Southeast Florida reef fish abundance and biology: Five year performance report

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FIVE-YEAR PERFORMANCE REPORT

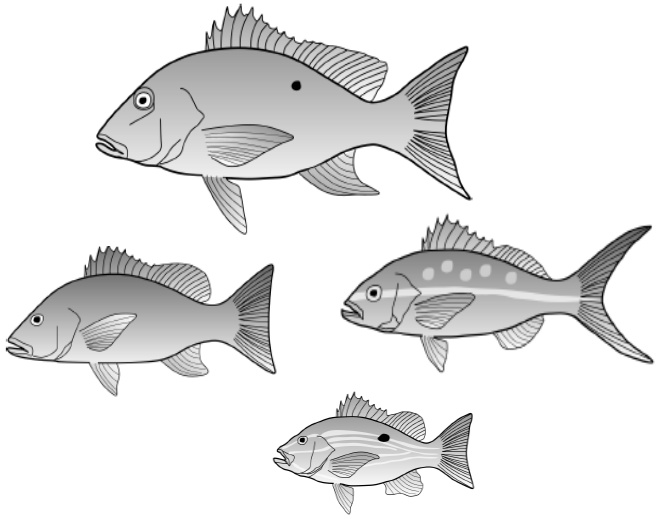
TO THE

U.S. DEPARTMENT OF INTERIOR
FISH AND WILDLIFE SERVICE

FROM THE

FLORIDA FISH AND WILDLIFE CONSERVATION COMMISSION
FLORIDA MARINE RESEARCH INSTITUTE

SOUTHEAST FLORIDA REEF FISH ABUNDANCE AND BIOLOGY



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PREFACE

SOUTHEAST FLORIDA REEF FISH ABUNDANCE AND BIOLOGY

This is an interim report on the first five years of an ongoing study of the biology, life history, and population dynamics of important reef fish in southeast Florida. This first phase of the grant included studies that focused on yellowtail snapper (*Ocyurus chrysurus*), gray snapper (*Lutjanus griseus*), mutton snapper (*L. analis*) and lane snapper (*L. synagris)*, all of which support important recreational (as well as commercial) reef fisheries in Florida. Studies on other species will be initiated in the future as additional species important to recreational reef fisheries in Florida are identified. Results presented in this report include manuscripts that have already been published as well as unpublished reports that address various project components (i.e., age and growth, reproduction, feeding habits, etc.). This report is organized in three main Sections: Section I includes the preliminary results of the study on age, growth, and reproduction of the four targeted snappers species listed above. Section II includes two separate studies on the feeding ecology of these same snapper species. Section III presents the results of the artificial reef monitoring program conducted in cooperation with Palm Beach County's Department of Environmental Resources Management.

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SECTION I – LIFE HISTORY

AGE, GROWTH AND REPRODUCTION OF RECREATIONALLY IMPORTANT SNAPPERS IN SOUTHEAST FLORIDA

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INTRODUCTION

Reef fishes of the snapper-grouper complex are among the most important commercial and recreational fisheries resources of the southeastern United States. This fish community consists of demersal tropical and subtropical species which generally occupy true coral reefs as well as "live-bottom" habitats and are caught by common fishing methods on continental shelf waters. Although the 1983 South Atlantic Fishery Management Council's snapper-grouper fishery management plan includes a total of 8 families, snappers (family Lutjanidae) and groupers (family Serranidae) are the most important in terms of number of species, desirability as food and sport fishes as well as in magnitude of catches. Along the Atlantic coast of the US, reef fisheries extend from Cape Hatteras, North Carolina to Key West, Florida, and consist of three major kinds of natural reef systems: (1) live-bottom reefs are scattered at depths of 20 to 100 m over the continental shelf from Cape Hatteras to Fort Pierce, Florida; (2) true hermatypic coral reefs become common south of Jupiter Inlet, Florida (26^{0}58' N) and occupy most of the narrow shelf south through the Florida Keys and Dry Tortugas; (3) deep shelf-edge and shelf-break reefs occur in a narrow band from about 100 to 250 m of depth throughout the region.

Important shallow-water (≤ 20 m) snapper fisheries—dominated by yellowtail, mutton and gray snappers—occur primarily in the true coral region of southeast Florida, where these species are the basis of important commercial and recreational fisheries. During the summer months these fisheries are particularly intense as they focus on large aggregations of fish that form along the outer reef tract. Most of the information on the reproductive biology of these species is either nonexistent, greatly outdated, or limited to the Gulf of Mexico and Caribbean. However, information on the spawning behavior of other lutjanids (e.g., lane snapper, *L. synagris,* and dog snapper, *Lutjanus jocu*) as well as preliminary data on the nocturnal occurrence of yellowtail, gray, and mutton snapper aggregations in southeast Florida suggest that the summer aggregations exploited by the fishery are spawning aggregations.

Spawning aggregations, because they are often persistent in time and space, are believed to be more susceptible to overexploitation. Although the damage caused by heavy fishing on these aggregations seem to be of particular concern for long-lived, hermaphroditic species like groupers, overfishing of shelf-edge spawning aggregations of mutton snapper has contributed to a major decline in landings and in some locations off Florida and Cuba, to a total collapse of the fishery. Data on the reproductive biology of yellowtail, gray, and mutton snappers, including information on the existence and temporal-spatial distribution of spawning aggregations, would greatly increase our ability to evaluate whether a similar problem might occur with these species in southeast Florida. Additionally, data on sex ratios, age- and size-specific maturity, and age- and size-specific fecundity would make it possible to estimate spawning potential ratios and, therefore, evaluate the effects of fishing on the egg production and spawning potential of these stocks.

Information on age and growth of snappers is also lacking for South Atlantic stocks. Although several studies have been conducted, the majority of samples were collected in the northeast Gulf of Mexico. Studies on age, growth, and mortality of gray snapper and lane snapper by Manooch and Matheson (1981) and Manooch and Mason (1984) covered the east coast of Florida. However, sampling was conducted 15-20 years ago (1978-1982) and may not be representative of current age and size compositions in this area. Results on age and growth of yellowtail, gray, lane, and mutton snappers generated by this study will fill this data gap and provide current information upon which to develop age-length keys, sex-specific growth parameters, and catch curve-based mortality estimates needed for stock assessment and rational management of these important reef species.

METHODS

Study Area

Southeast Florida contains a portion of reef habitat that spans the east coast of the United States from Cape Hatteras, North Carolina to Key West, Florida (Huntsman and Waters 1987). Providing structural shelter for many species of fish, and an abundant supply of food, reefs are home to a wide variety of both recreationally and commercially

important fish such as snapper (Alevizon and Bannerot 1990). The reef tract along this area, which lies on a north-south axis, is principally composed of live bottom and true coral habitat in depths of 20 m to 100 m. Live-bottom habitats are characterized by sedimentary rocks, with varying relief, covered by macro benthos such as sponges, sea fans, soft corals, and a small amount of hard corals (Huntsman and Waters 1987). True corals, or hermatypic reef-building corals, begin to appear around Jupiter Inlet (N 26^{o} 57') and continue south through the Florida Keys and Dry Tortugas (Huntsman and Waters 1987).

For the northern area (Tequesta) snapper collections were conducted in a 197 km^{2} area of the Atlantic Ocean off of Palm Beach and Martin Counties, Florida (Figure 1A). The northern boundary (N 27^{o} 05') and southern boundary (N 26^{o} 51') of the study area lie approximately between St. Lucie Inlet and Jupiter Inlet and between Jupiter Inlet and Lake Worth Inlet, respectively. The area north of Jupiter inlet is representative of the live bottom, rocky habitats typical of the northern region of southeast Florida. The area south of Jupiter inlet is characteristic of the coral reef habitats typical of the southern region of southeast Florida.

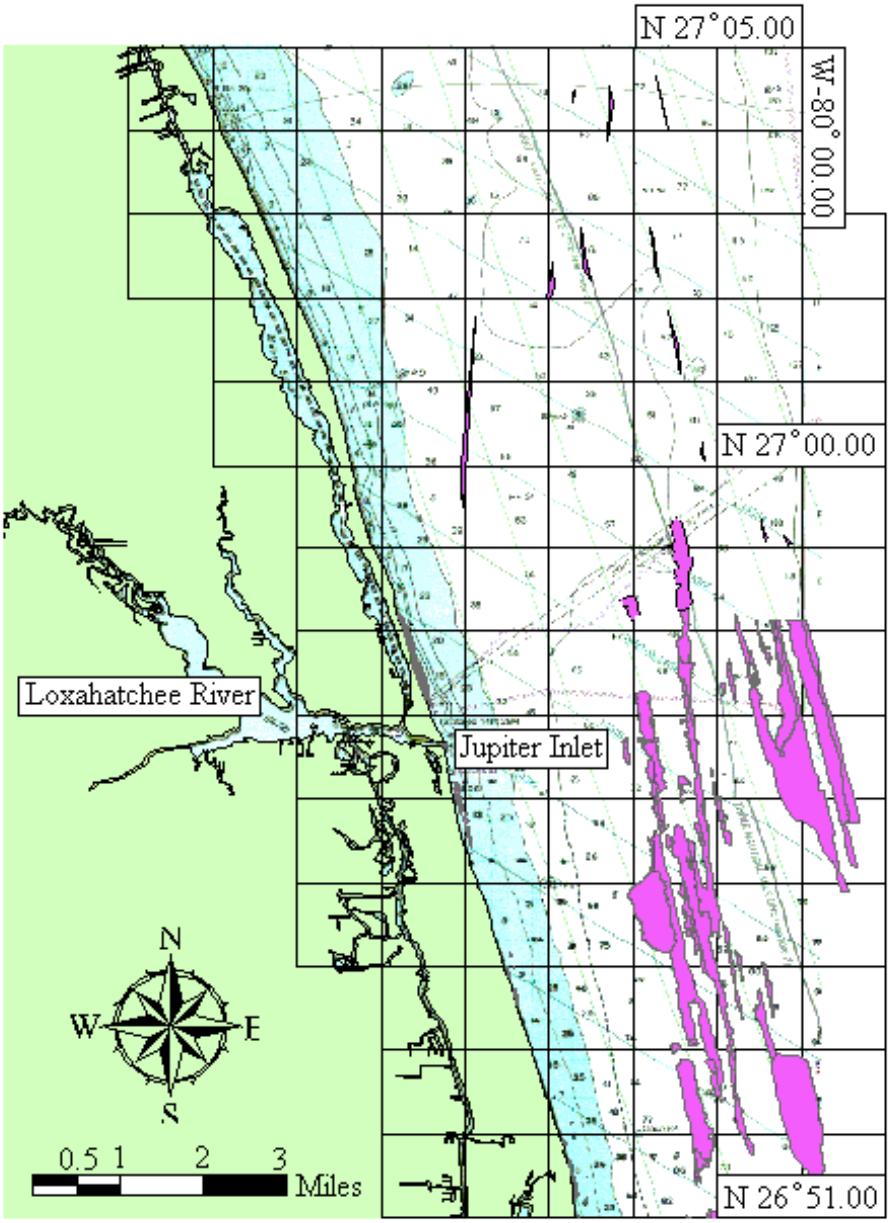

Figure 1A. Map of the area sampled in southeast Florida showing the 2.5 km^2 grids used for the stratified-random sampling program. Pink areas indicate hard bottom or structure. The northern-most portion of the eastern reef tract is not shown because mapping data were unavailable for that area.

