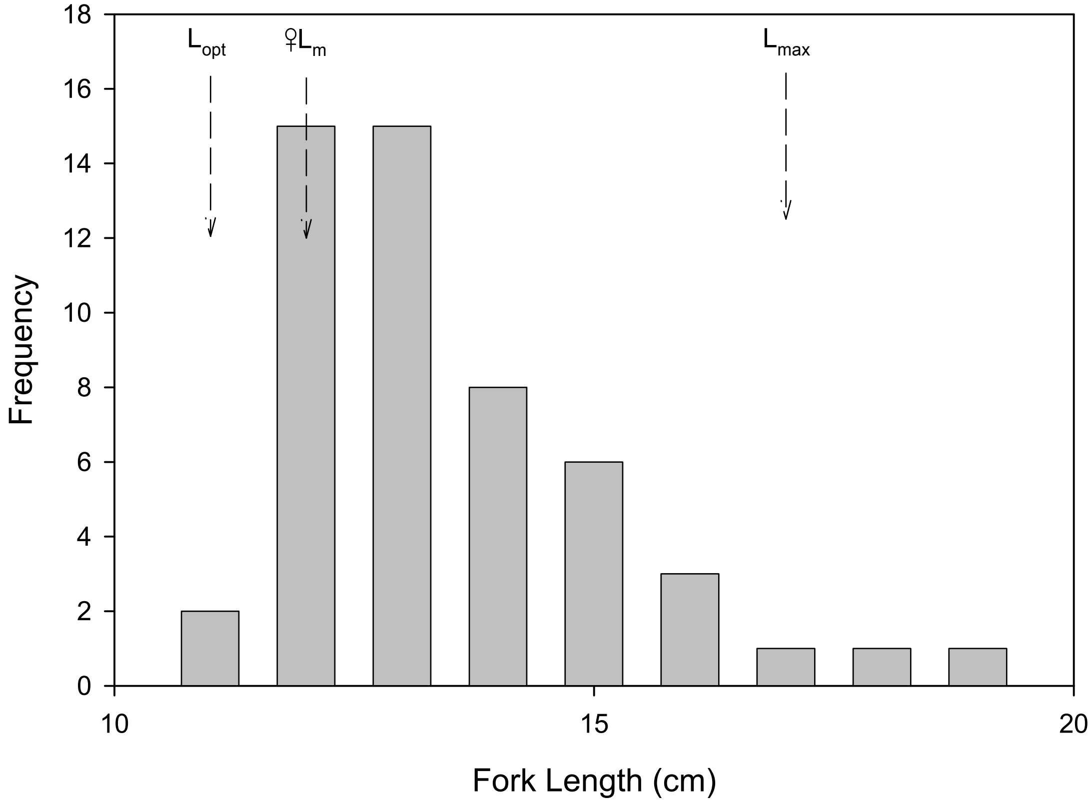

Figure 58. Size structure of *Myripristis violacea*.

Myripristis vittata (Valenciennes, 1831). Figure 59.

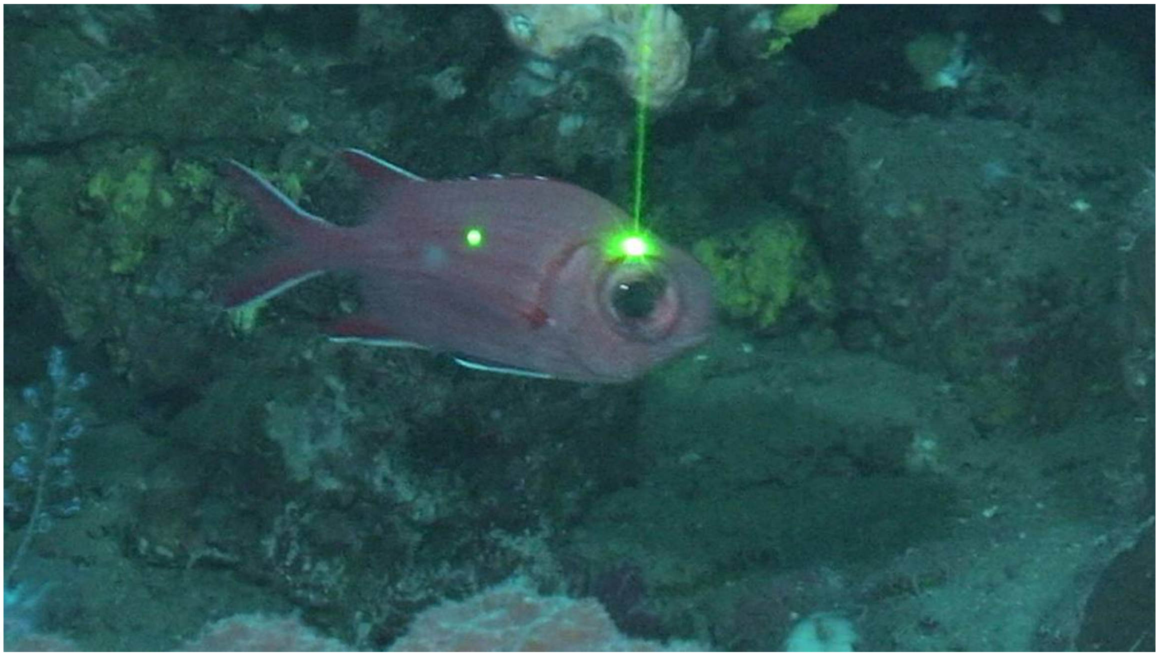

Figure 59. *Myripristis vittata*. Laser dots are separated by 36 mm.

One (1) specimen was added to our data set in 2011, yielding a combined total 20 individuals captured on video suitable for length estimation. The additional datum did not change our mean fork length estimate of 11 cm, which is 66% of the maximum reported length of 17 cm, 102% of the estimated optimum length of 11 cm and 94% of the estimated female L_m of 12 cm (Figure 60).

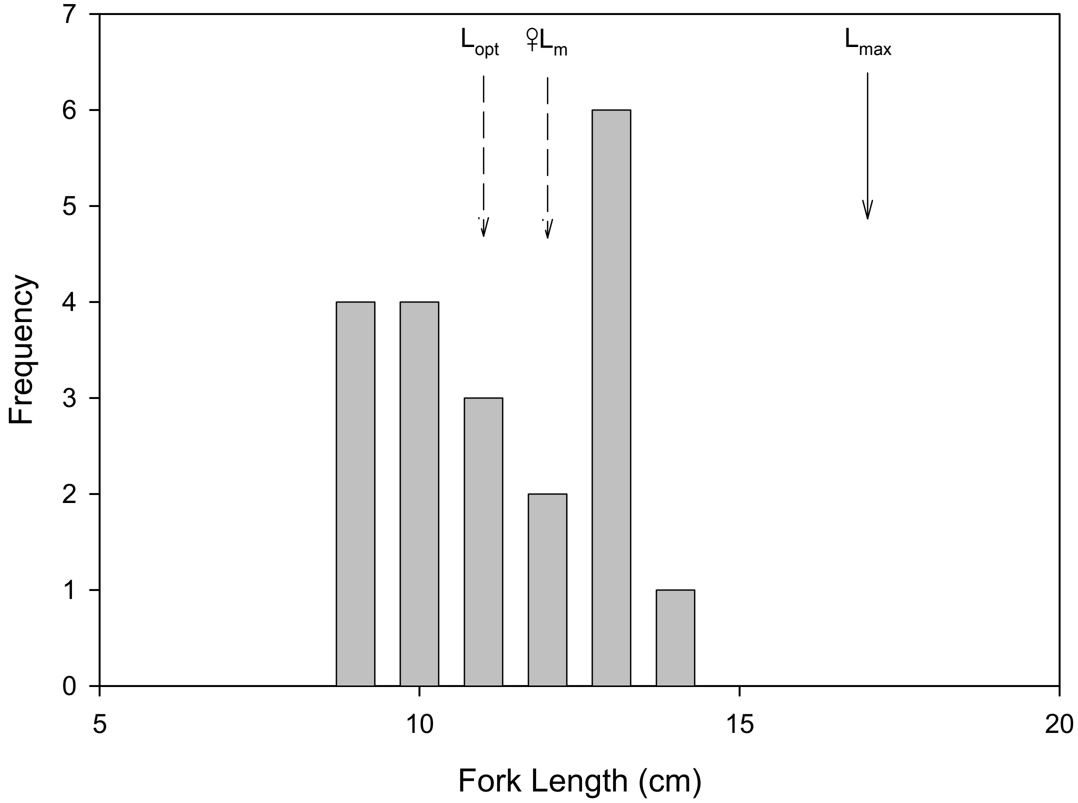

Figure 60. Size structure of *Myripristis vittata*.

Neoniphon sammara (Forsskål, 1775). Figure 61.

Figure 61. *Neoniphon sammara*. Laser dots are separated by 39 mm.

An additional four (4) specimens were added to our data set in 2011, yielding a total 14 individuals captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, the additional data did not change the mean fork length estimate of 14 cm. Mean size is 52% of the estimated maximum length of 27 cm, 83% of the estimated optimum length of 17 cm, and 177% of the published female L_m eight (8) cm. One-hundred percent of individuals had attained female L_m. Sex ratios have not been examined in this species, so the proportion of mature females cannot be estimated.

Sargocentron caudimaculatum (Rüppell, 1838). Figure 62.

Figure 62. *Sargocentron caudimaculatum*. Laser dots are separated by 31 mm.

A total five (5) individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean total length was 15 cm, which is 81% of the maximum reported length of 19 cm, 129% of the estimated optimum length of 12 cm, and 119% of the estimated female L_m of 13 cm.

<u>Kyphosidae</u>

Kyphosus cinerascens (Forsskål, 1775). Figure 63.

Figure 63. *Kyphosus cinerascens*. Laser dots are separated by 39 mm.

An additional 12 specimens were added to our data set in 2011, yielding a combined total 66 individuals captured on video suitable for length estimation. The additional data did not change the mean fork length estimate of 30 cm, which is 74% of the estimated maximum length of 41 cm, and 112% of estimates of optimum length and female L_m, both 27 cm (Figure 64).

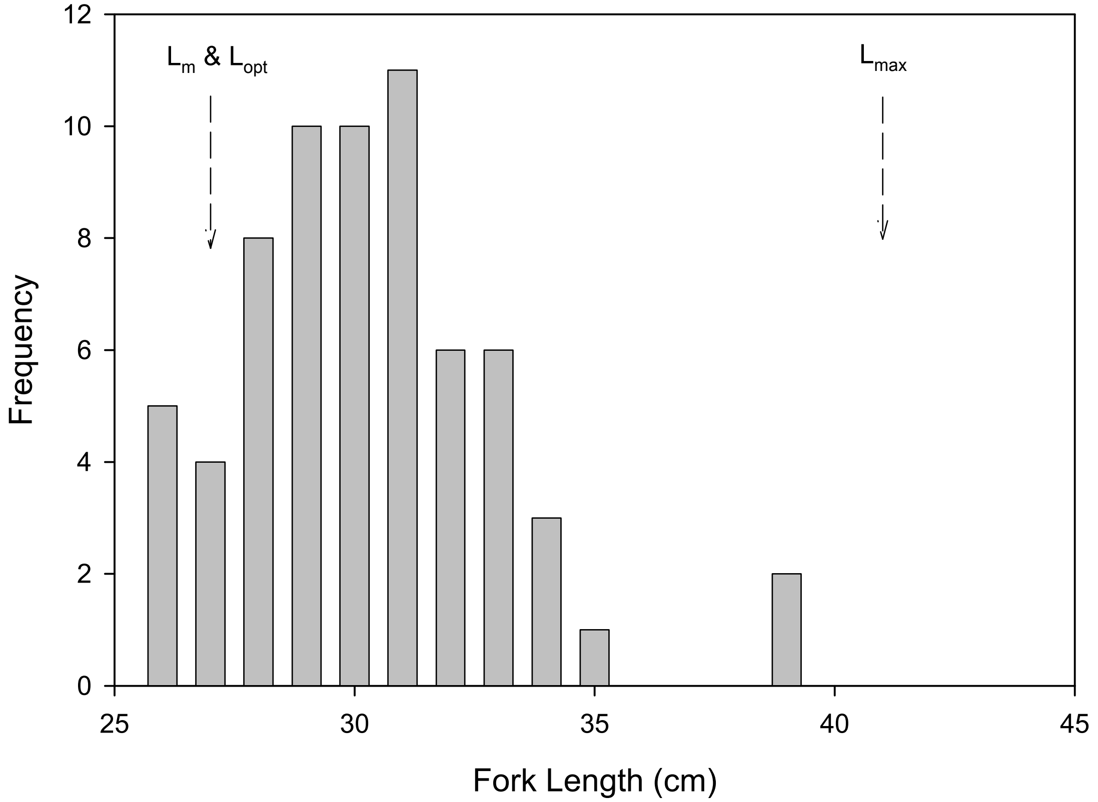

Figure 64. Size structure of *Kyphosus cinerascens*.

Kyphosus vaigiensis (Quoy and Gaimard, 1825). Figure 65.

Figure 65. *Kyphosus vaigiensis*. Laser dots are separated by 39 mm.

A total five (5) individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean fork length was 21 cm, which is 66% of the estimated maximum length of 56 cm, 100% of the estimated optimum length of 37 cm and 103% of the estimated female L_m of 36 cm.

Lethrinidae

Lethrinus erythropterus Valenciennes, 1830. Figure 66.

Figure 66. *Lethrinus erythropterus*. Laser dots are separated by 31 mm.

A total five (5) individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean fork length was 22 cm, which is 45% of the estimated maximum length of 48 cm, and 70% of estimates of optimum length and female L_m, both 31 cm.

Monotaxis grandoculis (Forsskål, 1775). Figure 67.

Figure 67. *Monotaxis grandoculis* juvenile (left) and adult (right).

An additional 18 specimens were added to our data set in 2011, yielding a combined total 61 individuals captured on video suitable for length estimation. The additional data shifted mean fork length to 25 from our 2010 estimate of 24 cm. The updated mean size is 45% of the estimated maximum length of 56 cm, 68% of the estimated optimum length of 37 cm and 70% of the estimated female L_m of 36 cm (Figure 68).

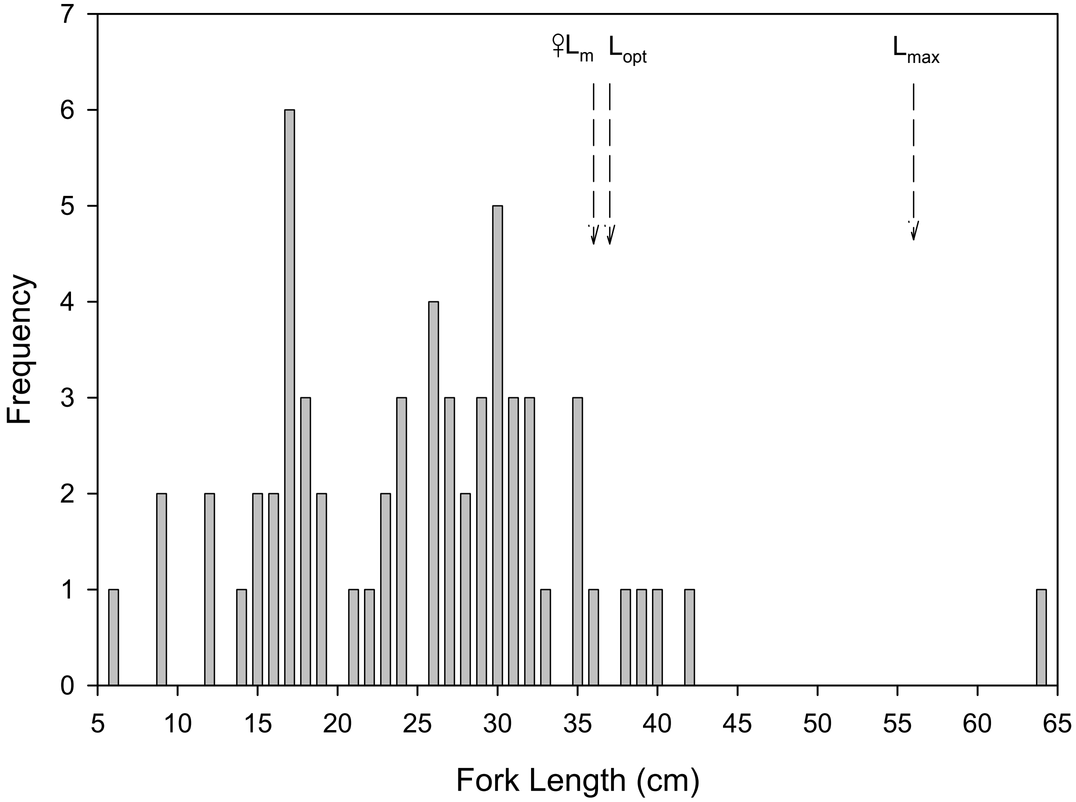

Figure 68. Size structure of *Monotaxis grandoculis*.

<u>Lutjanidae</u>

Lutjanus argentimaculatus (Forsskål, 1775). Figure 69.

Figure 69. *Lutjanus argentimaculatus*. Laser dots are separated by 36 mm.

One (1) additional specimen was added to our data set in 2011, yielding a total four (4) individuals captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. The additional datum shifted mean fork length to 48 cm from our 2010 estimate of 50 cm. The updated mean size is 41% of the estimated maximum reported length of 118 cm, 61% of the estimated optimum length of 79 cm and 91% of the published female L_{50} of 53 cm. The above information, when considered in light of the approximately 1:1 (♂:♀) sex-ratio, suggests that about 27% of the population is mature females.

Lutjanus biguttatus (Valenciennes, 1830). Figure 70.

Figure 70. ***Lutjanus biguttatus*****. Laser dots are separated by 39 mm.**

An additional 164 specimens were added to our data set in 2011, yielding a combined total 347 individuals captured on video suitable for length estimation. The additional data did not change our 2010 average fork length estimate of 14 cm. Mean size is 71% of the published maximum length of 19 cm, 117% of estimated optimum length of 12 cm and 88% of the published female L_{50} of 17 cm (Figure 71). Given that sex ratios are not significantly different from 1:1, about 15% of the population is mature females.