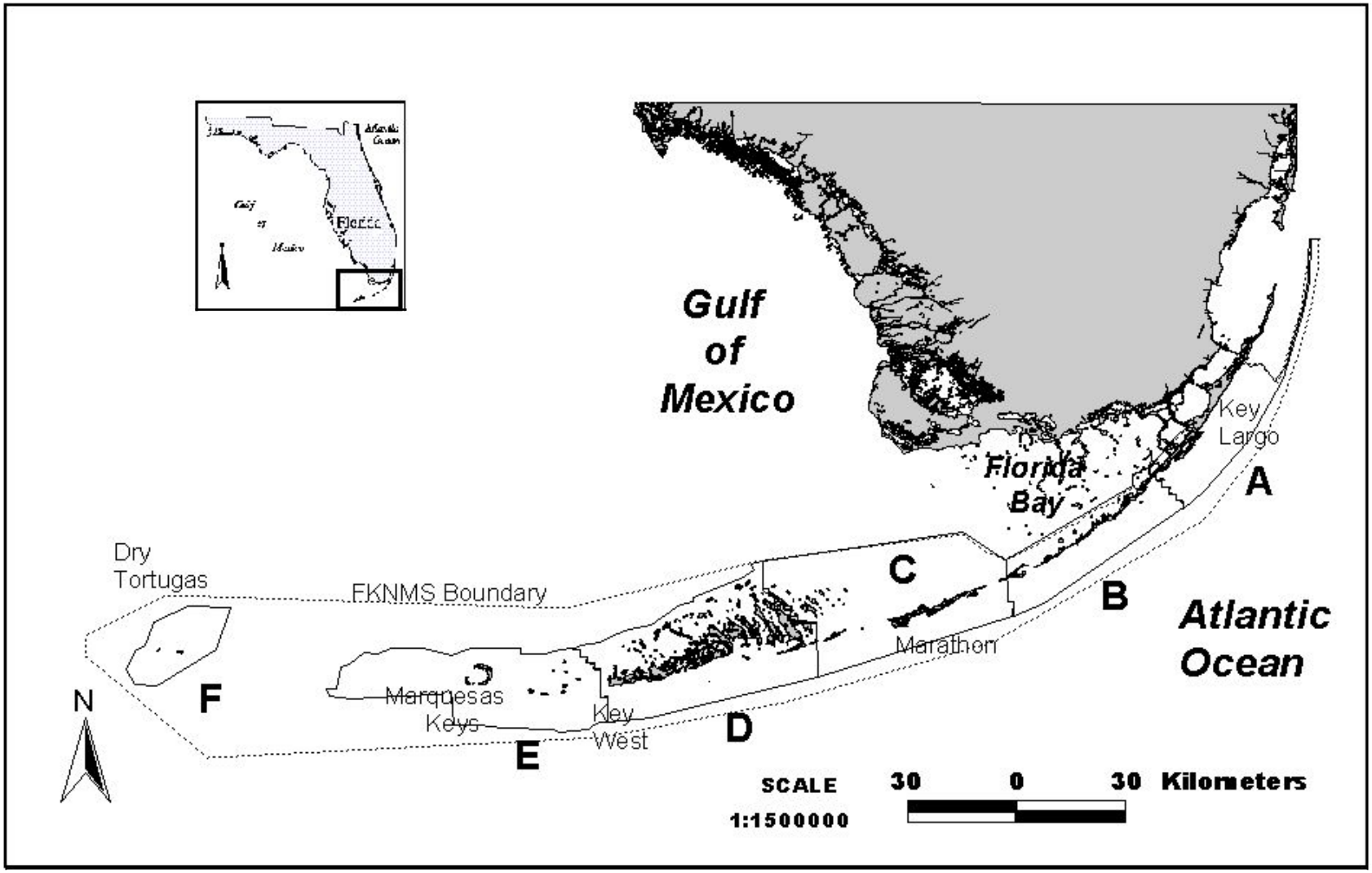

Figure 1B. Map of the sampling area in the Florida Keys National Marine Sanctuary.

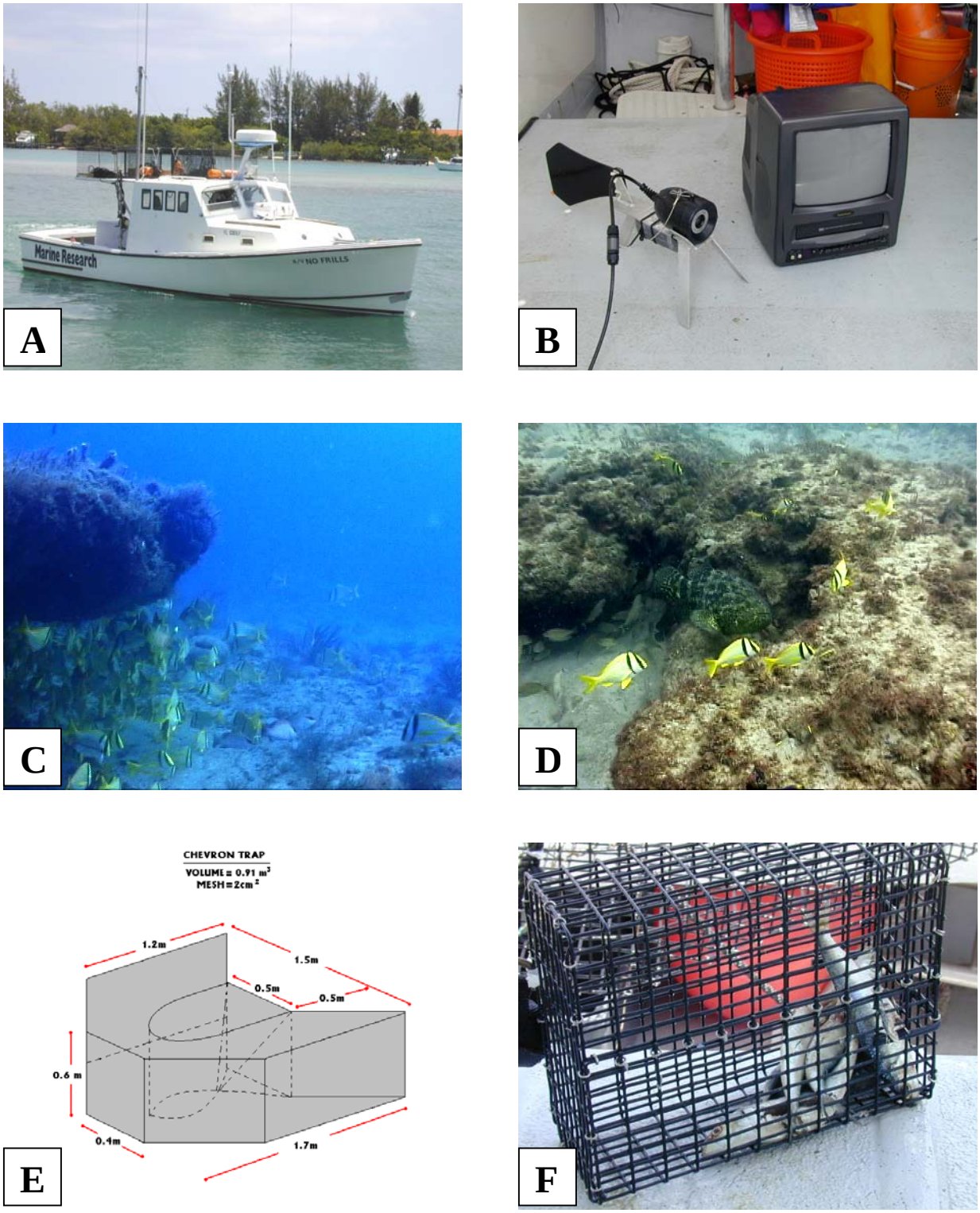

Figure 2. A. Research vessel *R/V No Frills*. B. Remote underwater video camera (SplashCam) and TV monitor. C. and D. Representative bottom type and fish assemblages recorded during pre-sampling uw survey with SplashCam. E. Chevron trap schematic. F. Bait cage used in conjunction with chevron trap deployment.

The eastern boundary (W 80^{o} 01') of the sampling area roughly corresponded to the 60 m depth contour, or the maximum suitable depth for sampling due to equipment limitations. Additionally, a sharp decline in snapper abundance is reported on reefs at depths greater than 30 m (Alevizon and Bannerot 1990). The western boundary was the east coast of Florida. The entire area or "zone" was divided into 2.5 km^2 grids, the boundaries of which fall on the latitude and longitude minute lines. Grids that were known to have only sand bottoms were eliminated from the sampling domain. The portions of reef tract covered in the study area included habitat typical of the areas where lane snapper fishery efforts are concentrated throughout southeast Florida.

In the Florida Keys region, collections were made within the Florida Keys National Marine Sanctuary (FKNMS). The FKNMS is one of the country's largest marine sanctuaries (9,500 km^2) and includes the only living barrier coral reef in the United States. The Florida Keys are a chain of limestone islands running to the south and then west from the tip of the Florida peninsula, extending from Key Biscayne, on the southeastern mainland coast, to the Dry Tortugas, over 360 km to the southwest. The coastal and marine areas adjacent to the Keys contain many mangrove islands and extensive seagrass meadows, while to the south and east is the Florida Reef Tract, the third largest barrier reef system in the world (Jaap 1984). Samples for the current project were collected from the reef tract, from patch reefs located between the reef tract and the Florida Keys, and from deep reef areas outside of the main reef tract at depths of 3-100 m in the area from Key Largo to the Marquesas Keys (Zones A-E in Fig. 1B). No collections were made from the Dry Tortugas region (Zone F). Samples were collected opportunistically from recreational and commercial fishers and by directed spearfishing and hook line collections made by project personnel.

Collection Methods

A stratified-random sampling program was employed to obtain samples for age and growth estimates (Figure 1A). Additional samples were obtained through fisheries dependent sampling and FMRI's fishery independent estuarine sampling program. These supplemental samples were used to aid in obtaining younger age classes and smaller sizes not yet available in reef habitat.

Stratified Random Sampling of Reef Habitat

A stratified-random sampling program utilizing chevron fish traps (Figure 3) and hook and line fishing gear was the primary source of specimens for this study. Collins (1990) compared multiple trap designs and determined that chevron traps were the most successful for capturing snappers. Traps were appropriate for this study because they present less bias for large fish than hook and line gear and thus include smaller individuals contributing to a more realistic representation of the lane snapper population. Hook-and-line fishing provides supplemental samples.

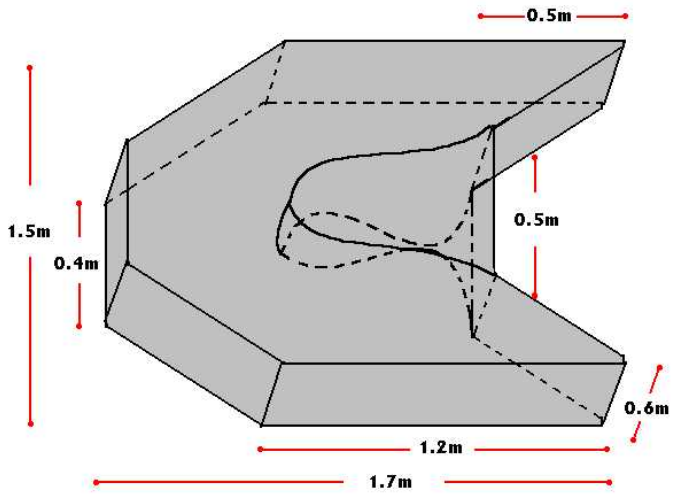

Figure 3. Detailed illustration of a chevron fish trap. The diagonal mesh size is 3.8cm.

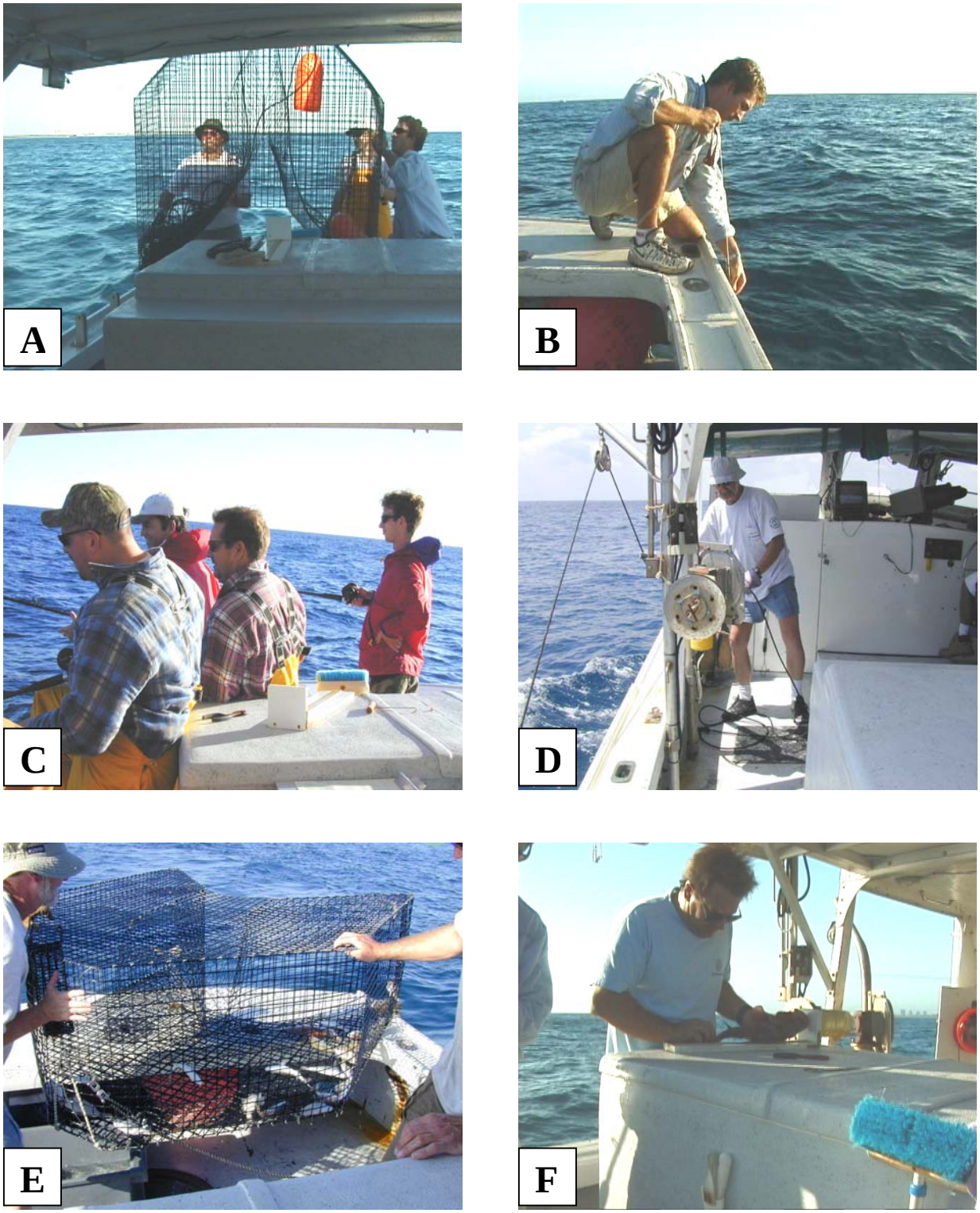

Figure 4. Chevron trap deployment. B. Environmental data collection (temperature, salinity, dissolved oxygen, visibility). C. Hook-and-line sampling during trap soak time. D. Chevron trap retrieval. E. Collecting specimens from trap. F. Measuring standard length of by-catch to be released.

The basic sample unit of the stratified-random sampling program was the catch from three traps soaked for at least 90 minutes in a randomly chosen grid, and fish captured by hook and line fishing while the traps soaked. Sampling occurred weekly from April 2000 to March 2002, unless a trip could not be made due to weather or boat mechanical problems. Two grids were sampled during each trip. Prior to the traps entering the water, the chosen grid was methodically searched with the depth finder and a remotely operated underwater video camera for deployment sites that would place the traps near live bottom or reef but would avoid damaging the habitat. Each trap was baited with six sardines and ¾ kg of menhaden chum. After the traps were deployed, multiple environmental parameters, which are not pertinent to this aging study, but may have use for future studies, were recorded. Date, time, latitude and longitude of each trap, and air temperature were measured in the field. Dissolved oxygen content of the seawater, salinity, and temperature were measured and recorded for the sea surface and bottom. Sea conditions and wind speed and direction were also estimated. Additional documented information included moon phase, times of sunrise and sunset, and tidal stage. The traps were retrieved and hook and line fishing ceased after a period of at least 90 minutes. All by-catch was counted, measured and released alive. All captured lane snapper were put into bags with tags indicating the time of day, location and method of capture, and were placed on ice and returned to the lab for later processing.

Fisheries-Dependent Sampling of Reef Habitat

Fishery-dependent lane snapper samples, obtained through the National Marine Fisheries Service (NMFS) headboat-monitoring program, were included to supplement fish numbers for age validation purposes. This ongoing program monitors the catches of headboats, which are chartered fishing vessels that carry six or more customers. Fish obtained from the 24 headboats between Miami and Ft. Pierce were weighed and measured at the dock. The gonads and otoliths were removed and placed in labeled plastic bags, put on ice, and taken to the lab to be processed. Headboats are restricted by recreational fishing limits and must release all lane snapper less than 200 mm. Information concerning the number and size of lane snapper released at sea was unavailable. Due to the potential bias for larger and older fish, these samples were not used for growth and mortality estimates.

Fishery-Independent Sampling of Estuarine Habitat

Small fish were necessary to determine the nature of the appearance of the first annulus as well for estimating the size and age at first sexual maturity. However, the stratified-random sampling gear and vessel were difficult to operate in the shallow estuarine areas. Additionally, the smaller fish are too small to be retained by the mesh of the chevron traps. Estuarine samples were provided by FMRI's Fisheries-Independent Monitoring Program (FIM), which uses a 183-m bag seine with a 2-cm mesh to monitor species diversity in the Indian River Lagoon and the Loxahatchee Estuary. The seine is used to randomly collect samples in the estuaries between Jupiter Inlet (N 26^{o} 57') and North Vero Beach (N 27^{o} 39'). Samples are obtained weekly from randomly selected, near-shore sample sites with depths less than or equal to 2.5 m of water. A random selection of the target snapper species sampled after each seine haul were placed in labeled plastic bags, put on ice, and returned whole to the laboratory for processing.

Figure 5. A. *In situ* workup during lane snapper diel periodicity event. B. Mutton snappers to be worked up in lab. C. Weight and length data being collected from target specimens. D. Otolith removal from lane snapper. E. Lobe of lane snapper ovary. F. Data analysis.