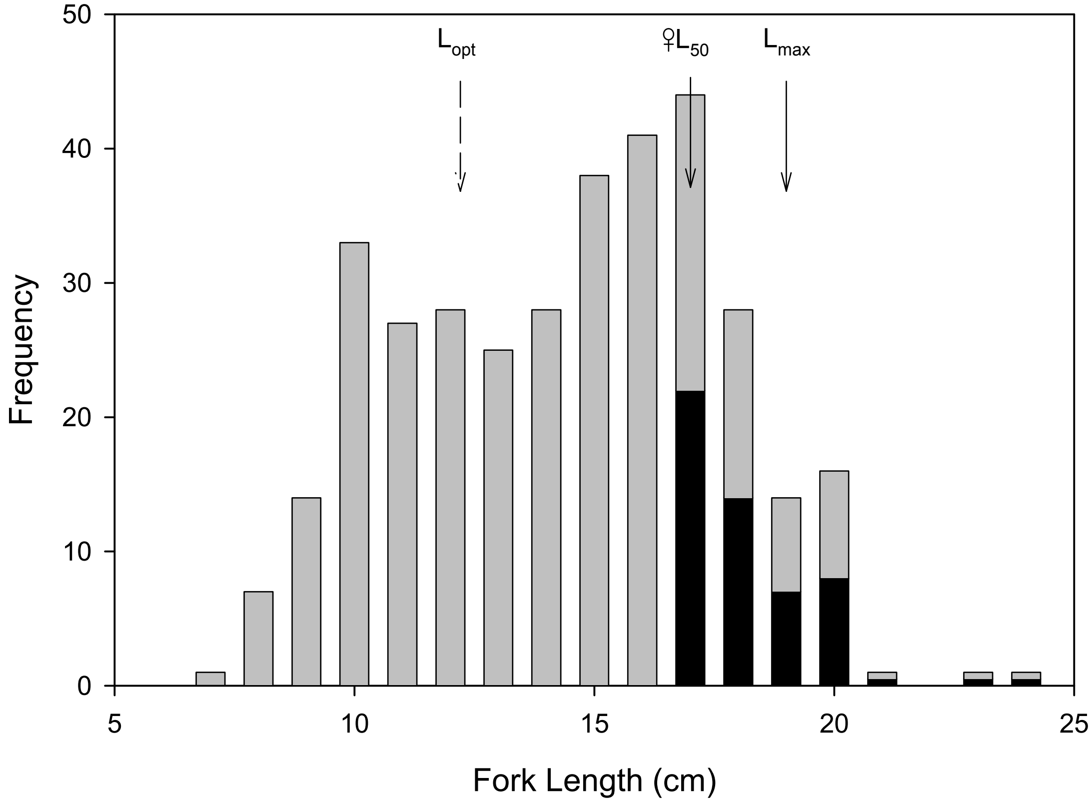

Figure 71. Size structure of *Lutjanus biguttatus*. The dark portion of bars represent estimated number of mature females, light portion represents all other individuals.

Lutjanus boutton (Lacepède, 1802). Figure 72.

Figure 72. *Lutjanus boutton*. Laser dots are separated by 39 mm.

An additional 18 specimens were added to our data set in 2011, yielding a combined total 159 individuals captured on video suitable for length estimation. The additional data did not change the 2010 mean fork length estimate of 14 cm, which is 49% of the estimated maximum length of 28 cm, 76% of the estimated optimum length of 18 cm and 72% of estimated female L_m of 19 (Figure 73).

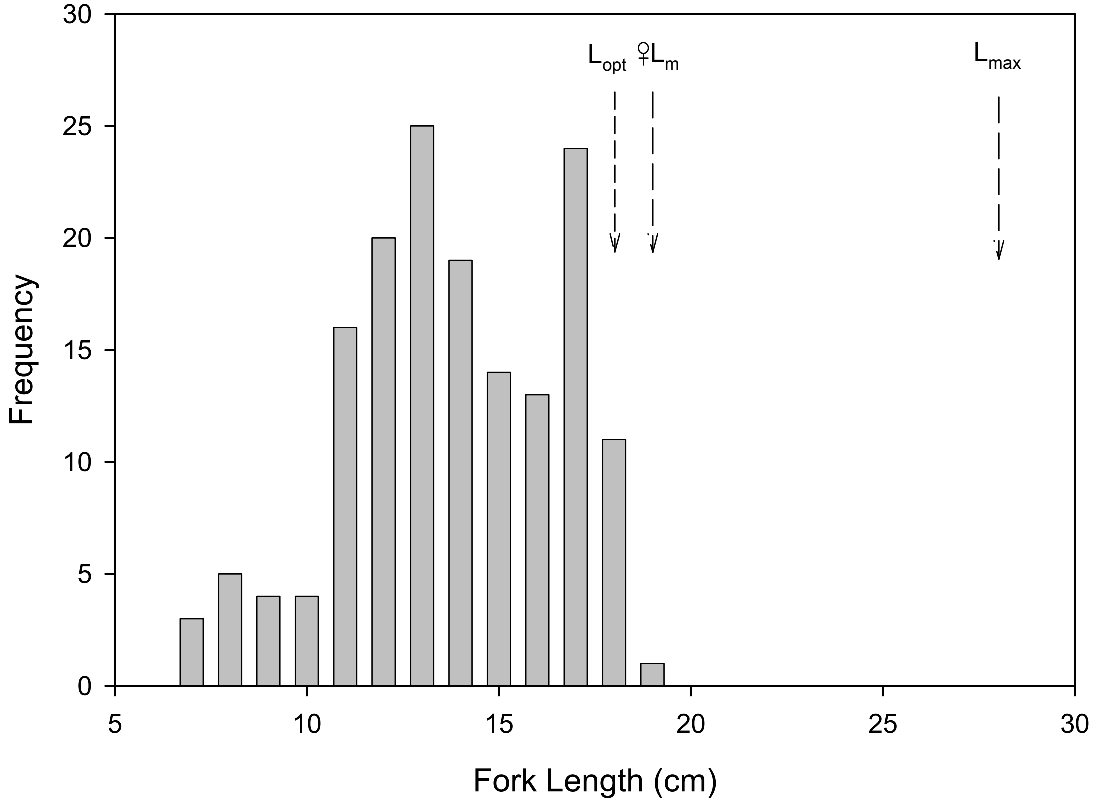

Figure 73. Size structure of *Lutjanus boutton*.

Lutjanus carponotatus (Richardson, 1842). Figure 74.

Figure 74. *Lutjanus carponotatus*.

An additional 13 specimens were added to our data set in 2011, yielding a combined total 28 individuals captured on video suitable for length estimation. The additional data shifted mean fork length to 20 cm from our 2010 estimate of 23 cm. The updated mean length is 52% of the maximum reported length of 38 cm, 80% of estimated optimum length of 25 cm and 108% of the published female L_{50} of 19 cm (Figure 75). The above information, when considered in light of the approximately 1:1 sex-ratio, suggests that about 23% of the population is mature females.

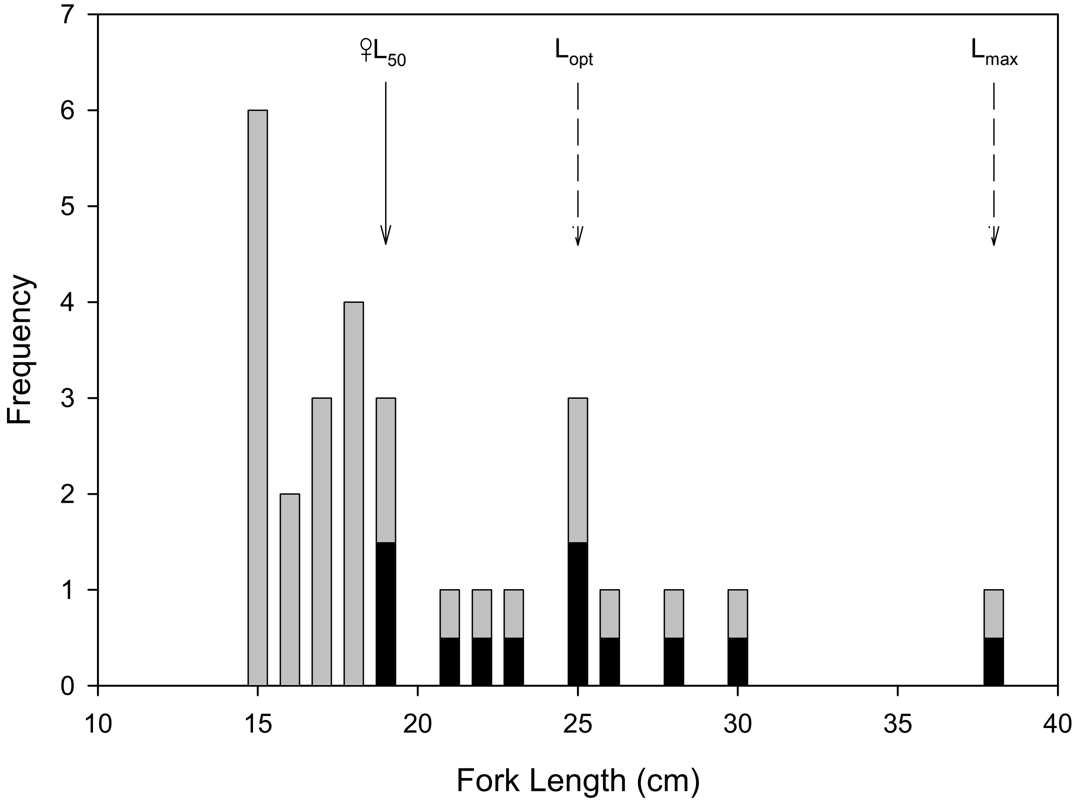

Figure 75. Size structure of *Lutjanus carponotatus*. The dark portion of bars represent estimated number of mature females, light portion represents all other individuals.

Lutjanus fulvus (Forster, 1801). Figure 76.

Figure 76. *Lutjanus fulvus*.

An additional six (6) specimens were added to our data set in 2011, yielding a combined total 39 individuals captured on video suitable for length estimation. The additional data did not change the 2010 mean fork length estimate of 18 cm, which is 47% of the estimated maximum reported length of 39 cm, 74% of the estimated optimum length of 25 cm and 71% of the estimated female L_m of 26 cm (Figure 77).

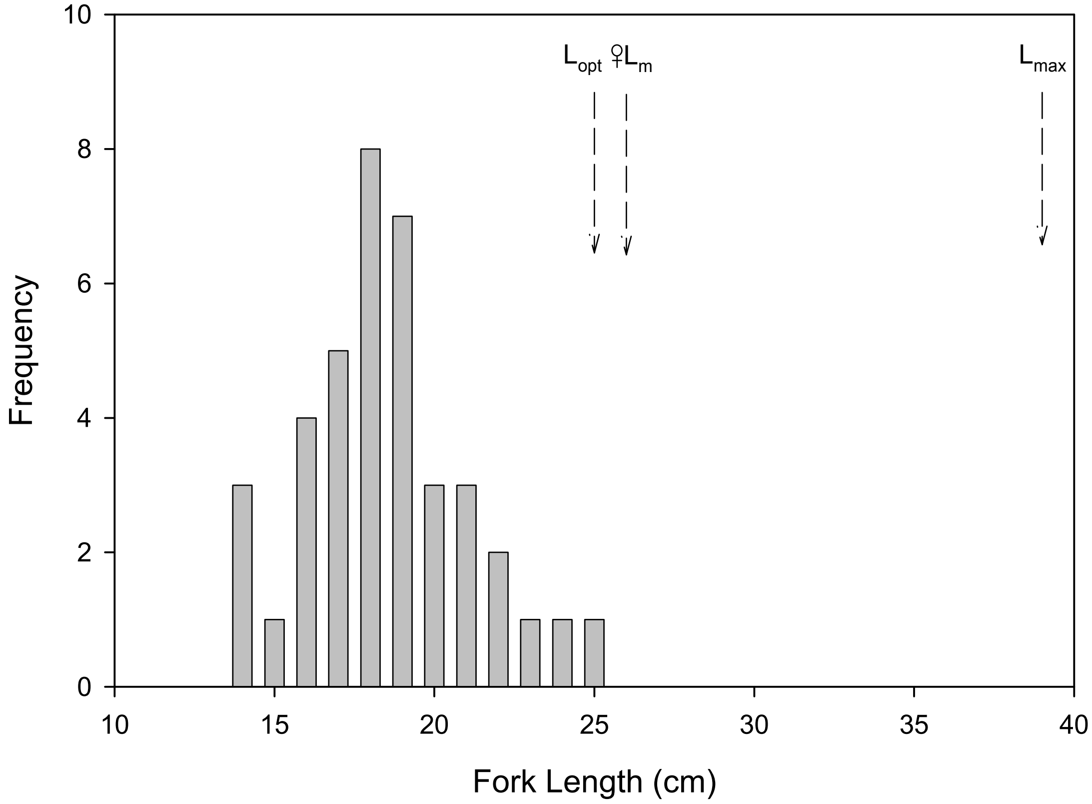

Figure 77. Size structure of *Lutjanus fulvus*.

Lutjanus gibbus (Forsskål, 1775). Figure 78.

Figure 78. *Lutjanus gibbus*. Laser dots are separated by 39 mm.

An additional five (5) specimens were added to our data set in 2011, yielding a combined total 20 individuals captured on video suitable for length estimation. The additional data shifted mean fork length to 21 cm from our 2010 estimated of 19 cm. The updated length estimate is 50% of the estimated maximum length of 42 cm, 77% of the estimated optimum length of 27 cm, and at least 131% of the published female L_m of ~16 cm (Figure 79). Because sex ratios have not been described in detail, the percentage of mature females cannot be estimated.

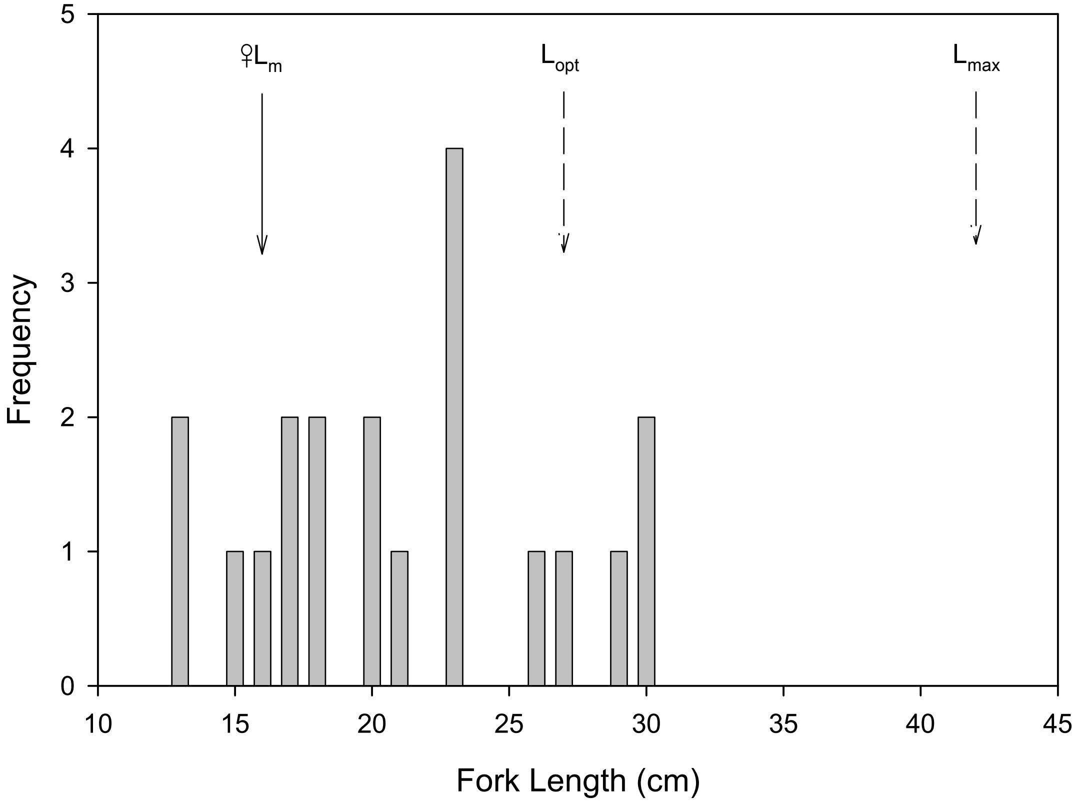

Figure 79. Size structure of *Lutjanus gibbus*.

Lutjanus kasmira (Forsskål, 1775). Figure 80

Figure 80. *Lutjanus kasmira*. Laser dots are separated by 36 mm.

A total three (3) individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean fork length was 15 cm, which is 46% of the published maximum length of 33 cm, 73% of the estimated optimum length of 21 cm and 153% of the published female L_m of 10 cm.

Lutjanus monostigma (Cuvier, 1828). Figure 81.

Figure 81. *Lutjanus monostigma*. Laser dots are separated by 31 mm.

A total four (4) individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean fork length was 21 cm, which is 43% of the estimated maximum length of 48 cm, and 67% of estimates of optimum length and female L_m, both 31 cm.

Lutjanus rivulatus (Cuvier, 1828). Figure 82.

Figure 82. *Lutjanus rivulatus*. Laser dots are separated by 39 mm.

A total four (4) individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean fork length was 31 cm, which is 49% of the estimated maximum length of 63 cm, 76% of the estimated optimum length of 41 cm and 78% of the estimated female L_m of 40 cm.

Lutjanus russellii (Bleeker, 1849). Figure 83.

Figure 83. *Lutjanus russellii*. Laser dots on the left fish are separated by 39 mm.

An additional two (2) specimens were added to our data set in 2011, yielding a combined total 75 individuals captured on video suitable for length estimation. The additional data did not change the mean fork length estimate of 22 cm, which is 50% of the estimated maximum length of 43 cm, 77% of the estimated optimum length of 28 cm, and 99% of the published female L_{50} of 22 cm (Figure 84).