Laboratory Processing

All fish were processed so that their otoliths and a representative sample of their reproductive organs were preserved and cataloged. A number was assigned to each fish that cross-referenced otoliths, otolith slides, histology samples, histology slides, and all information pertaining to that fish in an Access® database. All fish were measured for total length (TL) and standard length (SL) to the nearest mm, weighed for total weight (TW) to the nearest g and gonad weight (GW) to the nearest 0.1 g, sexed, and both otoliths (sagittae) removed, cleaned, and stored dry. The gonadosomatic index (GSI) was calculated for individual fish as:

$$GSI = (GW/(TW-GW)* 100)$$

Males were classified as sexually mature or immature. Females were assigned a gonad maturity stage based on macroscopic and microscopic criteria as described in Table 1. Whenever possible, the time of day each fish is collected was recorded to help evaluate the temporal occurrence of certain ovarian stages (e.g., gravid, running-ripe, and partially spent) and help determine the diel periodicity of spawning (Barbieri et al. 1994, Lowerre-Barbieri et al. 1996). An ovarian sample for histological analysis was taken from all females. For histological preparation, tissue samples were embedded in glycol-methacrylate, sectioned, stained with PAS/iron-hematoxylin, and counter-stained with metanil yellow by the Florida Marine Research Institute's histology lab staff (Quintero-Hunter et al. 1991). Histological classification of ovaries was based on the occurrence and relative abundance of six stages of oocyte development (primary growth, cortical alveoli, partially yolked, advanced yolked, final oocyte maturation (FOM) and hydrated), and on the occurrence and intensity of alpha (α) and beta (β) atresia. Terminology for stages of oocyte development and ovarian atresia will follow Wallace and Selman (1981), Hunter and Macewicz (1985) and Hunter et al. (1992).

To estimate mean length at first maturity (L_{50}) for males and females, the fraction of mature fish per 10 mm length intervals was fit to the logistic function by nonlinear regression (Marquardt method), using SAS (Statistical Analysis System version 8.0®). L_{50} (the mean size at first sexual maturity) was defined as the smallest length interval in which 50% of the individuals were sexually mature. Females were considered sexually mature if they were in gonad stages 2 (developing) or higher (Table 1). However, to avoid classifying resting (reproductively inactive) or early developing fish as immature, and thus getting biased estimates of L_{50}, only fish collected during the spawning season, when no resting or developing stages were found, were used for this analysis.

Because snappers are reported as being multiple (i.e., batch) spawners (Thresher 1984, Grimes 1987, Sadovy 1996), size- and age-specific fecundity were based on estimates of batch fecundity and spawning frequency. Batch fecundity will be estimated gravimetrically using the hydrated oocyte method (Hunter et al. 1985). Spawning frequency will be estimated using the postovulatory method and/or the percent hydrated method (Hunter and Macewicz 1985). Relationships of fecundity as a function of length, weight, and age will be developed using regression analysis.

Table 1. Description of ovarian developmental stages for gonochoristic multiple spawning fish. Macroscopic appearance refers to fresh ovaries. FOM = final oocyte maturation; POF's = postovulatory follicles (Modified from Barbieri et al. 1994 and Lowerre-Barbieri et al. 1996).

Stage	Macroscopic Appearance	Microscopic Appearance
1 - Immature	Ovaries very small, translucent, ribbon-like.	Only primary growth oocytes present; no atresia; ovarian membrane thin.
2 - Developing	Ovaries ranging from small to medium (≤ 25% of body cavity); light orange in color; no opaque (advanced yolked) oocytes present.	Mainly primary growth and cortical alveoli oocytes. A few partially yolked oocytes may be also present. There might be some atresia.
3 - Fully developed / Partially spent / Redeveloping	Ovaries ranging from medium (25-50% of body cavity) to large (50-75% of body cavity); pale (creamy) yellow to orange in color; opaque oocytes prevalent and easily detected; if partially spent, may have a 'ridge' (a red area along the dorsal ovarian edge) and some left-over clear (hydrated) oocytes may be present at the posterior end of the ovarian lumen.	Primary growth to advanced yolked oocytes present; may have some left-over hydrated oocytes and POFs from previous spawning; might have atresia of advanced yolked oocytes, but no major atresia of other oocytes.
4 - Gravid	Ovaries ranging from medium to very large (25-100% of body cavity); clear (hydrated) oocytes visible amongst opaque oocytes, giving a speckled appearance; late in season, ovaries may be smaller and reddish due to an increase in the ratio of clear to opaque oocytes and ovarian vascularization.	Primary growth to FOM/hydrated oocytes present; might have atresia of advanced yolked oocytes; hydrated oocytes unovulated. Remnant hydrated oocytes from a previous spawn or degenerating POFs may be present.
5 - Running-ripe	Ovaries ranging from medium to large (25-75% of body cavity); clear oocytes have been ovulated and are visible as a collective clear strip amongst the yolked oocytes; some may have been extruded; occasionally no opaque oocytes present.	Primary growth to ovulated, hydrated oocytes and POFs present; might have atresia of advanced yolked oocytes; occasionally only hydrated and primary growth oocytes present.
6 - Regressing	Ovaries quite flaccid and small (< 20% of body cavity); mustard yellow to orange, occasionally maroon; often contain clear fluid; can detect a few opaque oocytes.	Primary growth to advanced yolked oocytes present; however, major atresia of partially yolked and advanced yolked oocytes. May have remnant hydrated oocytes or degenerating POFs.
7 - Resting	Ovaries very small; dark orange to maroon in color; no opaque oocytes present; ovarian membrane thickened and more opaque than immature fish.	Most oocytes (> 90%) are primary growth; may have other oocytes in late stages of atresia; more follicular tissues than immature fish.

Otolith Removal and Storage

Sagittal otoliths were removed by pushing open the operculum, removing the gills, and opening the optic bulla with a wood chisel or an oyster shucker (Manooch and Matheson 1981). Forceps were used to gently remove the otoliths (Figure 6). Prior to storage, otoliths were rinsed with tap water to remove tissue and blood and wiped clean with a paper towel. They were placed dry into labeled 20 ml scintillation vials. The otoliths remained in the vials until they were sectioned.

Figure 6. Left sagittal otolith being removed from a lane snapper.

Otolith Sectioning and Mounting

Aging was performed using transverse otolith sections (Manooch and Matheson 1981, Johnson 1983) (Figure 4). All otoliths from the left side of the head (unless only the right otolith was available due to mishandling) were sectioned through the core using a Buehler low-speed Isomet saw. Sections were cut approximately 350 to 500 μm thick and mounted on glass slides with Flo-texx clear mounting medium. The slide labels corresponded to the fish identification numbers in the database. Otolith sectioning was performed at the Florida Marine Research Institute's Otolith Laboratory in St. Petersburg, Florida.

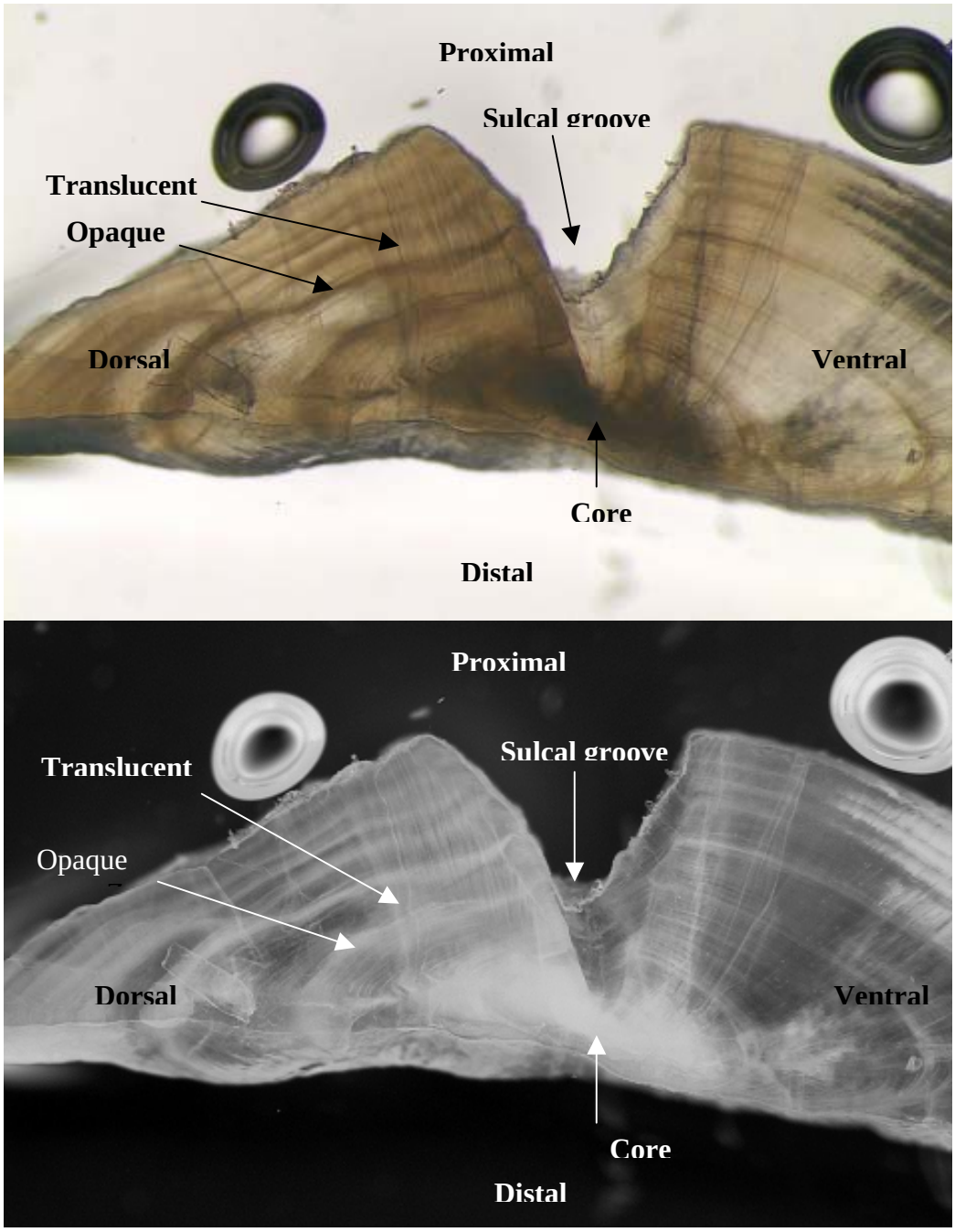

Figure 7. Transverse section through the core of the sagittal otolith of a seven-year- old gray snapper (*Lutjanus griseus)* collected in August 2001. The top image was taken with transmitted light; the bottom image was taken with reflected light. Magnification is 2.5×

Age Assignment

Some difficulties arise in aging sub-tropical fish due to environmental and biological factors that can cause the otoliths to have faint and difficult to interpret annuli (Manooch 1987). Annuli can only be identified when the change in calcium deposition in the otolith is great enough that it creates a zone with a greater optical density than the neighboring zone, thus creating the visual appearance of "rings" (Mina 1968). Changes in water temperature affect growth and the calcium deposition in the otoliths. In the tropics and sub-tropics, water temperatures are often uniform year round and great variations of calcium deposition do not occur in the otoliths (Pannella 1980, Manooch 1987).