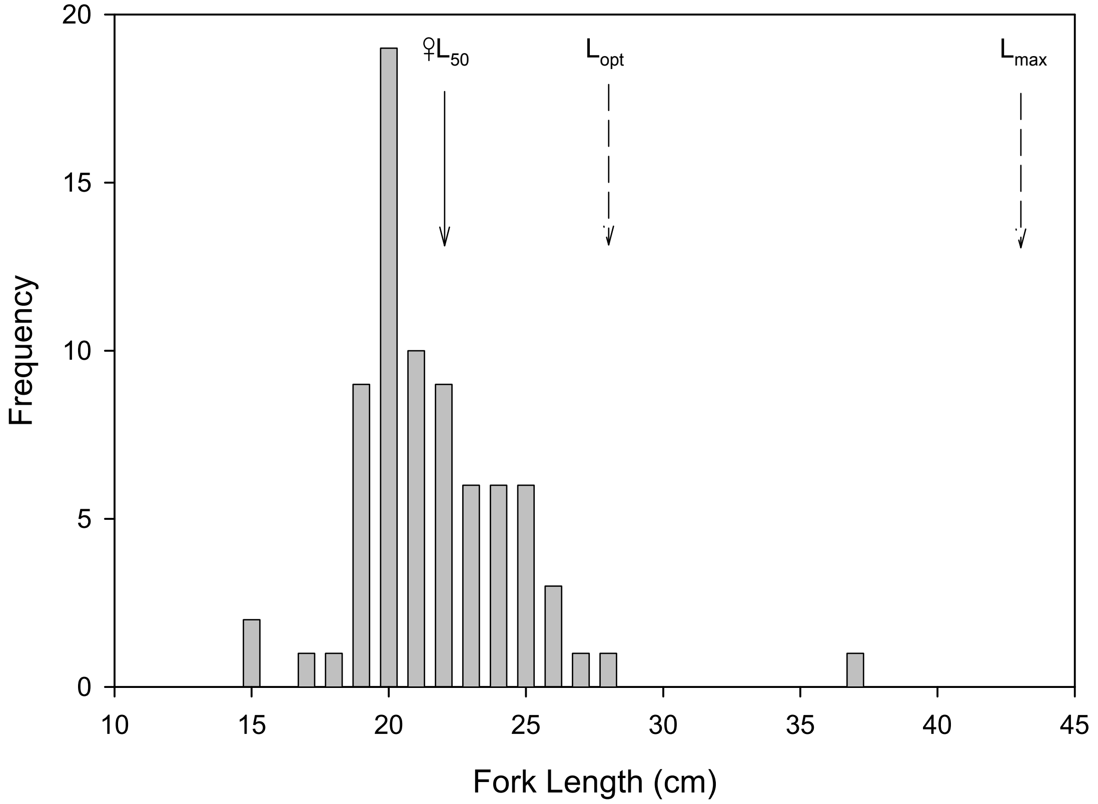

Figure 84. Size structure of *Lutjanus russellii*.

Lutjanus semicinctus Quoy & Gaimard, 1824. Figure 85.

Figure 85. *Lutjanus semicinctus*. Laser dots are separated by 39 mm.

An additional 19 specimens were added to our data set in 2011, yielding a combined total 42 individuals captured on video suitable for length estimation. The additional data shifted mean fork length to 20 from our 2010 estimate of 19 cm. The updated mean size estimate is 60% of the estimated maximum length of 34 cm, 92% of the estimated optimum length of 22 cm, and 96% of published female L_{50} of 21 cm. When the above information is considered in light of size-specific sex ratios (which could not be described with a regression equation) 15% of the individuals captured on video are mature females (Figure 86).

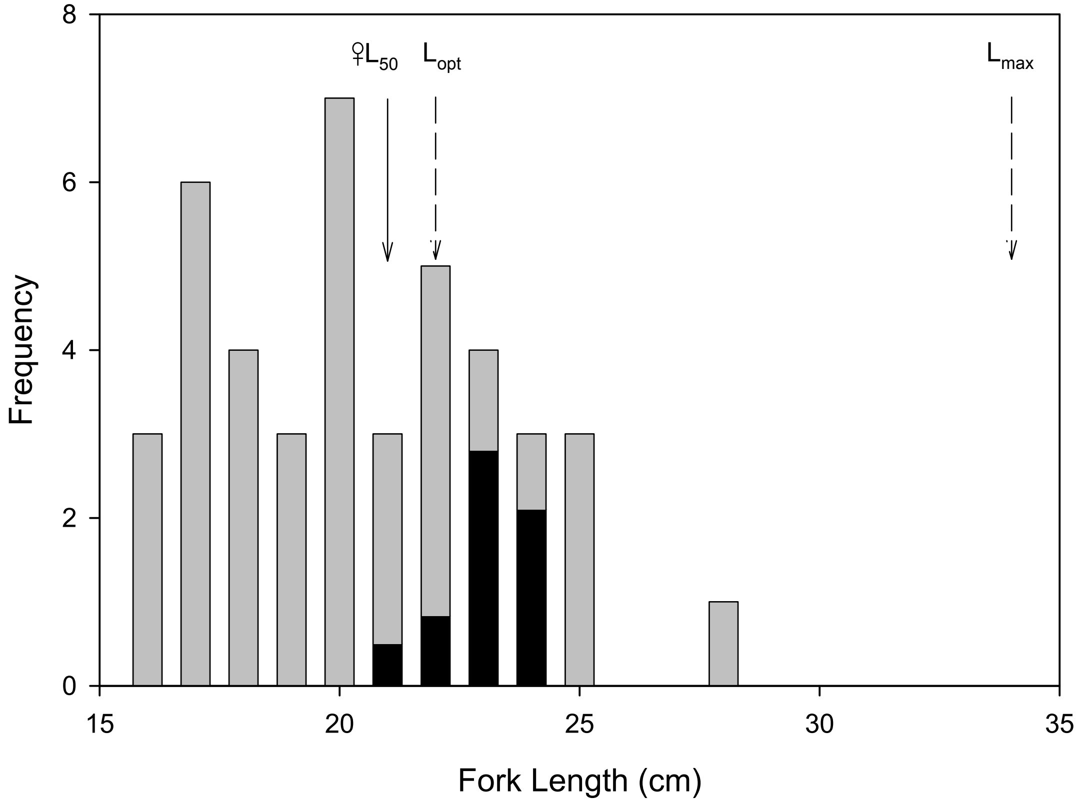

Figure 86. Size structure of *Lutjanus semicinctus*. The dark portion of bars represent estimated number of mature females, light portion represents all other individuals.

Lutjanus vitta (Quoy & Gaimard, 1824). Figure 87.

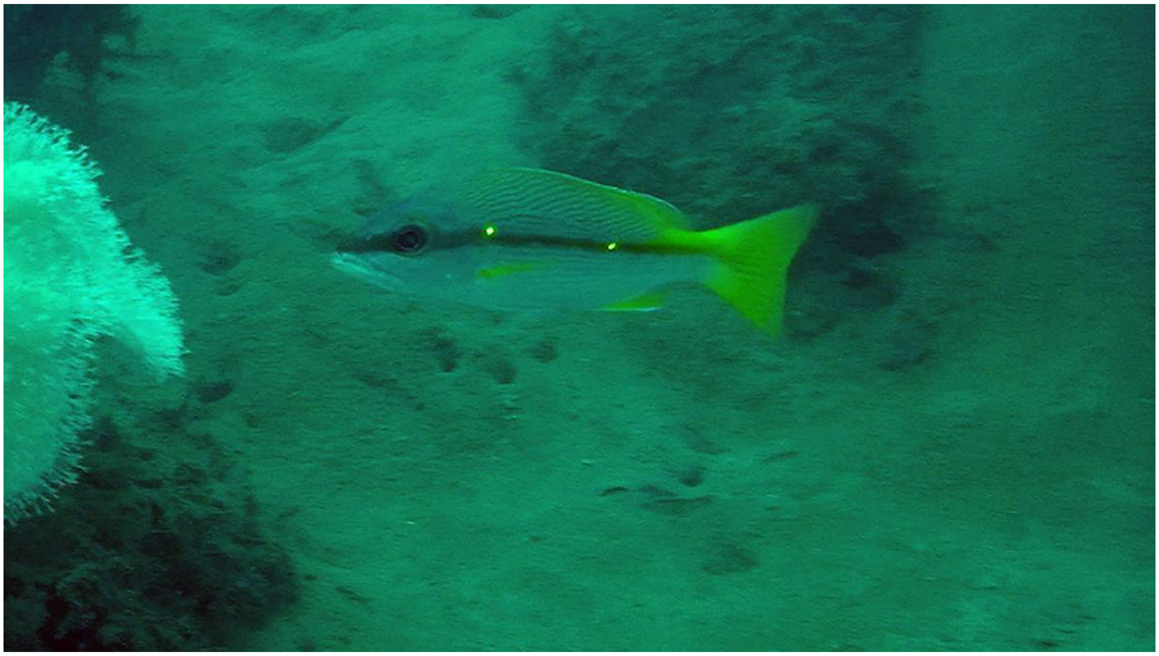

Figure 87. *Lutjanus vitta*. Laser dots are separated by 39 mm.

One (1) additional specimen was added to our data set in 2011, yielding a total 19 individuals captured on video suitable for length estimation. The mean fork length was shifted to 14 cm from our 2010 estimate of 15 cm. The updated mean length is 39% of the estimated maximum length of 37 cm, 60% of estimated optimum length of 24 cm and 96% of the published female L_{50} of 15 cm (Figure 88). The above information, when considered in light of size-specific sex ratios, suggests that about 24% of the population is mature females.

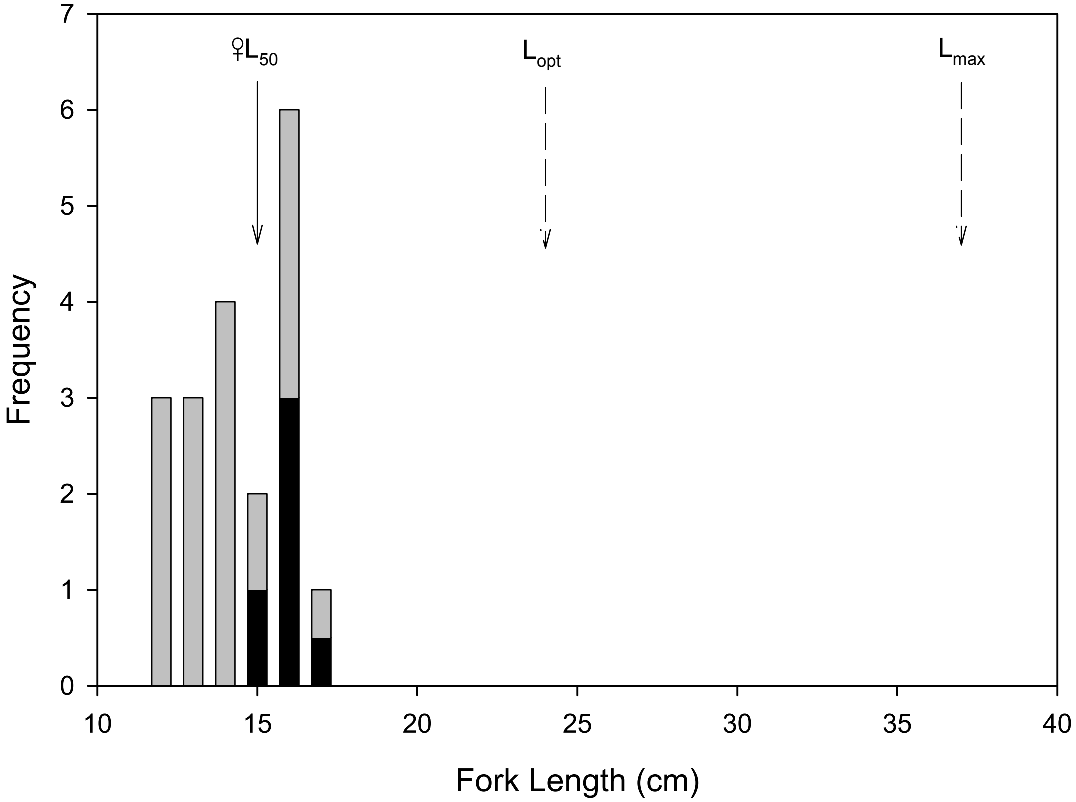

Figure 88. Size structure of *Lutjanus vitta*. The dark portion of bars represent estimated number of mature females, light portion represents all other individuals.

Macolor niger (Forsskål, 1775). Figure 89

Figure 89. *Macolor niger*. Laser dots are separated by 31 mm.

A total five (5) individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean fork length was 28 cm, which is 47% of the estimated maximum length of 60 cm, 72% of the estimated optimum length of 39 cm and 74% of the estimated female L_m of 38 cm.

Macolor macularis Fowler, 1931. Figure 90.

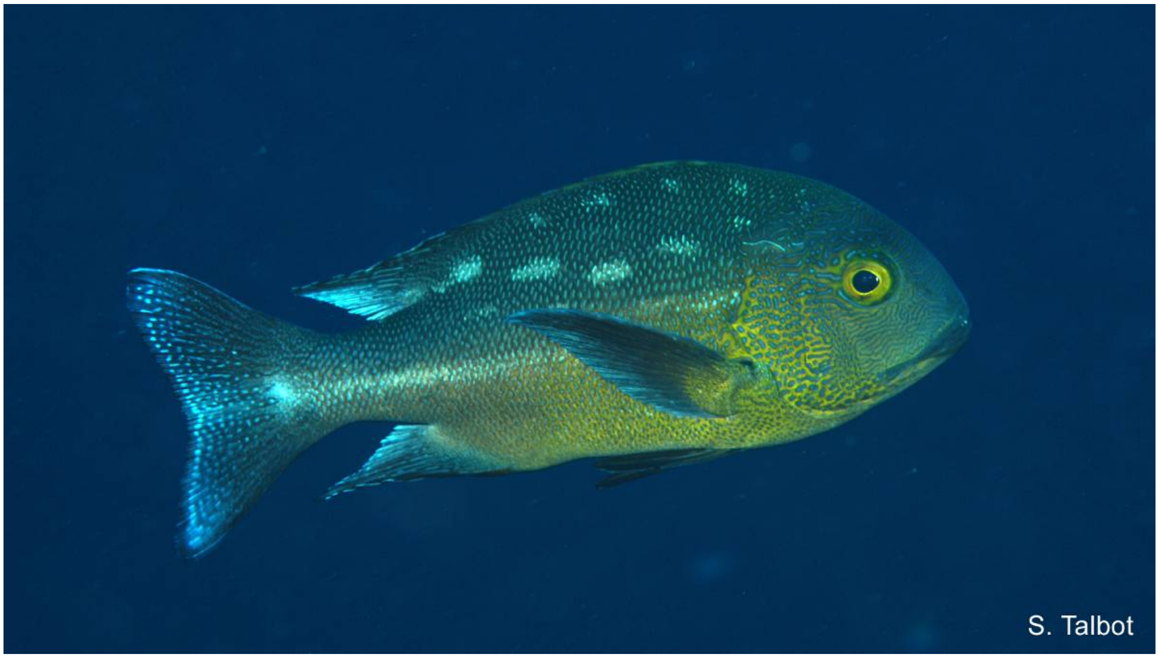

Figure 90. *Macolor macularis*.

An additional four (4) specimens were added to our data set in 2011, yielding a combined total 17 individuals captured on video suitable for length estimation. The additional data shifted mean fork length to 31 cm from our 2010 estimate of 30 cm. The updated mean size estimate is 56% of the estimated maximum length of 55 cm, 86% of the estimated optimum length of 36 cm, and 89% of the estimated female L_m of 35 cm (Figure 91).

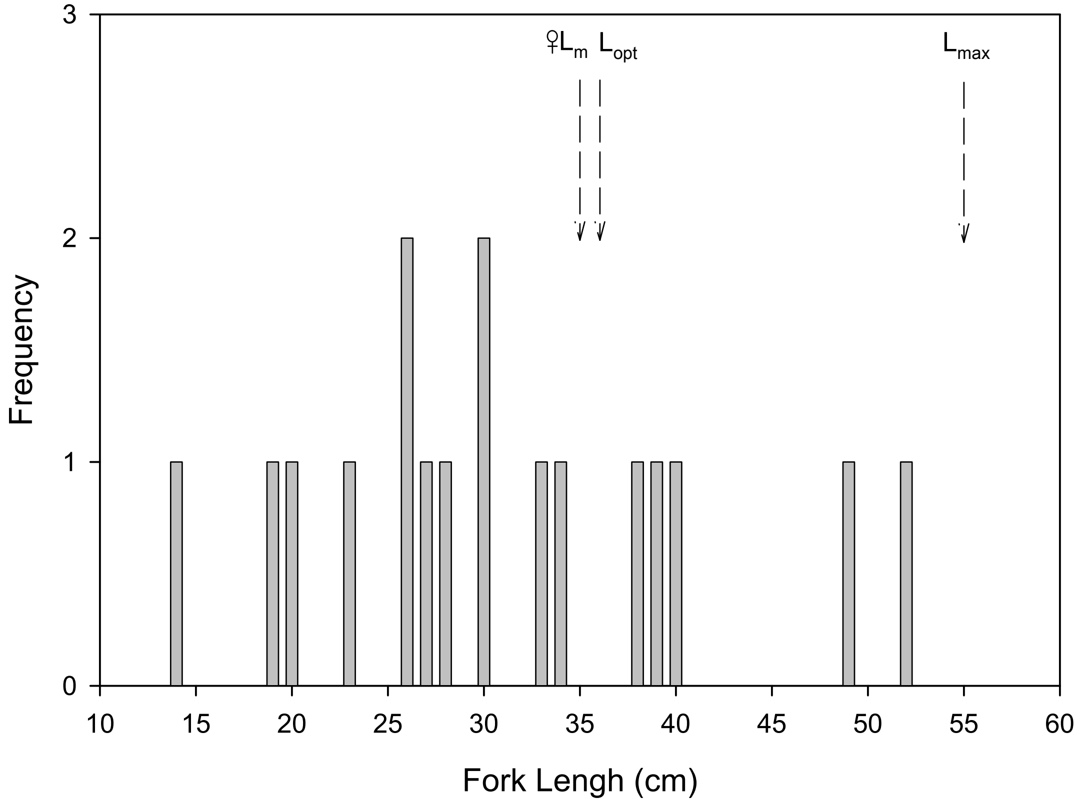

Figure 91. Size structure of *Macolor macularis*.

Mullidae

Mulloidichthys vanicolensis (Valenciennes, 1831). Figure 92.

Figure 92. *Mulloidichthys vanicolensis*. Laser dots are separated by 31 mm.

A total seven (7) individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean fork length was 21 cm, which is 62% of the estimated maximum length of 34 cm, 95% of the estimated optimum length of 22 cm, and 123% of the published female L_{50} of 17 cm.

Parupeneus barberinus (Lacepède, 1801). Figure 93.

Figure 93. *Parupeneus barberinus*. Laser dots are separated by 39 mm.

An additional 36 specimens were added to our data set in 2011, yielding a combined total 121 individuals captured on video suitable for length estimation. The additional data did not change our 2010 mean fork length estimate of 15 cm. Mean size is 34% of the estimated maximum length of 44 cm, 52% of the estimated optimum size of 29 cm and 126% of female L_m of 12 cm. The above information, when considered in light of size-specific sex ratios, suggests 44% of individuals captured on video are reproductive females (Figure 94).

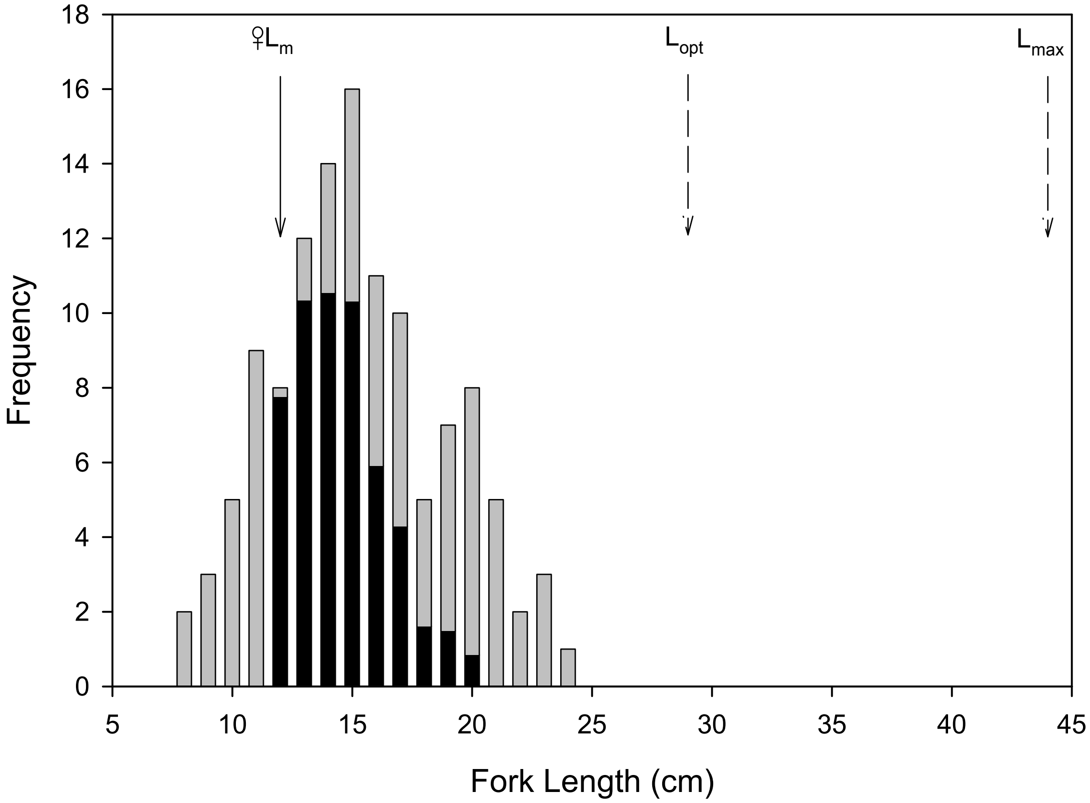

Figure 94. Size structure of *Parupeneus barberinus*.

Parupeneus cyclostomus (Lacepède, 1801). Figure 95.

Figure 95. *Parupeneus cyclostomus*.

An additional three (3) specimens were added to our data set in 2011, yielding a combined total 13 individuals captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, the additional data shifted mean fork length to 18 cm from our 2010 estimate of 19 cm. The updated mean size of the few individuals captured on video is 41% of the maximum reported length of 44 cm, and 62% of estimates of optimum length and female L_m, both 29 cm.

Parupeneus multifasciatus (Quoy & Gaimard, 1825). Figure 96.

Figure 96. *Parupeneus multifasciatus*.

An additional 19 specimens were added to our data set in 2011, yielding a combined total 69 individuals captured on video suitable for length estimation. The additional data did not change the mean fork length estimate of 14 cm, which is 54% of the maximum reported length of 26 cm, 82% of the estimated optimum length of 17 cm and 93% of the published female L_{50} of 15 cm (Figure 97). The above information, when considered in light of size-specific sex ratios and maximum female size (20 cm FL), suggests that about 28% of the population is mature females.

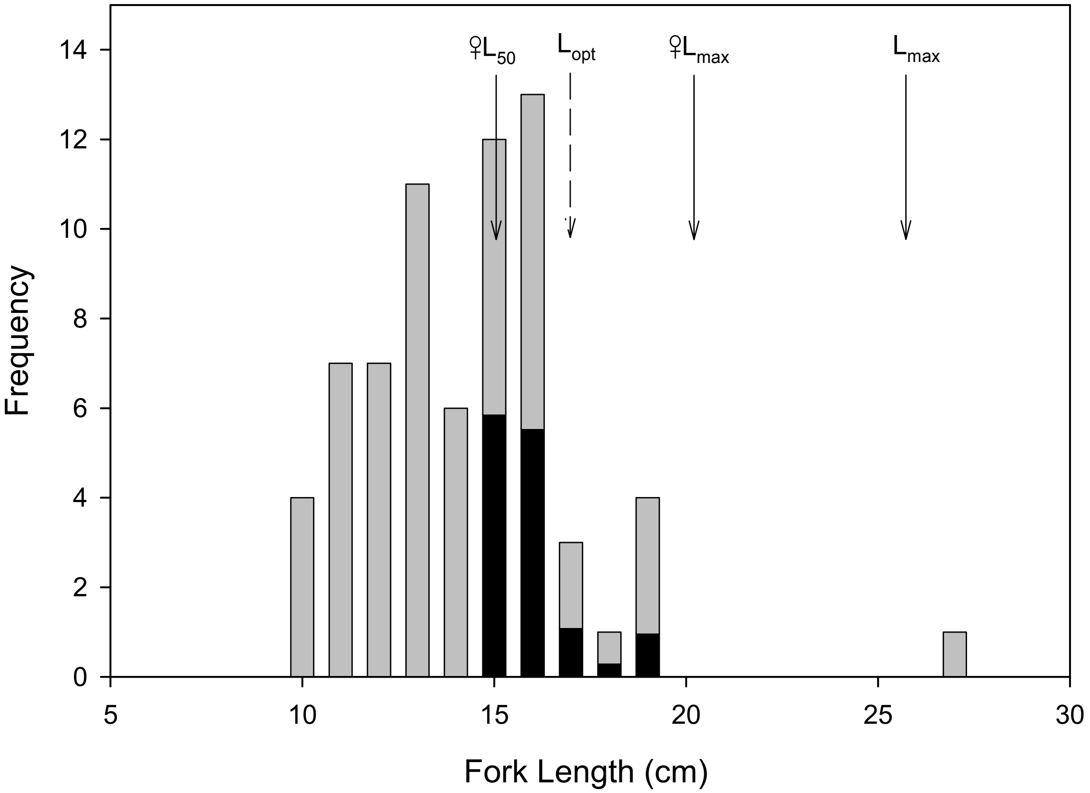

Figure 97. Size structure of *Parupeneus multifasciatus*. The dark portion of bars represent estimated number of mature females, light portion represents all other individuals.

Parupeneus trifasciatus (Lacepède, 1801). Figure 98.

Figure 98. *Parupeneus trifasciatus*. Laser dots are separated by 39 mm.

An additional 16 specimens were added to our data set in 2011yielding a total 28 individuals captured on video suitable for length estimation. The additional data did not change the mean fork length estimate of 20 cm. Mean size is 64% of the estimated maximum length of 31 cm and 100% of estimated optimum length (Figure 99). Mean length is 199% of the published female L_m of 10 cm, and 100% of individuals had attained this size. Sex ratios have not been examined in this species, so the proportion of mature females cannot be estimated.

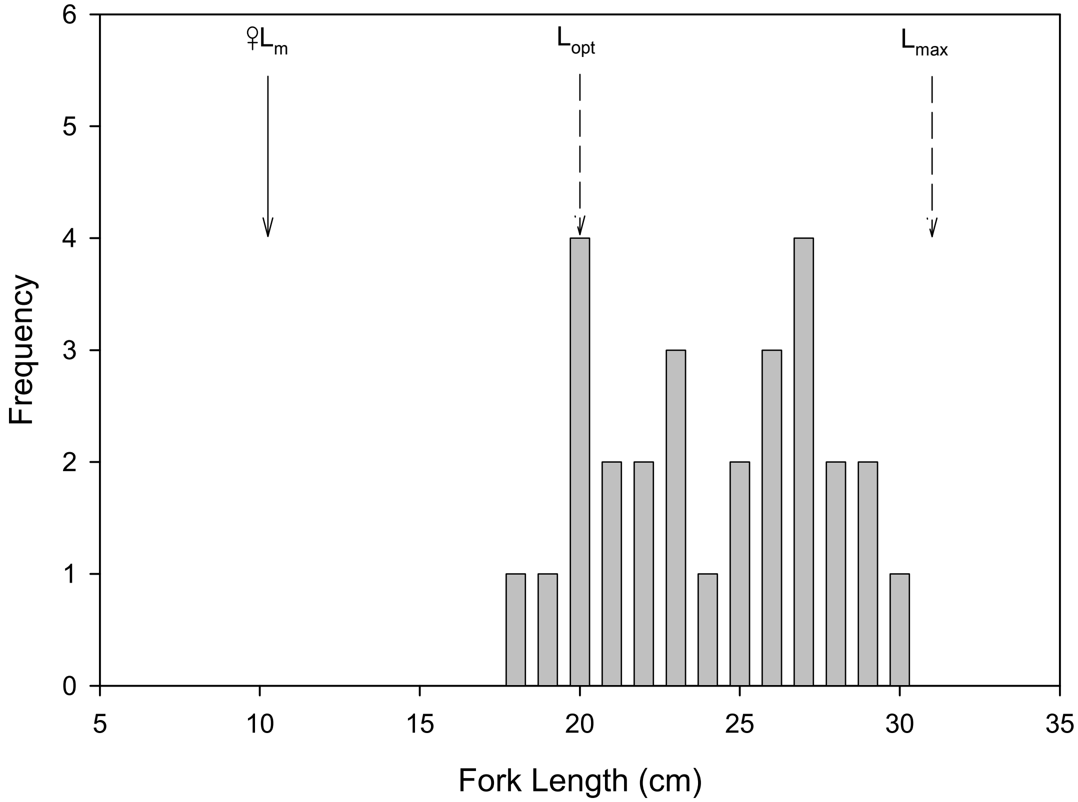

Figure 99. Size structure of *Parupeneus trifasciatus*.

Scaridae

Scarus flavipectoralis Schultz, 1958. Figure 100.

Figure 100. *Scarus flavipectoralis* initial phase (left) and terminal male (right). Laser dots are separated by 36 and 39 mm, respectively.

A total 13 individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean total length was 20 cm, which is 70% of the maximum reported length of 29 cm, and 107% of estimates of optimum length and female L_m, both 19 cm.

Scombridae

Gymnosarda unicolor (Rüppell, 1836). Figure 101.

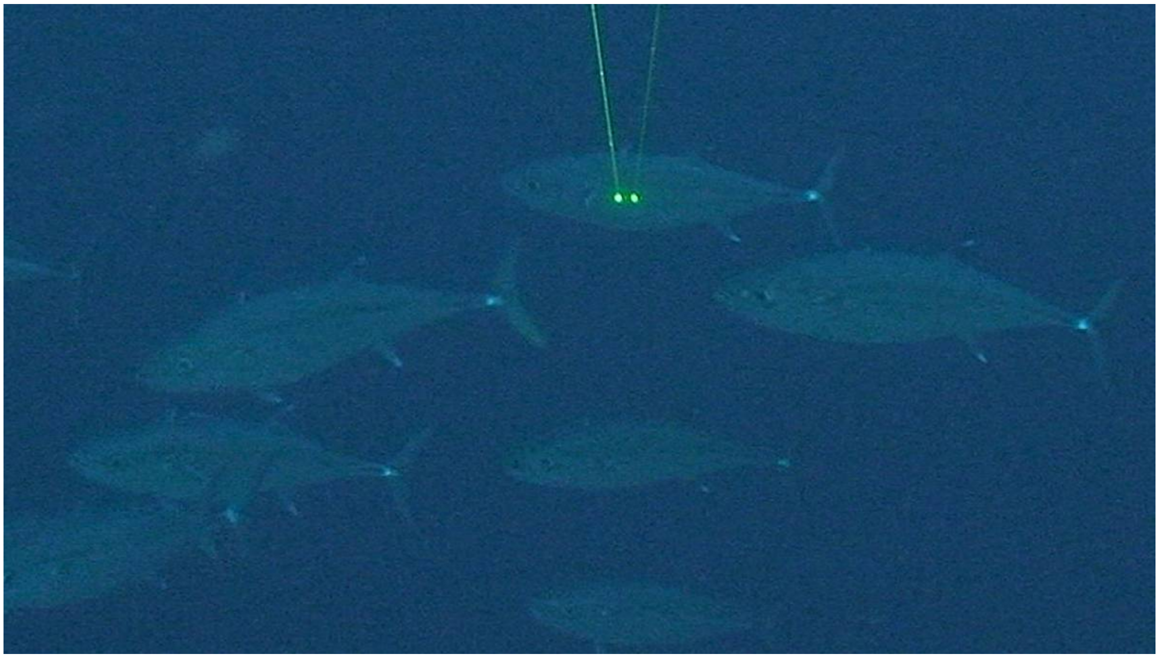

Figure 101. *Gymnosarda unicolor*. Laser dots are separated by 31 mm.

A total 17 specimens were captured on video suitable for length estimation. Mean fork length is 59 cm, which is 43% of the estimated maximum length of 137 cm, 64% of the estimated optimum length of 92 cm, and 85% of the published female L_m of 70 cm (Figure 102).

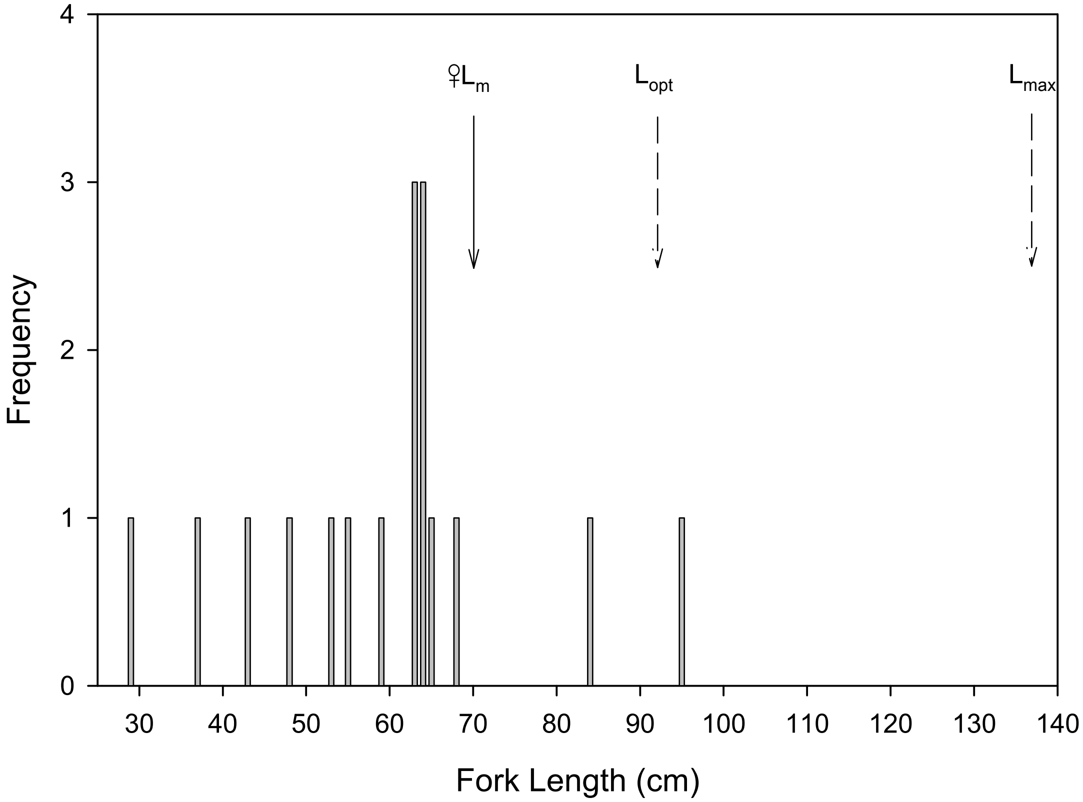

Figure 102. Size structure of *Gymnosarda unicolor*.

Scomberomorus commerson (Lacepède, 1800). Figure 103.

Figure 103. *Scomberomorus commerson*. Laser dots are separated by 31 mm.

A total four (4) individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean total length was 95 cm, which is 44% of the maximum reported length of 218 cm, 64% of the estimated optimum length of 148 cm, and 146% of the published female L_m of 65 cm. The above information, when considered in light of size-specific sex ratios, suggests that about 80% of the individuals captured on video were mature females.

Serranidae

Anyperodon leucogrammicus (Valenciennes, 1828). Figure 104.