Ages were assigned following the method described by Jearld (1983), which assigns an arbitrary birth date of January 1st. This method was chosen because the biological birth date coincides with the time of annulus deposition (summer) and thus may have caused inaccurate ages to be assigned. Ages were assigned by counting opaque annuli along the dorsal edge of the sulcus acousticus where marks appear much darker than on the ventral edge (Figure 4). A fish captured after January 1st, with a large translucent band on the margin would be assigned one age-class higher than the counted number of annuli (Figure 5). Fish with a translucent margin captured during or after the annulus deposition period had an age equivalent to the number of annuli. A fish with any opaqueness on its margin had an age equal to the number of annuli, counting the opaque margin as an annulus (Figure 6).

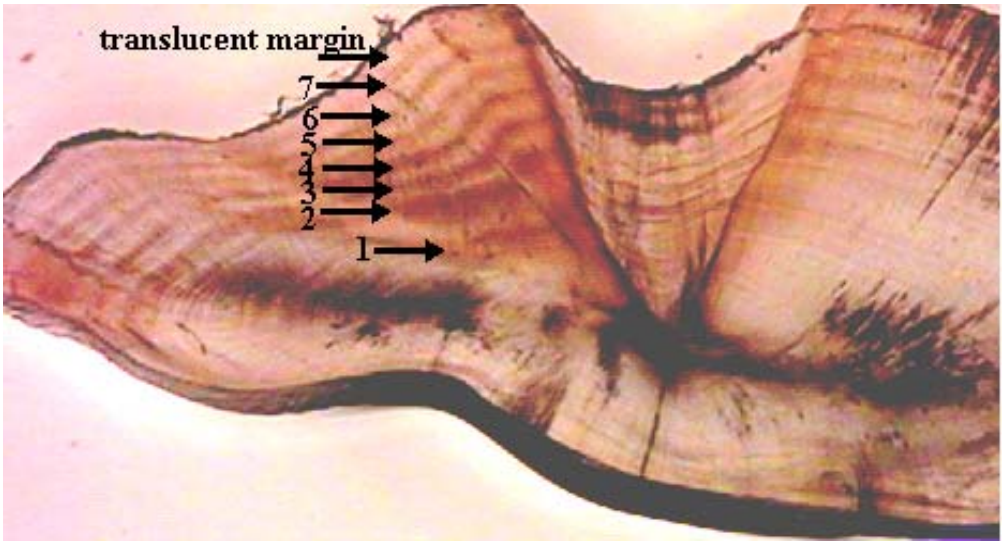

Figure 8. Transverse section through the core of an 8-year-old lane snapper sagittal otolith shown under transmitted light. The fish was captured after the arbitrary birth date in January 2000 and has 7 annuli.

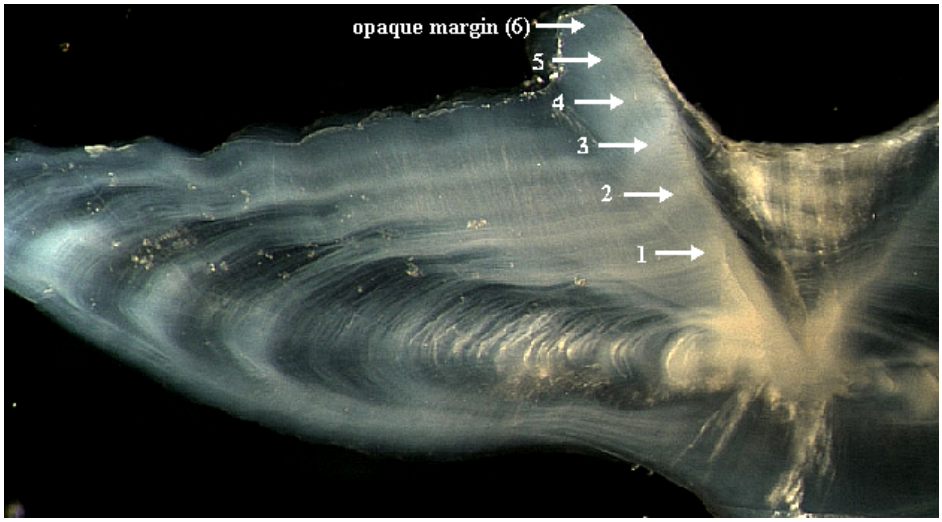

Figure 9. Transverse section through the core of a 6-year-old lane snapper sagittal otolith shown under reflected light. The fish was captured in June 2000 and has 6 annuli.

"Checks" or "false annuli" occasionally form between annuli and may be positioned so that they appear to be annuli (Manooch, 1987). All of the otolith sections were examined before an age was assigned so that a set of criteria for defining checks could be established. Checks, while not well understood, may be the result of reproductive activity or significant changes in diet or habitat.

To obtain the correct age of a fish, it is imperative that the first annulus be accurately identified. All of the snapper species studied have an extended spawning season (usually from April through August), allowing fish of the same year to experience different growth scenarios by the time they reach their first season of annulus deposition. Differences in growth of young-of-the-year fish cause great variation in the appearance of the first annulus. Examining otoliths from fish known to be young-of-the-year illuminated patterns of placement of the first annulus, as well as revealing that frequently there is a mark that forms near the core prior to deposition of the first annulus. To assist in identifying the location of the first annulus, measurements were made from the center of the core to the outside edge of the opaque area of the first annulus and to the pre-first annulus mark. Only otoliths with well-defined annuli and good core cuts were used for measurements.

The otolith slides were read with a Leica® MZ8 stereomicroscope. Magnification, light levels, and the light source were adjusted for every slide to provide maximum illumination of the annuli. An *Optimus*® Imaging System and an *Image Pro*® Imaging System were used as aids to display images for discussion, to measure distances, and to capture still images. All of the slides were examined to determine the nature of the appearance of the annuli and criteria were set to define annuli and checks based on these observations. Upon establishing aging criteria, the annual marks were counted and

recorded for each fish, unless the otolith was unable to be read due to poor slide preparation or unclear annuli.

Age Validation

Validation is the process that identifies the temporal frequency of annulus deposition (Geffen 1992), and is essential to properly calibrate an aging study (Beamish and McFarlane 1983). Several methods of validation are common including length frequency analysis, examination of fish known age through tagging or captive studies, comparison of multiple aging structures, and marginal increment analysis (Jearld 1983). Due to the great variations in lengths, limited resources for tagging or holding fish captive, and poor success of aging snapper with other structures such as scales (e.g., Reshetnikov and Claro 1976), marginal increment analysis was the most appropriate method of age validation for this study.

Marginal increment analysis was performed by examining the appearance of the outer margins of otolith cross-sections from fish captured over the period of an entire year (Williams and Bedford 1974). An otolith margin that was opaque indicated that annulus deposition was in progress at the time of capture. Graphing the presence or absence of opaque bands on the margins revealed the frequency and timing of annulus deposition for each snapper species.

Aging Precision

Precision is a measure of reproducibility. Each otolith was read twice by two independent readers. Precision, based on the method described by Beamish and Fournier (1981), was estimated between the two reads. Ages that differed between the two reads or between the two readers were re-evaluated and a final age was established. If a final age could not be determined with confidence, the otolith was removed from the data set.

Length and Weight Relationships

Relationships between length and weight were determined and reported so that unavailable length or weight information from a fish can be estimated from available length or weight information. Total length and standard length relationships were determined by linear regression. The relationships between total length and total weight and standard length and total weight were determined by log transforming the data and performing a linear regression. Differences between sexes were tested by Analysis of Covariance (ANCOVA) using SAS (Statistical Analysis System version 8.0®). If no differences between sexes were found, data were pooled. Rejection of the null hypothesis in statistical testes was based on α=0.05. F-tests in ANVOVA were based on Type III sums of squares (Freund and Littell 1986). Assumptions of linear models were checked by residual plots as described in Draper and Smith (1981).

Growth Estimates

Growth parameters were estimated using the von Bertalanffy growth model. Use of this model is advantageous because it is easily incorporated into stock assessment models. Fitting growth curves to observed age-length data allows the creation of mathematical expressions that give the length of a fish at any given age, thus showing the growth over a given period of time (Gulland 1983). Observed lengths at age were fit to the von Bertalanffy growth model:

$$L_t = L_\infty (1 - e^{-K(t-to)})$$

with nonlinear regression using SAS version 8.0® and the Marquadt Method (Ricker 1975). Model parameters as described by Ricker (1975) are:

L_t = fish length
t = age (years)
L_∞ = mean asymptotic total length
K = the Brody growth coefficient
t_0 = hypothetical age at which fish would have 0 mm length

Mortality Estimates

Total instantaneous mortality (*Z*) is an estimate of the proportion of fish lost from a cohort each year due to natural mortality (*M*, which is due to factors such as predation, disease, etc.) and fishing mortality (*F*). Mortality over a year varies greatly. Catch curve analysis considers the rate of mortality by comparing fish cohorts that are one year apart and that are captured at approximately the same time. The total decline of abundance between the two years reflects the proportion of mortality over the year and encompasses variations that occur during the 12-month period. Total instantaneous mortality (*Z*) was estimated by calculating the slope of the regression of the catch curve as described in Ricker (1975) and Gulland (1983):

$$N_t = N_o e^{-z t}$$

where: N_t = number of fish at age t

N_o = number of fish at age 0
t = age (years)

Actual total mortality (*A*) rate, which estimates the total percent of loss from the population during the given time period was estimated by the relationship $A = 1 - e^{-z}$.

RESULTS

Numbers and Sizes of Fish Sampled

A total of 6,869 snappers were sampled from both sampling areas (i.e., Tequesta and Florida Keys) during the course of this study. A breakdown of the sample sizes for each species by area sampled is presented in Table 2. A summary of the size distribution for each species by area is presented in Table 3 and in Figures 10-13 below.

Table 2. Numbers of snappers collected in each sampling area for life history and population dynamics studies conducted during Sport Fish Restoration Grant F-73.

Species Sampled	Tequesta	Florida Keys	Totals
Gray snapper	1,083	979	2,062
Lane snapper	1,508	734	2,242
Mutton snapper	634	298	932
Yellowtail snapper	972	661	1633
Totals	4,197	2,672	6,869

Table 3. A summary of the sizes of snappers collected in each sampling area for life history and population dynamics studies conducted during Sport Fish Restoration Grant F-73.

Species	Location	Mean TL (mm)	Min. TL (mm)	Max. TL (mm)
Gray snapper	FL Keys	358	141	606
	Tequesta	291	71	670
Lane snapper	FL Keys	220	85	368
	Tequesta	252	104	450
Mutton snapper	FL Keys	472	190	820
	Tequesta	390	99	815
Yellowtail snapper	FL Keys	358	176	649
	Tequesta	347	127	603

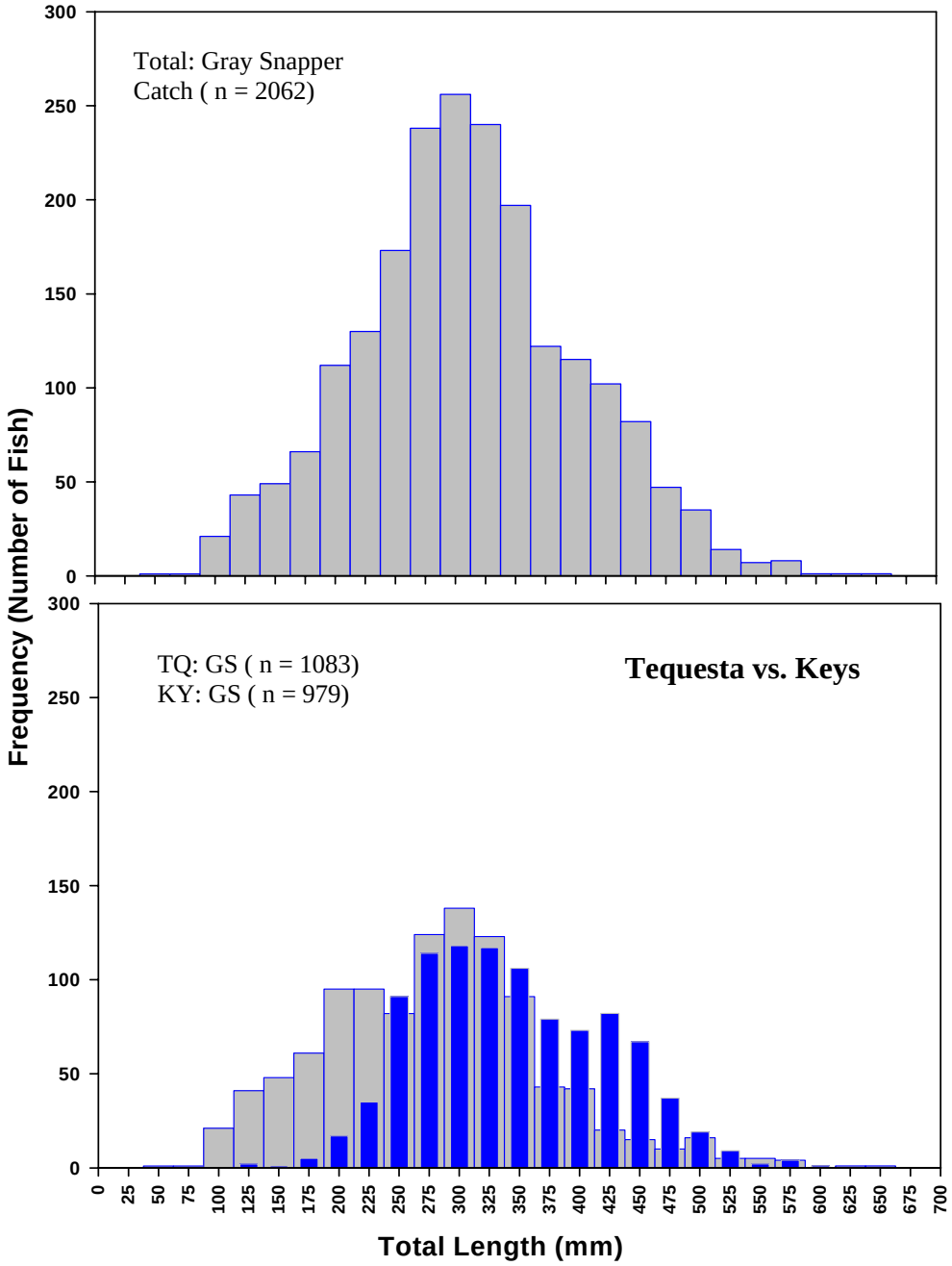

Figure 10. Length frequency distribution for all gray snapper sampled during this study (top graph) and length frequency distributions by area sampled (bottom graph).

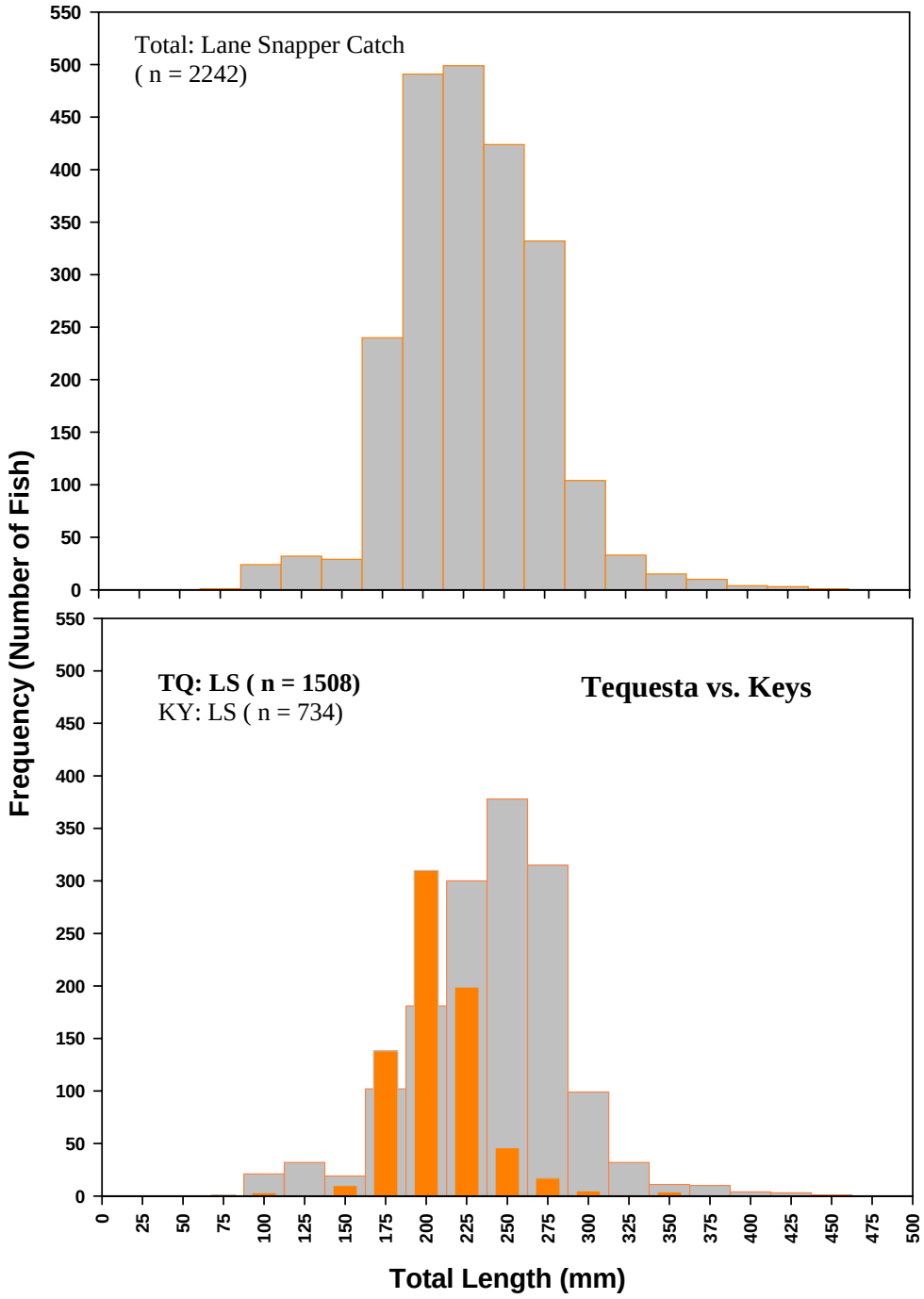

Figure 11. Length frequency distribution for all lane snapper sampled during this study (top graph) and length frequency distributions by area sampled (bottom graph).