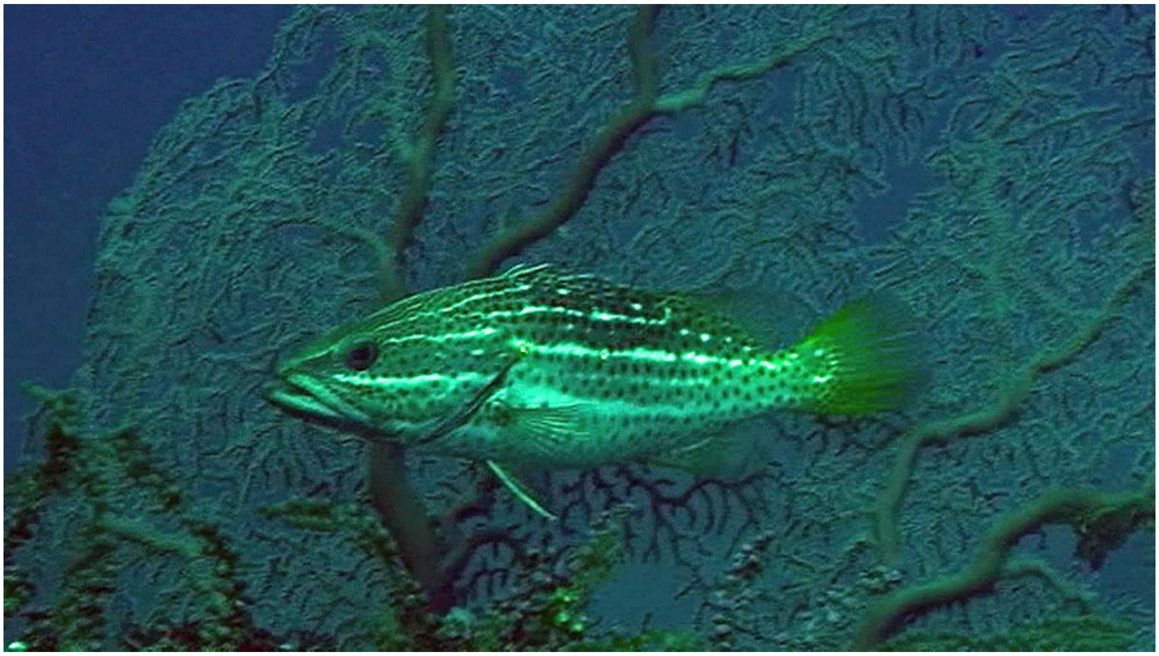

Figure 104. *Anyperodon leucogrammicus*. Laser dots are separated by 39 mm.

An additional three (3) specimens were added to our data set in 2011, yielding a combined total 11 individuals captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, the additional data shifted mean length to 26 cm from our 2010 estimate of 25 cm. The updated mean size is 50% of the maximum reported length of 52 cm. 77% of the estimated optimum length of 34 cm and 79% of the estimated female L_m of 33 cm.

Cephalopholis boenak (Bloch, 1790). Figure 105.

Figure 105. *Cephalopholis boenak*.

No new specimens were added to our data set in 2011, leaving a total 10 individuals captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean total length was 17 cm, which is 70% of the maximum reported length of 24 cm and 111% of the estimated optimum length and the published female L_{50}, both 15 cm. Because sex change occurs in this species (~ 16 cm) and size-specific sex ratios are not known, the proportion of mature females cannot be reliably estimated.

Cephalopholis cyanostigma (Valenciennes, 1828). Figure 106.


S. Talbot

Figure 106. *Cephalopholis cyanostigma*.

An additional 16 specimens were added to our data set in 2011, yielding a combined total 46 individuals captured on video suitable for length estimation. The additional data did not change the mean total length estimate of 19 cm, which is 54% of the maximum reported length of 35 cm and 82% of estimated optimum length and published female L_{50}, both 23 cm. Given L_{50}, size-specific sex ratios (present study) and the maximum female size of 26 cm (Moss *et al*. 2002), 0.9% are mature females. However, if minimum size at female maturity (17 cm, present study) is considered, up to 39% of individuals captured on video may be mature females (Figure 107).

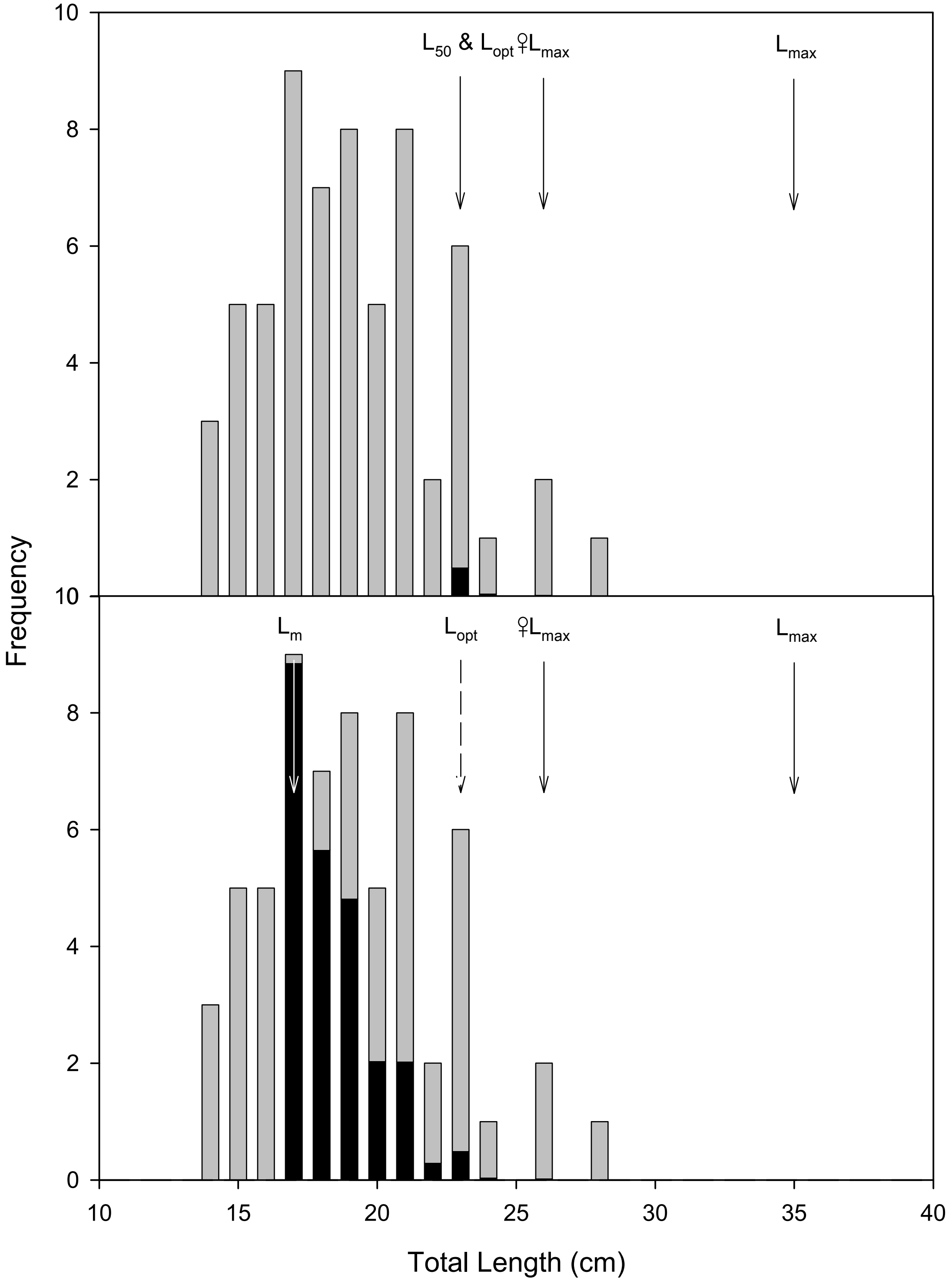

Figure 107. Size structure of *Cephalopholis cyanostigma*. The dark portion of bars represent estimated number of mature females if L_{50} is considered (top) of if L_m is considered (bottom), light portion represents all other individuals.

Cephalopholis microprion (Bleeker, 1852). Figure 108.

Figure 108. *Cephalopholis microprion*. Laser dots are separated by 39 mm.

An additional seven (7) specimens were added to our data set in 2011, yielding a combined total 20 individuals captured on video suitable for length estimation. The additional data did not shift our 2010 estimate of 13 cm. Mean size is 56% of the maximum reported length of 23 cm, 86% of the estimated optimum length of 15 cm and 81% of the estimated female L_m of 16 cm (Figure 109).

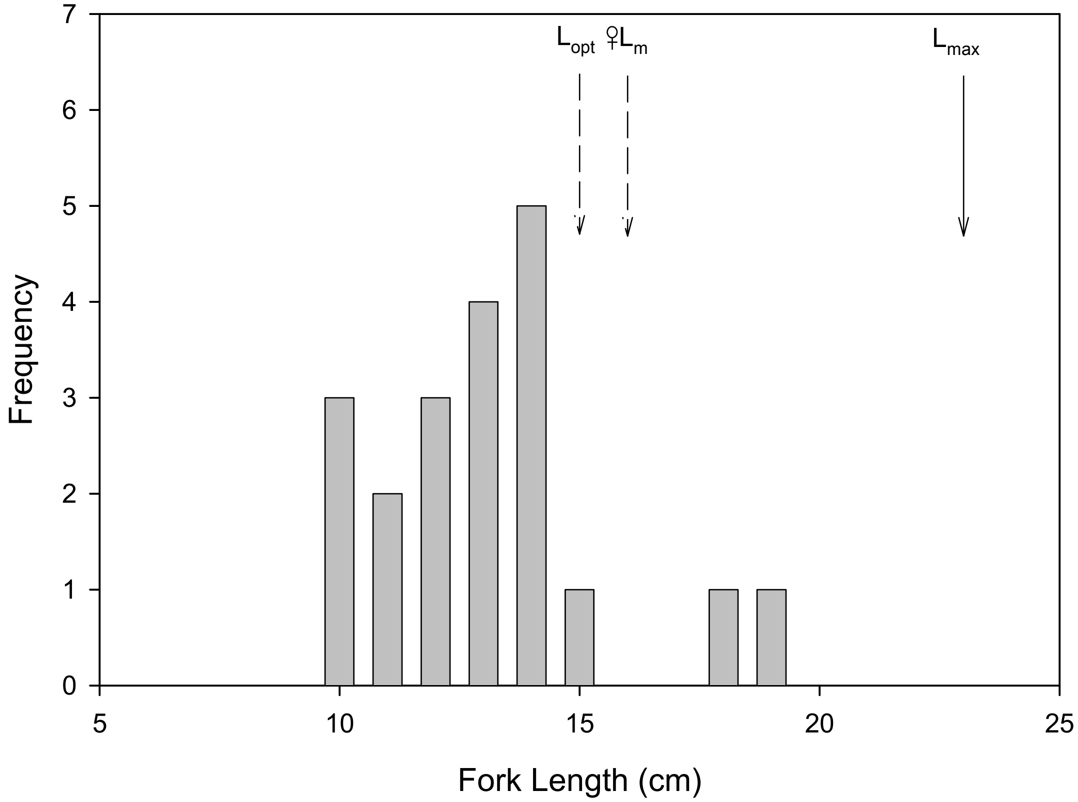

Figure 109. Size structure of *Cephalopholis microprion*.

Cephalopholis sexmaculata (Rüppell, 1830). Figure 110.

Figure 110. *Cephalopholis sexmaculata*. Laser dots are separated by 36 mm.

A total three (3) individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean fork length was 21 cm, which is 45% of the published maximum length of 47 cm, 69 % of the estimated optimum length of 31 cm and 89% of the published female L_m of 24 cm.

Cephalopholis urodeta (Forster, 1801). Figure 111.

Figure 111. *Cephalopholis urodeta*. Laser dots are separated by 39 mm.

An additional two (2) specimens were added to our data set in 2011, yielding a combined total six (6) individuals captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, the additional data shifted the mean total length estimate to 18 cm from our 2010 estimate of 17 cm. The updated mean length is 65% of the maximum reported length of 27 cm, 104% of estimated optimum length of 17 cm, and 97% of estimated female L_m of 18 cm.

Plectropomus areolatus (Rüppell, 1830). Figure 112.

Figure 112. *Plectropomus areolatus*. Laser dots are separated by 39 mm.

An additional 10 specimens were added to our data set in 2011, yielding a total 15 individuals captured on video suitable for length estimation. The additional data shifted mean length to 18 cm from our 2010 estimate of 15 cm. The updated mean size is 22% of the maximum reported length of 70 cm, 38% of the estimated optimum length of 46 cm, and 44% of the published female L_{50} of 40 cm (Figure 113). Apparently, none of the individuals captured on video had attained reproductive size.

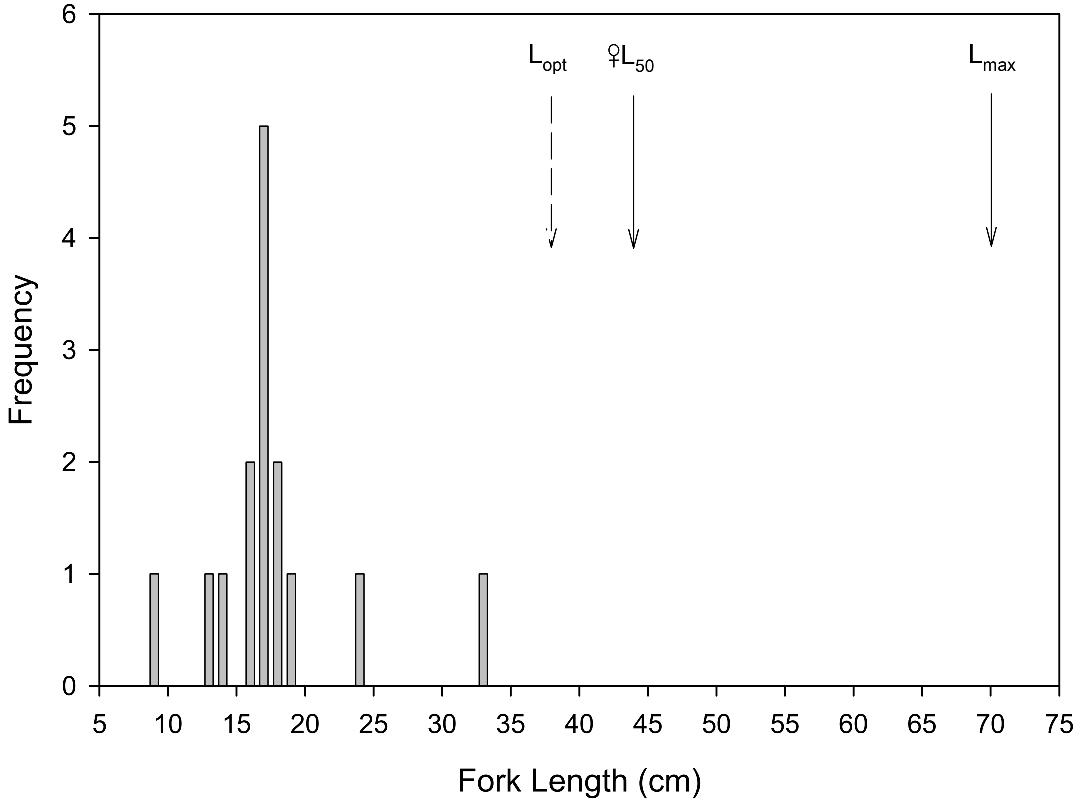

Figure 113. Size structure of *Plectropomus areolatus.*

Plectropomus leopardus (Lacepède, 1802). Figure 114.

Figure 114. *Plectropomus leopardus*. Laser dots are separated by 36 mm.

An additional three (3) individuals were added to our data set in 2011, yielding a total six (6) individuals captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, the additional data shifted mean total length to 34 cm from our 2010 estimate of 30 cm. The updated mean size is 50% of the estimated maximum length of 68 cm, 76% of the estimated optimum length of 45 cm, and 106% of the published female L_{50} of 32 cm. The above information, when considered in light of size-specific sex ratios, suggests that about 67% of the individuals captured on video are mature females.

Plectropomus oligacanthus (Bleeker, 1854). Figure 115.

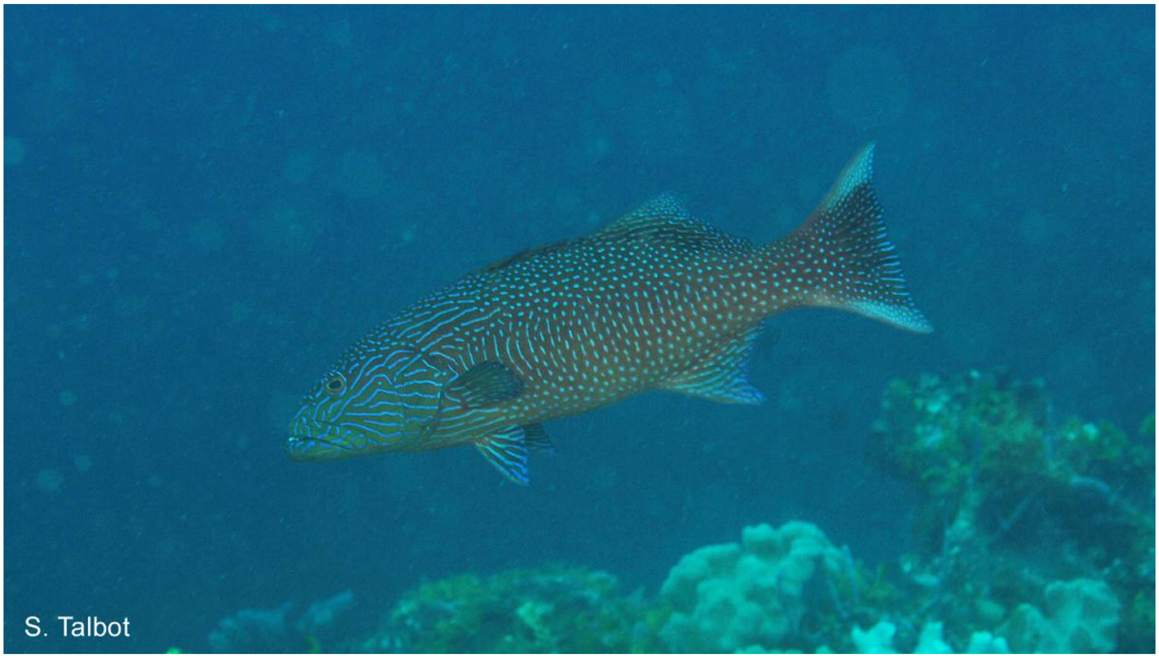

Figure 115. *Plectropomus oligacanthus*.

An additional four (4) specimens were added to our data set in 2011, yielding a combined total 41 individuals captured on video suitable for length estimation. The additional data shifted mean fork length to 32 cm from our 2010 estimate of 31 cm. The updated mean size is 50% of the maximum reported length of 65 cm, 75% of the estimated optimum length of 43 cm, and 79% of the estimated L_m of 42 cm (Figure 116).

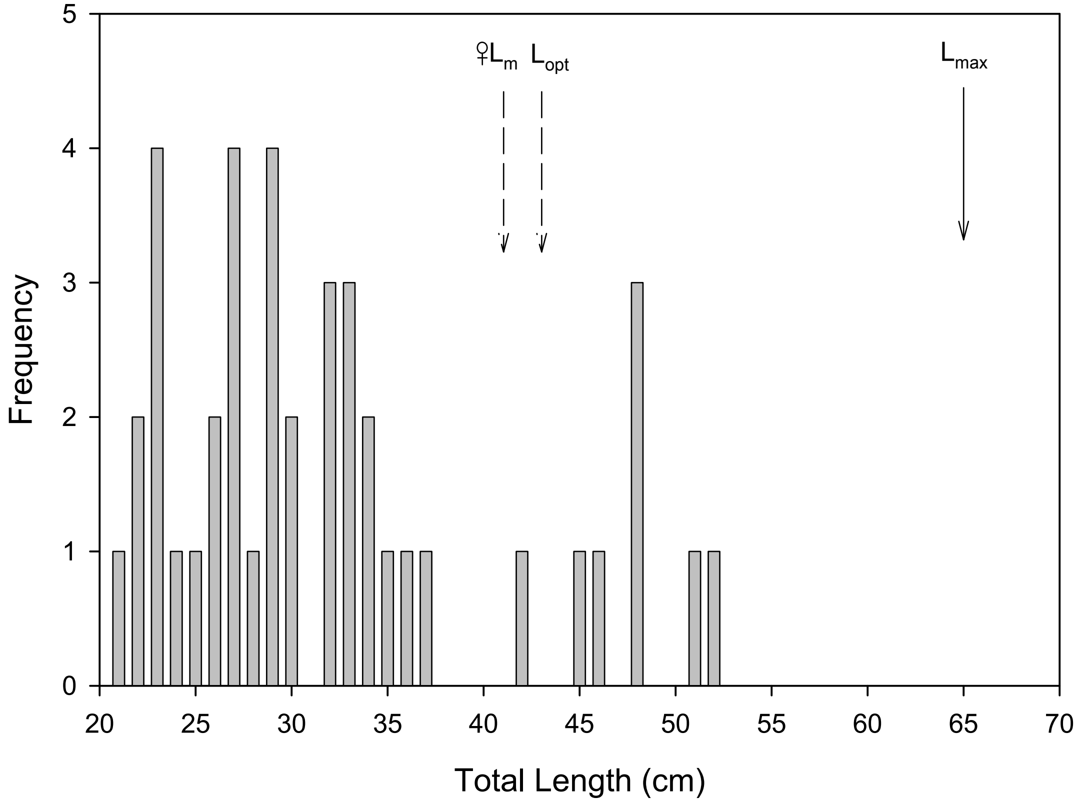

Figure 116. Size structure of *Plectropomus oligacanthus*.

Siganidae

Siganus javus (Linnaeus, 1766). Figure 117.

Figure 117. *Siganus javus*. Laser dots are separated by 39 mm.

No new specimens were added to our data set in 2011, leaving a total 33 individuals captured on video suitable for length estimation. Mean “fork” length was 25 cm, which is 47% of the maximum reported total length of 53 cm, 72% of the estimated optimum length of 35 cm, and 74% of the estimated female L_m of 34 cm (Figure 118). The percentage presented here is a slight underestimate because the caudal fin of this species is emarginate, thus total length is longer than “fork” length (distance to the end of the middle caudal ray used throughout this study).

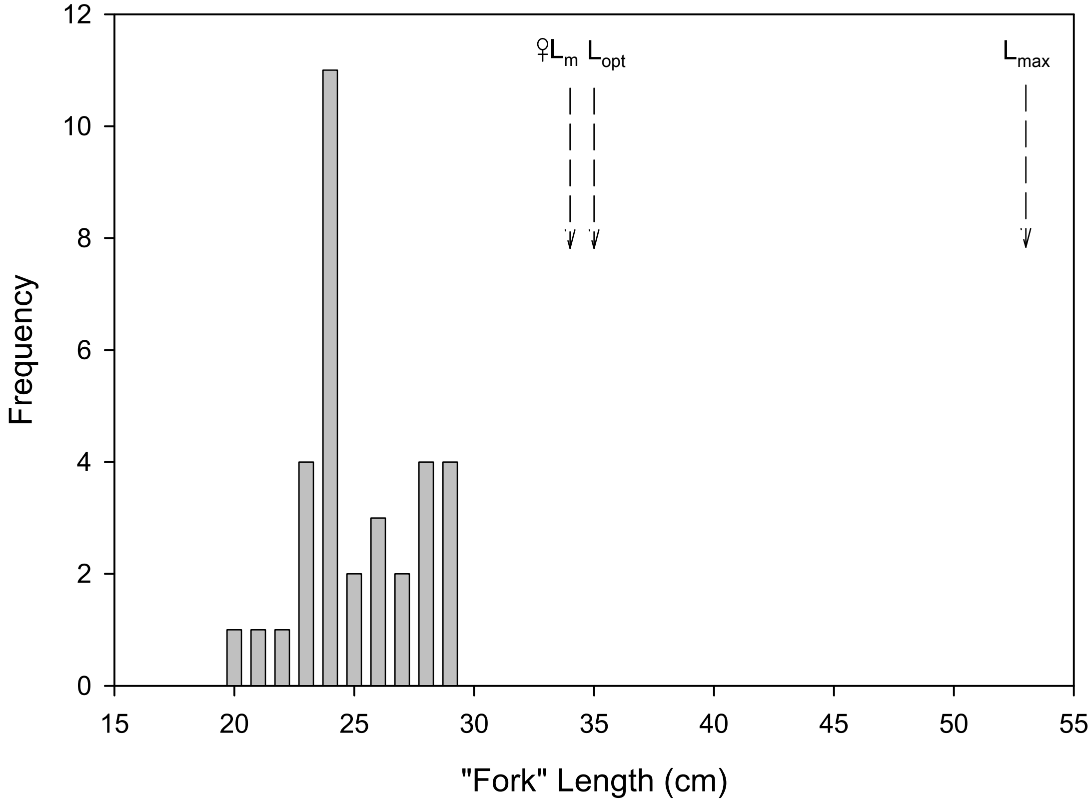

Figure 118. Size structure of *Siganus javus*.

Siganus lineatus (Valenciennes, 1835). Figure 119.

Figure 119. *Siganus lineatus*.

An additional 26 specimens were added to our data set in 2011, yielding a combined total 65 individuals captured on video suitable for length estimation. The additional data did not change our 2010 mean "fork" length estimate of 26 cm. Mean size estimate is 63% of the estimated maximum "fork" length of 41 cm, 95% of the estimated optimum length of 27 cm, and 107% of published female L_{50} of 24 cm. The above information, when considered in light of size-specific sex ratios and maximum published female length (29 cm), suggests 31% of the individuals captured on video are mature females (Figure 120).

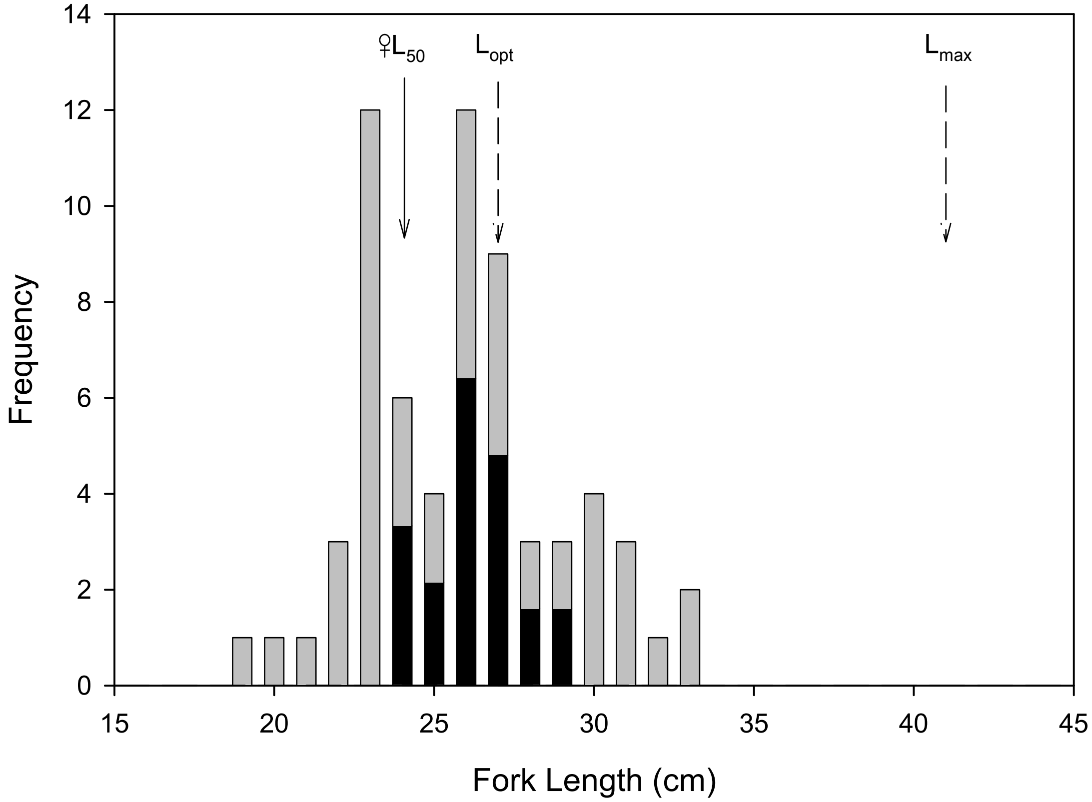

Figure 120. Size structure of *Siganus lineatus*. The dark portion of bars represent estimated number of mature females, light portion represents all other individuals.

Siganus puellus (Schlegel, 1852). Figure 121.

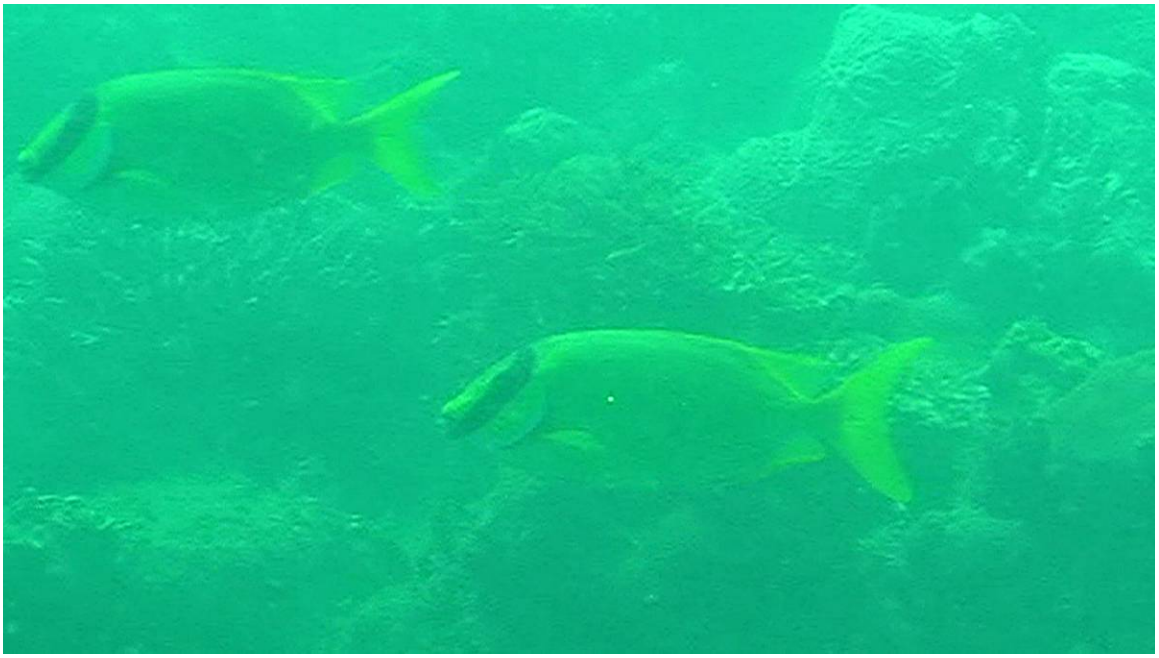

Figure 121. *Siganus puellus*. Laser dots are separated by 39 mm.

A total three (3) individuals were captured on video suitable for length estimation. Due to low sample size, a size distribution is not presented. However, mean fork length was 22 cm, which is 57% of the estimated maximum length of 38 cm, and 87% of estimates of optimum length and female L_m, both 25 cm.

Fishery Selectivity

We had data to compare catch with populations at-large for four species (Figure 122). Catch of *Cephalopholis cyanostigma* averaged 19.7 cm, slightly larger than at-large population mean of 18.9 cm; however, no significant difference was detected with a t-test. Catch of *Lutjanus semicinctus* averaged 17.4 cm; a t-test indicated mean length was significantly lower than the at-large population mean of 20.3 cm. Catch of *Parupeneus barberinus* averaged 16.5 cm; a t-test on log-transformed data indicates this is significantly larger than the mean size of the at-large population (15.2 cm). Catch of *Siganus lineatus* averaged 23.9 cm, which is smaller than the at-large population mean of 26.0 cm. Data could not be transformed to meet assumptions of parametric statistics; however, a Mann-Whitney test indicates population medians are significantly different.

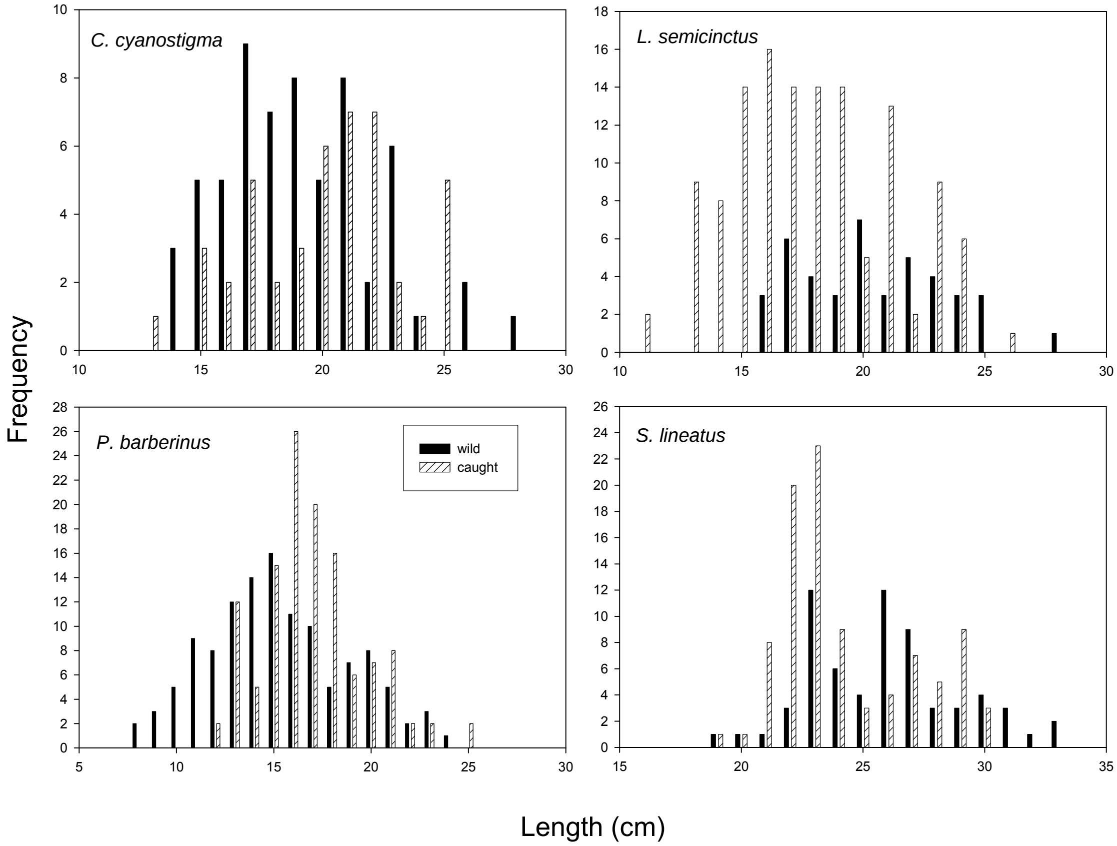

Figure 122. Size structure of fish catch (dark bars) and at-large populations (hashed bars) for four species at Kamiali Wildlife Management Area.

DISCUSSION

Reproductive Analysis

We successfully generated preliminary, histology-based reproductive information for five exploited fishes at Kamiali Wildlife Management Area (KWMA). All five of these species have broad geographic ranges. Thus, the results of our reproductive analyses provide crucial information for the conservation and management of reef fishes elsewhere in the Indo-Pacific region.

During a previous, unsuccessful attempt to generate a similar amount of information (Longenecker *et al*. 2010), we identified our primary problem to be the limited time we allowed for collecting specimens (only two weeks). We attribute our success in the current study to village participation, where residents permitted us to measure and remove gonads from their catch. Importantly, villagers had four months to collect specimens before we began histological work.

We histologically examined a total 477 specimens in 2011. For 386 of these, work (embedding, sectioning, and microscopic evaluation) was done during a two-week field trip during which the overwhelming majority of our time was spent preparing for and conducting technical dives for laser-videogrammetry surveys. The remaining 91 specimens were embedded at Kamiali, but were transported to Hawaii for sectioning and evaluation.