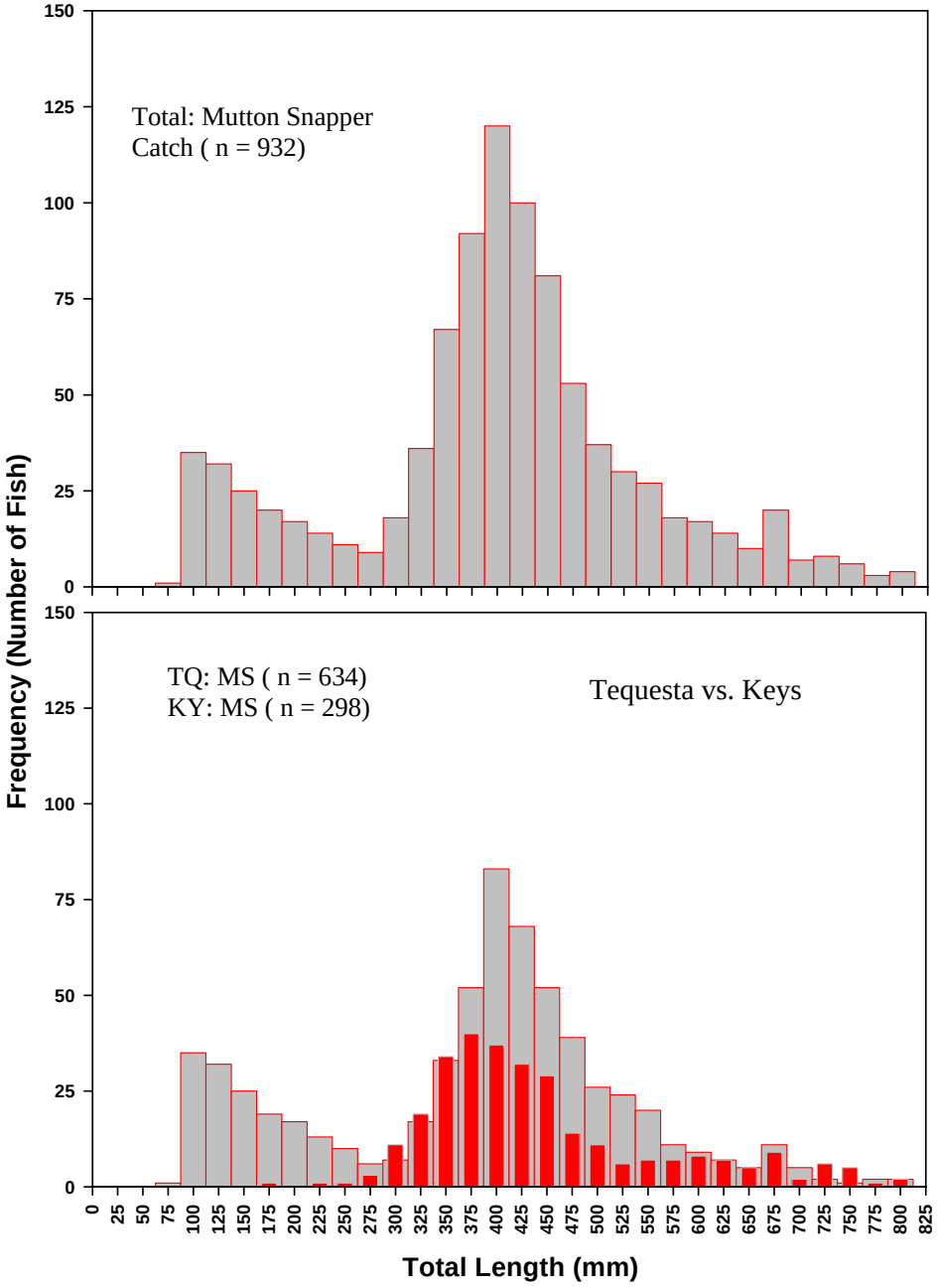

Figure 12. Length frequency distribution for all mutton snapper sampled during this study (top graph) and length frequency distributions by area sampled (bottom graph).

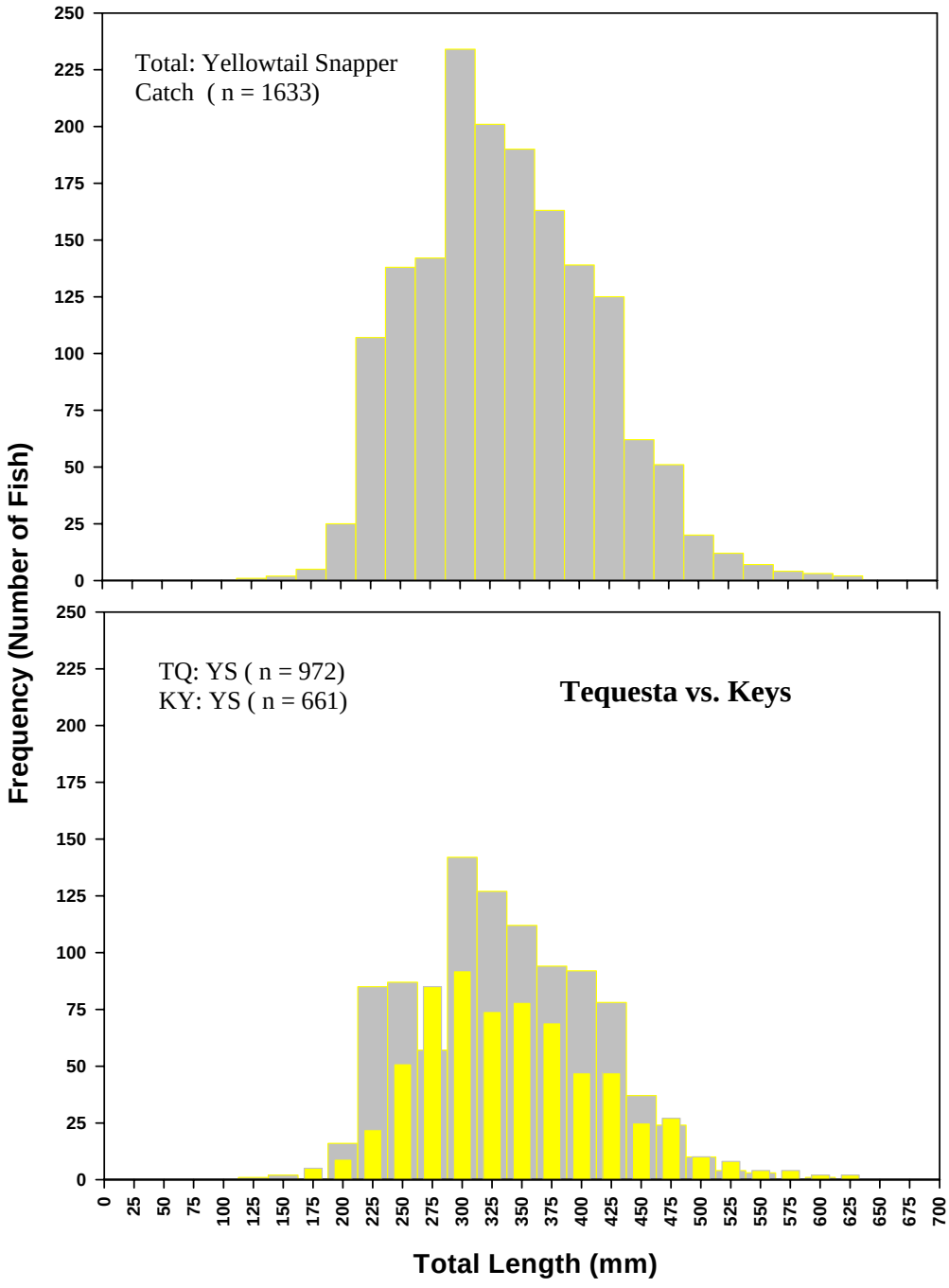

Figure 13. Length frequency distribution for all yellowtail snapper sampled during this study (top graph) and length frequency distributions by area sampled (bottom graph).

Age Determination

Despite some variability among species, transverse otolith sections for all four snapper species showed clear, easily identified marks that can be used for ageing. Typical sections have an opaque core followed by an alternating pattern of narrow opaque bands (the annuli) and wider translucent bands outside the proximal margin of the core. For most species annuli were more clearly defined and easier to identify along the dorsal side of the sulcus acousticus (Figures 14-17). All four species, but particularly lane and mutton snappers, showed two dominant patterns of first annulus deposition. A well-defined band separated from the core by a translucent area is the most common first annulus deposition pattern (Figure 18; bottom panel). Occasionally, the first annulus may be a blurred band, continuous with the core (Figure 18; top panel).

Checks or false annuli were rare for most of the snapper species studied, but occurred in 18% of lane snapper otoliths aged. The majority of all the checks (about 84%) occurred between the first and the second annuli. Most of the checks were thinner and fainter relative to the other annuli in addition to meeting other criteria. Of the 237 lane snapper otoliths excluded from the study, 52% were deemed unreadable because checks could not be distinguished from annuli (Figure 19).

Growth

Body-Size Relationships

Length and weight relationships were estimated to allow predictions of weight or length to be made if fish were missing measurements and to evaluate the hypothesis of isometric growth. Table 4 below shows the TL-SL equations that were derived for individual snapper species. No differences in TL-SL relationships were found between males and females, therefore, the equations below represent data pooled for both sexes. All four species showed a strong linear relationship between total length (TL) and standard length (SL) indicating that values from one variable can confidently be predicted from the other (Figures 20-23).

Table 4. Total length (TL) to standard length (SL) relationships for snappers captured in southeast Florida and the Florida Keys. Sexes are pooled.

Species	n	Equation	r^2	P-value
Gray	2073	SL = -3.48 + 0.79 TL	0.99	P<0.0001
Lane	2285	SL = -3.98 + 0.79 TL	0.99	P<0.0001
Mutton	977	SL = -5.54 + 0.79 TL	0.98	P<0.0001
Yellowtail	1610	SL = 4.52 + 0.69 TL	0.96	P<0.0001