We experienced a minor problem with fecundity analyses. Two weeks was too short for Gilson's fluid to liberate oocytes from fixed ovaries. Specimens for fecundity analysis had to be shipped to Hawaii before this aspect of the study was completed. Researchers attempting similar analyses could more-effectively use limited field time by taking and weighing ovarian subsamples, returning them to fixative (which is easier to ship), shipping them to a laboratory, and then transferring samples to Gilson's Fluid for subsequent analysis.

Our results indicate reef fish at KWMA have a variety of reproductive characteristics. One species (*Cephalopholis cyanostigma*) is a protogynous hermaphrodite (*i.e.*, changes sex from female to male), whereas the other four are apparently gonochoristic (do not change sex). Male minimum size at maturity (L_m) is smaller than L_m for females in four species, whereas male L_m is larger than female L_m for *Parupeneus barberinus*. Two species (*Cephalopholis cyanostigma* and *Parupeneus barberinus*) become increasingly male-biased with length, and one species (*Siganus lineatus*) appears to have a nearly 1:1 sex ratio. We did not have enough specimens to reliably describe sex ratios in the remaining two species (*Lutjanus semicinctus* and *Lutjanus timorensis*). In four of five species batch fecundity is an approximately cubic function of length, whereas we could not construct a descriptive equation for the fifth species (*Cephalopholis cyanostigma*).

Below we discuss the results of our reproductive analyses on the three species for which some reproductive information is available. We could not find any published information for the snappers *Lutjanus semicinctus* or *Lutjanus timorensis*.

Cephalopholis cyanostigma

Our reproductive analysis of *Cephalopholis cyanostigma* is based on a small number (44) of individuals. Despite the limitations of a low sample size, we are able to report new reproductive information for the species. Sex ratios in this grouper vary predictably with size; females dominate at smaller sizes and are absent in larger size classes. This pattern may be expected given the protogynous reproductive mode (Moss *et al*. 2002, Heemstra & Randall 1993, present study). Moss *et al*. (2002) report that sex change in *Cephalopholis cyanostigma* occurs from 16 – 26 cm. We found a single transitional male at 19.8 cm TL, well within this range.

Unlike reproductive analysis of Great Barrier Reef populations by Moss *et al*. (2002), we found immature individuals throughout the female size range. All specimens examined by Moss *et al*. (2002) were ≥ 14 cm and all were mature. The presence of immature individuals in our study permitted estimation of female L_{50} at 23 cm TL; however, this result is driven by a single mature female in the largest female size class. When data were organized into larger (2 cm) size classes, no more than 25% of females in any size class were mature. Thus, our female L_{50} value is tentative. Also tentative is our finding that fecundity is not predictably related to female size. Spawning season has not been described for this species. It is possible that the specimens we used for reproductive analysis were collected outside of their spawning period. This may be the reason why our L_{50} and fecundity results are not robust; it is sometimes difficult to reliably distinguish females who have not yet reached reproductive maturity from those who have previously spawned but regressed to an inactive state at the end of a spawning season. Also, we may not have collected specimens from throughout the female size range. Moss *et al*. (2002) report females as large as 28 cm, whereas our largest female was 24.6 cm TL. The presence of larger females in our collection may have resulted in better L_{50} and fecundity curves.

Parupeneus barberinus

Despite a larger sample size (123 individuals) and having collected specimens during the latter part of its spawning season of October – May (Anand & Pillai 2002), we could not construct L_{50} curves for *Parupeneus barberinus*. However, our L_m values for females and males (12 and 14 cm FL, respectively) are remarkably similar to those of Anand & Pillai (2002) who report 12 and 16 cm, respectively for populations from India.

Our analyses did yield size-fecundity and size-specific sex ratio equations. Smaller size classes of *Parupeneus barberinus* are dominated by females, and females are absent from larger size classes. This results in a sex-based bimodal size distribution, which is one sign of protogynous hermaphroditism (female-to-male sex change) in fishes. We also found a single female with spermatogenic tissue, which can be a sign of protogynous sex-change. However, gonads containing both ovarian and testicular tissue (ovotestes) are known to occur in both hermaphroditic and gonochoristic species. In gonochores, ovotestes are typically non-functional as either sex and thus contain only pre-vitellogenic oocytes. Also, testes of mature males typically do not retain anatomical evidence of previous ovarian function (*e.g.*, vestigial ovarian lumen or brown bodies - thought to represent atretic oocytes). Presence of ovotestes in gonochoristic species is often regarded as an abnormal artifact of physiological stress (*e.g.*, high stocking densities or high water temperature) or as a natural process of gonad differentiation in immature individuals (*e.g.*, Asoh *et al*. 2001) In protogynous species, ovotestes are most numerous within intermediate size-classes and may contain mature oocytes, spermatozoa, or both. In addition, gonads of mature males typically retain anatomical evidence of their ovarian origin. We found no evidence of brown bodies or lumina within the testes of mature male *Parupeneus barberinus*. Further, the single ovotestis did not contain mature gametes of either sex, and came from one of the smallest specimens (12.9 cm FL) examined. Thus we concluded that *Parupeneus barberinus* is a gonochore.

Siganus lineatus

Because *Siganus lineatus* spawns year-round (Hamilton *et al*. 2004), the 93 specimens we processed for reproductive analysis should provide reliable reproductive data. We were able to construct size-fecundity and size-specific sex ratio equations. Although we could not estimate male L_{50} (all but one male in our collection were mature) we did estimate female L_{50} at 24 cm FL. This value is remarkably close to Woodland's (1990) observation that the smallest spawning individual was 23 cm. Our results suggest *Siganus lineatus* does not changes sex and agree with Chan & Sadovy (2002) that this species is a gonochore.

The results of our reproductive analyses, plus those published elsewhere, suggest the empirically derived equations of Froese & Binohlan (2000) should be viewed with caution when estimating female L_m. Figure 32 shows that Froese & Binohlan's equation overestimates the female L_m of 10 species for which L_m is known. Further, the degree of overestimation increases as size increases. Given that size at 50% maturity (L_{50}) should generally be expected to be larger than L_m, we find it even more remarkable that L_m based on Froese & Binohlan's equation is higher than 12 of 14 observed values for female L_{50} (Figure 33). As above, the degree of overestimation increases as size increases. We fully recognize the value of Froese & Binohlan's equation; we think it is far better to have an approximation of reproductive size, based on empirical evidence, than to devise fishery management and conservation plans without reference to reproductive biology (in fact, we rely on their equations for the vast majority of analyses in the present study). However, the above comparisons highlight the need for continued life history work. We suggest that, with regard to marine resource management and conservation, outcomes are more likely to match expectations when the latter are based on accurate information rather than approximations with known biases.

Catch Characteristics

The value of life history analysis is further demonstrated by our ability to model the outcome of fishery management/conservation proposals relative to current fishing practices. These models allow us to explore ways that subsistence fishers can maintain their current harvest levels while simultaneously promoting larger fish populations. We can present information in terms of weight (important to villagers that depend on fish for their primary source of protein) and number of eggs released in a single spawning event (likely to influence the size of future fish populations). More importantly, this information can be easily understood by non-specialists (*e.g.*, village residents who control marine resources at KWMA and will ultimately be responsible for any conservation/management decisions).

Below we compare the effects of current fishing practices to a combination of two of Froese's (2004) suggested fishing practices (all fish in the catch are mature and within 10% of estimated L_{opt}). With somewhat reliable estimates of size at maturity, size-specific sex ratios, size-fecundity relationships, length-weight relationships; we can estimate reproductive output from a hypothetical population after fish have been harvested. The hypothetical populations we construct have the same relative size structure observed in at-large populations (via laser videogrammetry); we simply multiply the number of individuals in each size class by a constant number so that each hypothetical size class contains enough individuals to accommodate the greater of observed or proposed harvest. We had adequate information for three species, none of which were harvested in a manner consistent with Froese's (2004) criteria.

Harvest of *Cephalopholis cyanostigma* at KWMA appears non-selective; there was no significant difference between the average size of a fish caught and the average size of an at-large individual. A total 44 fish harvested yielded 5.62 kg. Our hypothetical population would produce 564,376 eggs after those 44 individuals were removed. Lengths within 10% of L_{opt} are 21 – 25 cm TL, but because L_{50} is 23 cm TL, harvest consistent with Froese's (2004) guidelines is 23 – 25 cm TL. Residents can obtain the same 5.62 kg by harvesting only 25 fish equally distributed among 23 – 25 cm size classes. Under this scenario, our hypothetical population would produce an additional 30,105 eggs per spawning event.

Harvest of *Parupeneus barberinus* at KWMA appears to select larger individuals; average size of a fish caught was significantly bigger than the average size of an at-large individual. Interestingly, harvest meets Froese's (2004) criterion that all fish should have reached size at maturity, however no fish was within 10% of L_{opt}. A total 123 fish harvested yielded 11.08 kg. Our hypothetical population would produce 1,436,044 eggs after those 44 individuals were removed.

Lengths within 10% of Lopt are 26 – 32 cm FL, and all individuals within this size range would be mature. Residents can obtain the same 11.08 kg by harvesting only 26 fish equally distributed among 26 – 32 mm size classes. Under this scenario, our hypothetical population would produce an additional 543,442 eggs per spawning event.

Harvest of *Siganus lineatus* at KWMA appears to select smaller individuals; average size of a fish caught was significantly shorter the than the average size of an at-large individual. A total 92 fish harvested yielded 29.32 kg. Our hypothetical population would produce 82,465,199 eggs after those 92 individuals were removed. Lengths within 10% of Lopt are 24 – 30 cm FL, and all individuals within this size range would be mature. Residents can obtain the same 29.32 kg by harvesting only 67 fish equally distributed among 24 – 30 mm size classes. Under this scenario, our hypothetical population would produce 6,472,181 fewer eggs per spawning event.

Discrepancies in the above results may be related to differences in patterns of size-specific sex ratios. Average female size is smaller than average male size for *Cephalopholis cyanostigma* and *Parupeneus barberinus*. Harvest guidelines based on Froese's (2004) criteria would protect most female *Cephalopholis cyanostigma* and all female *Parupeneus barberinus* (maximum female length = 21 cm FL). Thus an immediate increase in reproductive output would be seen if fishing practices changed. On the other hand, sex-ratio is approximately 1:1 in *Siganus lineatus*, and there is no significant difference in male and female size. Thus, fishing based on Froese's criteria does not preferentially protect females and our model does not indicate an immediate increase in reproductive output should be expected.

Our model does suggest future increases in reproductive output, however. Because no immature fish are harvested under Froese's criteria, there are more individuals available to join the mature segment of the population in the future. If we make the simplistic assumption that all fish grow 1 centimeter (and that current fishing patterns remain exactly the same), the population remaining after a second round of harvesting under current fishing practices would produce 96,291,039 eggs per spawning event, whereas when fished according to Froese's criteria, the same hypothetical population would produce 100,739,653 eggs. Our models suggest future benefits would be seen for *Cephalopholis cyanostigma* and *Parupeneus barberinus* as well, with 31,887 and 560,222 more eggs produced per spawning event, respectively, when fished according to Froese's criteria.

Given the apparent benefits of using Froese's criteria as fishing guidelines, we present those for the two species we could not model. A total 122 *Lutjanus semicinctus* harvested yielded 12.47 kg. Residents can obtain the same 12.47 kg by harvesting only 61 fish equally distributed among 21 – 24 cm Fl size classes and can satisfy the criteria of all individuals being mature and within 10% of L_{opt}. For all of the above species, guidelines insure individuals are at female L_{50} (or larger) before capture. However, we could not reliably estimate female L_{50} for *Lutjanus timorensis*. A total 120 *Lutjanus timorensis* harvested yielded 67.56 kg. Residents can obtain the same 67.56 kg by harvesting 113 fish equally distributed among 30 – 36 cm FL size classes. This size range is within 10% of L_{opt} (30 – 36 cm FL) and also insures individuals reach at least minimum size at maturity for females (L_m). We present this size range as a beginning guideline for sustainable fishing on *Lutjanus timorensis*, with the caveat that the lower size limit would probably be better aligned with female L_{50}, which our results suggest is almost certainly higher than L_m (Figure 14).

Fishery Surveys

Most of the size structure information presented above should be viewed as preliminary. For 68% of the species included in our laser-videogrammetry surveys, we captured too few individuals on video to describe population size structure or mean size changed with the addition of new specimens in 2011. For these species, additional data would lead to more robust population characterizations. For 18 species, there was no change in average length estimates between years. This suggests that our population characterizations are suitably robust for these species. We include *Caesio cuning*, *Caranx melampygus*, *Plectorhinchus lineatus*, *Myripristis adusta*, *Myripristis kuntee*, *Myripristis violacea*, *Myripristis vittata*, *Kyphosus cinerascens*, *Lutjanus biguttatus*, *Lutjanus boutton*, *Lutjanus fulvus*, *Lutjanus russelli*, *Parupeneus barberinus*, *Parupeneus multifasciatus*, *Parupeneus trifasciatus*, *Cephalopholis cyanostigma*, *Cephalopholis microprion*, and *Siganus lineatus* in this group.

Results from a literature review indicate that remarkably little is known about reproductive parameters for these coral reef fishes. In 2009, size at maturity was known for only 27% of species examined (Longenecker *et al*. 2009). In 2010, the number increased to 41% (Longenecker *et al*. 2010). In 2011, there was a slight increase to 42%. This small increase is a function of adding 16 species to our fishery surveys. This increase in species number diluted the impact of the rapid reproductive analyses we conducted for five (5) species in the present study. Thus, reproductive parameters continue to be unknown for nearly 60% of the exploited reef-associated fishes examined at Kamiali Wildlife Management Area. This lack of information is a common problem for coral-reef fisheries, even in developed countries; Longenecker *et al*. (2008a) report that size at maturity is unknown for 38% of the 13 most-heavily exploited reef fishes in Hawaii. It is impossible to evaluate the breeding status of a population or create biologically meaningful management strategies when this information is lacking.

Estimating the proportion of mature females in a population is further hindered by the scarcity of information on size-specific sex ratios. For six of 12 species for which sex ratios are known (Davis & West 1992, Ferreira 1995, Kritzer 2004, Longenecker & Langston 2008, Heupel *et al*. 2009, Longenecker *et al*. 2010, present study), data suggest the proportion of males in a population increases with length. The same trend would be expected for protogynous fishes (*e.g.*, Scaridae, Serranidae, and Labridae) and is seen in many groupers (Loubens 1980). Elsewhere in the Pacific the same pattern was found in each of three species examined (Longenecker & Langston 2008, Longenecker *et al*. 2008b) with a fourth species becoming increasingly female-biased with length (Langston *et al*. 2009). Because females can be absent from larger size classes of these species, the reproductive status of any population would be better understood if size-specific sex ratios are known.

Given the above caveats, a typical individual in the exploited reef-fish community at Kamiali Wildlife Management Area is 52% of its maximum length (the same value observed in 2010, Longenecker *et al*. 2010) and 84% of its estimated optimum length. In the subset of 14 species for which female L_{50} is known, a typical individual is 91% of female reproductive size (a decrease from our 2010 estimate of 104%, Longenecker *et al*. 2010). Notably, no individual of one of the largest species considered in this subset (*Plectropomus areolatus*), was of mature size. Considering sex ratios (known for only 12 species) suggests that approximately 25% of a population consists of reproductively mature females (an increase from our 2010 estimate of 20%, Longenecker *et al*. 2010). The interannual fluctuations in information relating to % mature females suggests more reproductive analysis is needed before robust statements about the reproductive status of exploited fish populations at KWMA can be made.

The above information (relative to maximum and optimum lengths) provides important baselines that can be used to detect future shifts in reef-fish populations. To give the same information immediate conservation relevance, it must be viewed in the context of the village's subsistence fishing needs. Longenecker *et al*. (2008c) reported an average of two canoes engaged in fishing at any one time during the day. Kamiali's approximately 600 residents appear to obtain their primary source of dietary protein with relative ease. We suggest this observation is evidence that overfishing is not occurring on the coral reefs of Kamiali Wildlife Management Area (with the possible exception of some larger-bodied species for which we rarely observed reproductively sized individuals). If our assertion is correct, average lengths of ½ the maximum size can be used as evidence of robust fish populations.

Despite the apparent lack of overfishing at Kamiali Wildlife Management Area, residents do not consider themselves practitioners of reef-fish conservation. Longenecker *et al*. (2009) report a lack of gear restrictions, creel limits, minimum or maximum size limits, or seasonal closures for any species. Nor are Kamiali residents prohibited from fishing in any part of the wildlife management area. Finally, because of severe barotrauma to fish caught by handline in deeper water (Longenecker *et al*. 2008c), small individuals are not returned to the water. In other words, life-history-based fishery management methods are not currently used at Kamiali. We suggest that such methods would be appropriate for the larger-bodied species for which reproductively sized individuals are rare; however sufficient life-history information must first be generated for those species.

Until the time that life-history-based management techniques can be enacted, we think preserving aspects of village life consistent with marine conservation will be the most effective way to promote robust fish populations. Several characteristics of the village and its fishery appear to reduce the risk of overfishing. The following is updated from Longenecker *et al*. (2009):

1) Customary tenure. Outsiders are prohibited from fishing within Kamiali Wildlife Management Area, making it a *de facto* limited-entry fishery.

2) Distance to commercial markets. Kamiali is 64 km from the city of Lae, the nearest place where fish can be sold commercially. Cinner & McClanahan (2006) suggest proximity to markets (<16 km) increases the likelihood of overfishing in Papua New Guinea. Commercial fishing in Kamiali presents an economic challenge. Because there are no roads, individuals selling fish must have a motorized vessel to transport fish to market. The cost of operating these is high; a liter of fuel can cost up to $2 (US). Based on our own travels to the village on these vessels, approximately 100 liters of fuel is used in a typical round trip, resulting in an overhead cost of about $200 (US) per commercial sale. Because there is no electrical service in Kamiali, ice must be purchased in Lae. Therefore, economic success in commercial fishing requires that a sufficient quantity of fish

3) Subsistence economy. Because cash is limited, technologies that may lead to fishery overexploitation are cost-prohibitive. Fishing is done primarily from small, human-powered, handmade, outrigger canoes (Longenecker *et al*. 2008c). Transportation to bottom-fishing sites and propulsion while trolling requires a significant input of human energy. Hook-and-line fishing with homemade handreels and weights, or handcrafted outriggers, is the dominant fishing technique. Two spearing methods are also used. Most common is aerial hand-launching of bamboo poles fitted with metal tines (Longenecker *et al*. 2008c). Catching fish by this method appears to be infrequent. Less common are homemade spearguns used while freediving. Because dive fins are not used, a depth refuge from spearing exists. Gillnets are rare, and we have not seen traps or weirs at Kamiali. Finally, lack of refrigeration reduces the motivation to catch more than can be used within a few days.

4) Plant-based diet. Although fish is the major source of dietary protein consumed by Kamiali residents, the majority of their calories are derived from fruits and vegetables grown in swidden gardens. Time spent fishing is limited by the need to conduct labor-intensive gardening.

5) Family and community obligations. As above, time spent fishing must be balanced against other time-intensive activities. These include building and repairing houses and canoes (both made from materials harvested from the surrounding forests), and attending community meetings.

6) Tidal cycles. Poison fishing is limited. The use of *Derris*, a native plant containing the non-selective ichthyocide rotenone, is limited to reef flats during lowest-low tides. This timing appears to be driven by the desire to maximize catch; extreme low tides create pools of still water where poison can be concentrated but fish cannot escape. Higher water during the majority of a lunar cycle effectively prohibits the method most of the time.

The factors listed above do not act in isolation. Distance to market is negatively related to the likelihood that a community will exclude outsiders from exploiting its marine environment. On the other hand, communities that subsist on marine resources may be more likely to exclude outsiders (Cinner 2005).

Ongoing and anticipated changes at Kamiali may threaten the sustainable use of its coral-reef fishes. The community is undergoing a transformation from a common-property system to a cash-based economy (Wagner 2002), and lower dependence on marine resources may reduce the likelihood that a community employs exclusionary marine tenure regimes (Cinner 2005). Cinner *et al*. (2007) indicate that customary management is at risk during economic modernization such as that underway at Kamiali Wildlife

Management Area. They suggest that marine conservation initiatives based on customary tenure are more likely to succeed if organizations help reduce the impact of socioeconomic transformations. The Kamiali Initiative, by establishing a pathway to economic development that is based on effective environmental conservation, is helping to maintain a traditional lifestyle as the village economy changes.

One way that science and customary marine tenure can be effectively combined is in a developing commercial fishery at KWMA. Kamiali residents have overcome economic barriers to commercial fishing by establishing fishing cooperatives. A few motorized-vessel owners transport to and sell at a commercial market the fish caught by a larger group. The majority of fishing at KWMA continues to be diffuse and low-technology, done from human-powered canoes with hand-made gear. However, all fish destined for commercial sale are, at some point, in the possession of one of a few vessel owners. This arrangement provides an excellent opportunity to monitor fish catch. Longenecker (2011) developed a community fish-monitoring program geared toward Kamiali's school students. However, the program was designed to be easily adapted to other situations. In the present case, measuring and recording fish lengths just before transport and sale represents an ideal way for village residents to monitor their catch and identify any undesirable changes in the same.

Continued conservation success at Kamiali will be sustained by information, such as that outlined above, necessary to make science-based environmental management decisions. Currently, one of the biggest information gaps at Kamiali and elsewhere in the Indo-Pacific is the scarcity of even the most-basic life history information for many reef-associated fishes. We suggest that more life history research is the most productive pathway to future reef-fish conservation at Kamiali Wildlife Management Area and throughout the extensive region where humans use coral reef fishes as the basis of their diet.

ACKNOWLEDGMENTS

An anonymous private foundation generously provided financial support for this study. Kassi Cole provided access to her histology laboratory to complete processing of *Siganus lineatus* gonads. We thank the residents of Kamiali for their hospitality, openness, and willingness to have their environment and fishing practices examined. We wish to extend thanks to the men, women, and children who participated in our specimen sampling program. Without them, we could not have conducted the reproductive analyses presented in this report.

LITERATURE CITED

Agger, P., O. Bagge, O. Hansen, E. Hoffman, M.J. Holder, G.L. Kesteven, H. Knudsen, D.F.S. Raitt, A. Saville, and T. Williams. 1974. Manual of fisheries science part 2 – methods of resource investigation and their application. FAO Fisheries Technical Paper T115 (Rev. 1). 255 pp.

Allen, G.R. 1985. FAO species catalogue. Vol. 6. Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date. FAO Fisheries Synopsis No. 125 Vol. 6. 208 pp.

Allen, G.R., and R. Swainston. 1993. *Reef Fishes of New Guinea: A Field Guide for Divers, Anglers and Naturalists*. Christensen Research Institute, Madang. 132 pp.

Anand, P.E.V., and N.G.K. Pillai. 2002. Reproductive biology of some common coral reef fishes of the Indian EEZ. Journal of the Marine Biological Association of India 44(1&2):122-135.

Anderson, Jr., W.D., and G.R. Allen. 2001. Lutjanidae: Snappers (jobfishes). Pp 2840-2918 *in* Carpenter, K.E., and V.H. Niem (eds). *FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 5. Bony Fishes Part 3 (Menidae to Pomacentridae)*. FAO, Rome.

Asoh, K, T. Yoshikawa and M. Kasuya. 2001. Gonadal development and non-functional protogyny in a coral-reef damselfish, *Dascyllus albisella* Gill. Journal of Fish Biology 58(6):1601-1616.

Carpenter, K.E. 1988. FAO species catalogue. Vol. 8. Fusilier fishes of the world. An annotated and illustrated catalogue of caesionid species known to date. FAO Fisheries Synopsis No. 125 Vol. 8. 75 pp.

Chan, T.T.C., and Y. Sadovy. 2002. Reproductive biology, age and growth in the chocolate hind, *Cephalopholis boenak* (Bloch, 1790), in Hong Kong. Marine and Freshwater Research 53:791-803.

Choat, J.H., and D.R. Robertson. 2002. Age-based studies on coral reef fishes. Pp 57-80 *in* P.F. Sale (ed). *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. Academic Press, San Diego.

Cinner, J.E. 2005. Socioeconomic factors influencing customary marine tenure in the Indo-Pacific. Ecology and Society 10(1):36.

Cinner, J.E., and T.R. McClanahan. 2006. Socioeconomic factors that lead to overfishing in small-scale coral reef fisheries of Papua New Guinea. Environmental Conservation 33(1):73-80.

Cinner, J.E., S.G. Sutton and T.G. Bond. 2007. Socioeconomic thresholds that affect use of customary fisheries management tools. Conservation Biology 21(6):1603-1611.

Cole, K.S. 2008. Assessment of reproductive status and reproductive output of three Hawaiian goatfish species, *Mulloidichthys flavolineatus* (yellowstripe goatfish), *M. vanicolensis* (yellowfin goatfish), and *Parupeneus porphyreus* (whitesaddle goatfish) (family Mullidae). DAR Dingel Johnson Grant Report for 2007-2008 Award. http://hawaii.gov/dlnr/dar/coral/pdfs/COLE%20FINAL%20REPORT%20JULY%2030%2008.pdf

Collette, B.B. and C.E. Nauen. 1983. FAO Species Catalogue. Vol. 2. Scombrids of the world. An annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date. FAO Fisheries Synopsis No. 125 Vol. 2. 137 p.

Davis, T.L.O., and G.J. West. 1993. Maturation, reproductive seasonality, fecundity, and spawning frequency in *Lutjanus vittus* (Quoy and Gaimard) from the North West Shelf of Australia. Fishery Bulletin 91:224-236.

Ferreira, B.P. 1995. Reproduction of the common coral trout *Plectropomus leopardus* (Serranidae : Epinephelinae) from the central and northern Great Barrier Reef, Australia. Bulletin of Marine Science 56(2):653-669.

Friedlander, A.M., J.D. Parrish and R.C. DeFelice. 2002. Ecology of the introduced snapper *Lutjanus kasmira* (Forsskal) in the reef fish assemblage of a Hawaiian Bay. Journal of Fish Biology 60:28-48.

Froese, R. 2004. Keep it simple: three indicators to deal with overfishing. Fish and Fisheries 5:86-91.

Froese, R., and C. Binohlan. 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. Journal of Fish Biology 56:758-773.

Froese, R., and D. Pauly (eds). 2011. FishBase. World Wide Web electronic publication. www.fishbase.org, version (10/2011). Accessed 10/2011.

Grandcourt E.M., T.Z. Al Abdessalaam, A.T. Al Shamsi and F. Francis. 2006. Biology and assessment of the painted sweetlips (*Diagramma pictum* (Thunberg, 1792)) and the spangled emperor (*Lethrinus nebulosus* (Forsskål)) in the southern Arabian Gulf. Fishery Bulletin 104:75-88.

Grandcourt E.M., T.Z. Al Abdessalaam, F. Francis and A.T. Al Shamsi. 2011. Reproductive biology and implications for management of the painted sweetlips *Diagramma pictum* in the southern Arabian Gulf. Journal of Fish Biology 79:615-632.

Hamilton, R.J., M. Matawai and T. Potuku. 2004. Spawning aggregations of coral reef fish in New Ireland and Manus Provinces, Papua New Guinea: Local knowledge field survey report. (UNRESTRICTED ACCESS VERSION). Report prepared for the Pacific Island Countries Coastal Marine Program, The Nature Conservancy. TNC Pacific Island Countries Report No. 4/04.

Heemstra P.C., and J.E. Randall. 1999. Serranidae: Groupers and sea basses (also, soapfishes, anthiines, etc.). Pp 2442-2548 *in* Carpenter, K.E., and V.H. Niem (eds). *FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 4. Bony Fishes Part 2 (Mugilidae to Carangidae)*. FAO, Rome.

Heemstra, P.C., and J.E. Randall. 1993. FAO species catalogue. Vol. 16. Groupers of the world (family Serranidae, subfamily Epinephelinae). An annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper and lyretail species known to date. FAO Fisheries Synopsis No. 125 Vol. 16. 382 pp.

Heupel, M.R., L.M. Currey, A.J. Williams, C.A. Simpendorfer, A.C. Ballagh and A.L. Penny. 2009. The comparative biology of lutjanid species on the Great Barrier Reef. Project Milestone Report. Report to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre Limited, Cairns. 30 pp.

Jehangeer, M.I. 2003 Some population parameters of the goatfish, *Mulloidichthys vanicolensis* from the lagoon of Maurituis. Pp 82-88. *in* M.L.D. Palomares, B. Samb, T. Diouf, J.M. Vakily and D. Pauly (eds). *Fish Biodiversity: Local Studies as Basis for Global Inferences*. ACP-EU Fisheries Research Report 14. 281pp.

Johannes, R.E. 1998. The case for data-less marine resource management: examples from tropical nearshore finfisheries. Trends in Ecology and Evolution. 13(6): 243-246.

Kritzer, J.P. 2002. Biology and management of small snappers on the Great Barrier Reef. Pp 66-84 *in* A.J. Williams, D.J. Welch, G. Muldoon, R. Marriott, J.P. Kritzer and S.A. Adams (eds). *Bridging the gap: A Workshop Linking Student Research with Fisheries Stakeholders*. CRC Reef Research Centre Technical Report #48. CRC Reef Research Centre, Townsville.

Kritzer, J.P. 2004. Sex-specific growth and mortality, spawning season, and female maturation of the stripey bass (*Lutjanus carponotatus*) on the Great Barrier Reef. Fishery Bulletin 102:94-107.

Langston, R., K. Longenecker, and J. Claisse. 2009. Growth, mortality and reproduction of kole, *Ctenochaetus strigosus*. Hawaii Biological Survey Contribution 2009-005. 25 pp.

Lewis, A.D., B.R. Smith and R.E. Kearney. 1974. Studies on tunas and baitfish in Papua New Guinea waters. Research Bulletin #11. Department of Agriculture, Stocks, and Fisheries, Port Moresby. 12 pp.

Longenecker, K. 2008. Relationships Between otolith- and body-size for Hawaiian reef fishes. Pacific Science 62(4):533-539.

Longenecker, K. 2011. Development and delivery of a school-based fishery-monitoring program for a remote village in Papua New Guinea. Bishop Museum Technical Report 53. 42 pp.

Longenecker, K., and R. Langston. 2008. A rapid, low-cost technique for describing the population structure of reef fishes. Hawaii Biological Survey Contribution 2008-002. 34 pp.

Longenecker, K., R. Langston and B. Barrett. 2008a. A compendium of life history information for some exploited Hawaiian reef fishes. Bishop Museum Technical Report 44. 67 pp.

Longenecker, K., R. Langston, and J. Eble. 2008b. Reproduction, growth, and mortality of manini, *Acanthurus triostegus sandvicensis*. Hawaii Biological Survey Contribution 2008-006. 23 pp.

Longenecker, K., A. Allison and H. Bolick. 2008c. A preliminary account of marine fish diversity and exploitation at Kamiali Wildlife Management Area, Papua New Guinea. Bishop Museum Technical Report 46. 116 pp.

Longenecker, K., A. Allison, H. Bolick, S. James, R. Langston, R. Pyle, D. Pence and S. Talbot. 2009. A preliminary assessment of exploited reef-fish populations at Kamiali Wildlife Management Area, Papua New Guinea. Bishop Museum Technical Report 49. 75 pp.

Longenecker, K, R Langston, H Bolick & A Allison. 2010. Population Size Structure and Rapid Reproductive Analysis of Exploited Reef-fish Populations at Kamiali Wildlife Management Area, Papua New Guinea. Bishop Museum Technical Report 52. 101 pp.

Loubens, G. 1980. *Biologie de quelques espèces de poisons du lagon néo-calédonien*. II. *Sexualité et reproduction*. Cahiers de l’Indo-pacifique II(1):41-72.

Mackie, M.C., Gaughan, D.J. and Buckworth, R.C. 2003 Stock assessment of narrow-barred Spanish mackerel (Scomberomorus commerson) in Western Australia. Final Report FRDC Project No. 1999/151. 242 pp.

Moss, J.W., S. Adams and D.J. Welch. 2002. Bommie cod, (*Cephalopholis cyanostigma*): a big surprise from a little fish. Pp 94-107 *in* A.J. Williams, D.J. Welch, G. Muldoon, R. Marriott, J.P. Kritzer and S.A. Adams (eds). *Bridging the gap: A Workshop Linking Student Research with Fisheries Stakeholders*. CRC Reef Research Centre Technical Report #48. CRC Reef Research Centre, Townsville.

Munro, J.L. and D. McB. Williams. 1985. Assessment and management of coral reef fisheries: biological, environmental and socio-economic aspects. Pp 543-578 *in Proceedings of the Fifth International Coral Reef Congress, Tahiti, 27 May-1 June 1985*. 4. Antenne Museum-EPHE, Moonea, French Polynesia.

Nagahama, Y. 1983. *The Functional Morphology of Teleost Gonads*. Fish Physiology, Academic Press. IXA:223-275.

Pakoa, K. 1998. Vital statistics of marine fishes of Vanuatu. Naga 21:27-29.

Randall, J.E. 2001. Mullidae: Goatfishes (surmullets). Pp 3175-3200 *in* Carpenter, K.E., and V.H. Niem (eds). *FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 5. Bony Fishes Part 3 (Menidae to Pomacentridae)*. FAO, Rome.

Randall, J.E., G.R. Allen and R.C. Steene. 1990. *Fishes of the Great Barrier Reef and Coral Sea*. University of Hawaii Press, Honolulu. 507 pp.

Rasband, W.S. 2009. ImageJ, National Institutes of Health, Bethesda, MD. http://rsb.info.nih.gov/ij/

Rhodes, K.L., and M.H. Tupper. 2007. Preliminary market-based analysis of the Pohnpei, Micronesia, grouper (Serranidae: Epinephelinae) fishery reveals unsustainable fishing practices. Coral Reefs 26:335-344.

Roberts, C.M., and N.V.C. Polunin. 1993. Marine reserves: simple solutions to managing complex fisheries? Ambio 22(6):363-368.

Russell, D.J., and A.J. McDougall. 2008. Reproductive biology of mangrove jack (*Lutjanus argentimaculatus*) in northeastern Queensland, Australia. New Zealand Journal of Marine and Freshwater Research 43(2):219-232.

Sadovy, Y., and D.Y. Shapiro. 1987. Criteria for the diagnosis of hermaphroditism in fishes. Copeia 1987:135-156.

Shakeel, H, and H Ahmed. 1996. Exploitation of reef resources: grouper and other food fishes. Pp 117-136 *in* Nickerson, D. J. and Maniku, M.H. (eds). *Report and Proceedings of the Maldives/FAO National Workshop on Integrated Reef Resources Management in the Maldives. Male, 16-20 March, 1996, Madras*. BOBP,Report No. 76. 250 pp.

Sheaves, M. 1995. Large lutjanid and serranid fishes in tropical estuaries: Are they adults or juveniles? Marine Ecology Progress Series. 129:31-40.

Sivadas, M., and A. Anasukoya. 2005. On the fishery and some aspects of the biology of dogtooth tuna, *Gymnosarda unicolor* (Ruppell) from Minicoy, Lakshadweep. Journal of the Marine Biological Association of India 47:111-113.

Sudekum, A.E., J.D. Parrish, R.L. Radke and S. Ralston. 1991. Life history and ecology of large jacks in undisturbed, shallow oceanic communities. Fishery Bulletin 89:493-513.

Thresher, R.E. 1984. *Reproduction in Reef Fishes*. T.F.H. Publications, Inc. Ltd., Neptune City, New Jersey. 399 pp.

Wagner, J. 2002. Commons in transition: an analysis of social and ecological change in a coastal rainforest environment in rural Papua New Guinea. PhD dissertation. McGill University, Montreal. 340 pp.

Wallace, R.A., and K. Sellman. 1981. Cellular and dynamic aspects of oocyte growth and maturation in teleosts. American Zoologist 21:325-343.

Woodland, D.J. 1990. Revision of the fish family Siganidae with descriptions of two new species and comments on distribution and biology. Indo-Pacific Fishes 19. 136 pp.

Woodland D.J. 2001. Siganidae: Rabbitfishes (spinefoots). Pp 3627-3650 *in* Carpenter, K.E., and V.H. Niem (eds). *FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 6. Bony Fishes Part 4 (Labridae to Latimeridae)*. FAO, Rome.