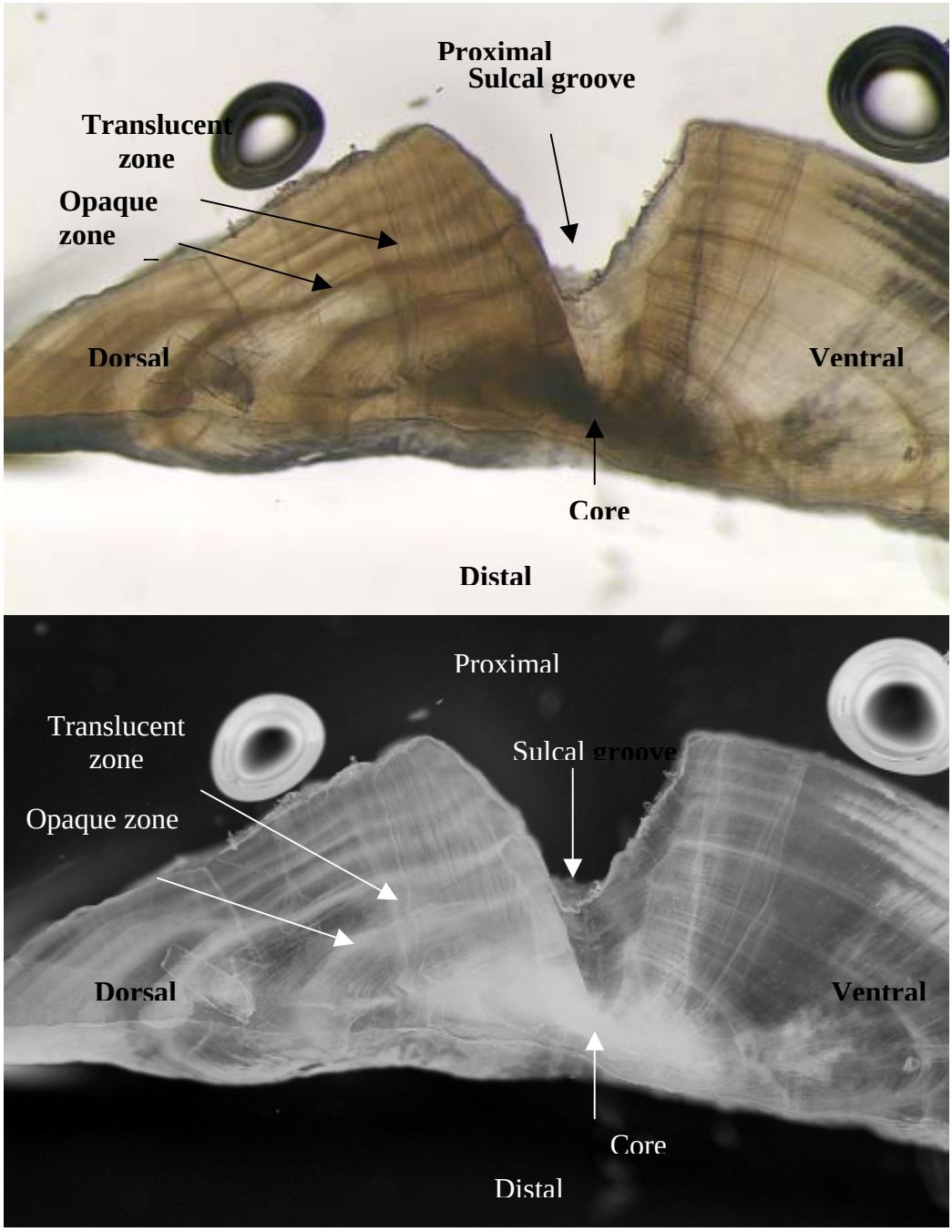

Figure 14. Transverse section through the core of the sagittal otolith of a seven-year-old gray snapper (*Lutjanus griseus)* collected in August 2001. The top image was taken with transmitted light; the bottom image was taken with reflected light. 2.5x

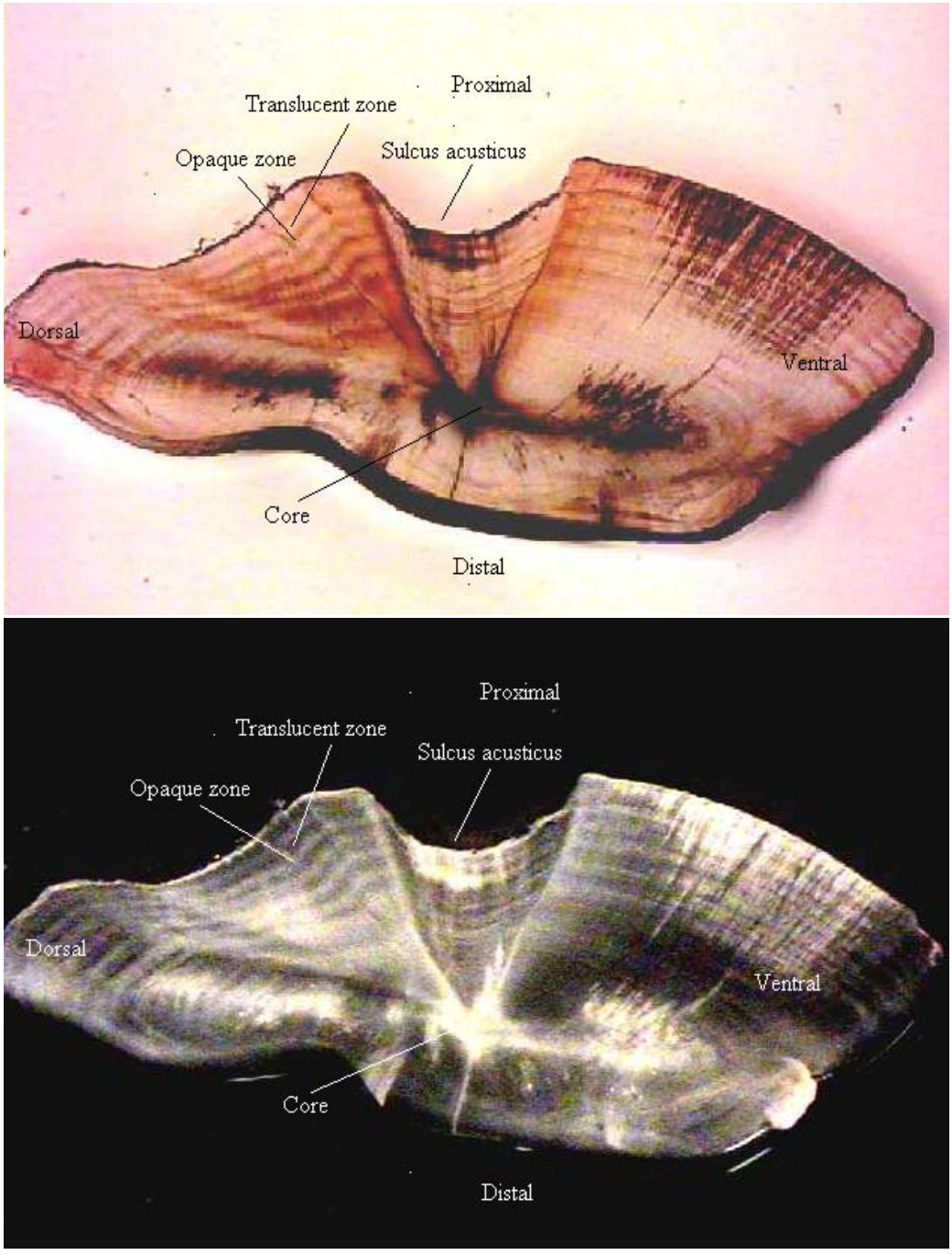

Figure 15. Transverse section through the core of the sagitta of an eight-year- old *Lutjanus synagris* collected in January 1999. The top image was taken with transmitted light; the bottom image was taken with reflected light. 2.5x

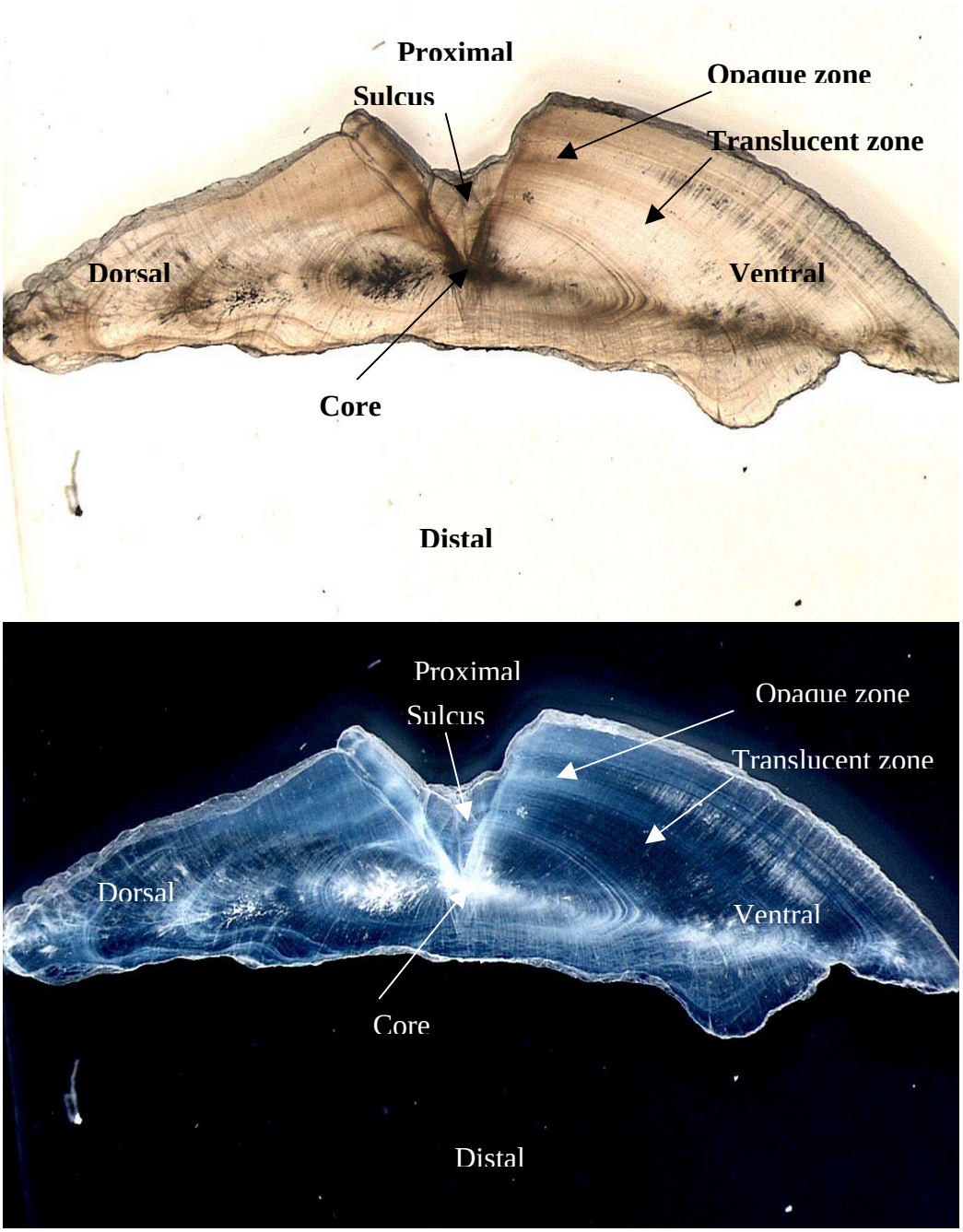

Figure 16. Transverse section through the core of the sagitta of a four-year-old *Lutjanus analis* collected in March 1999. The top image was taken with transmitted light; the bottom image was taken with reflected light. 2.5x

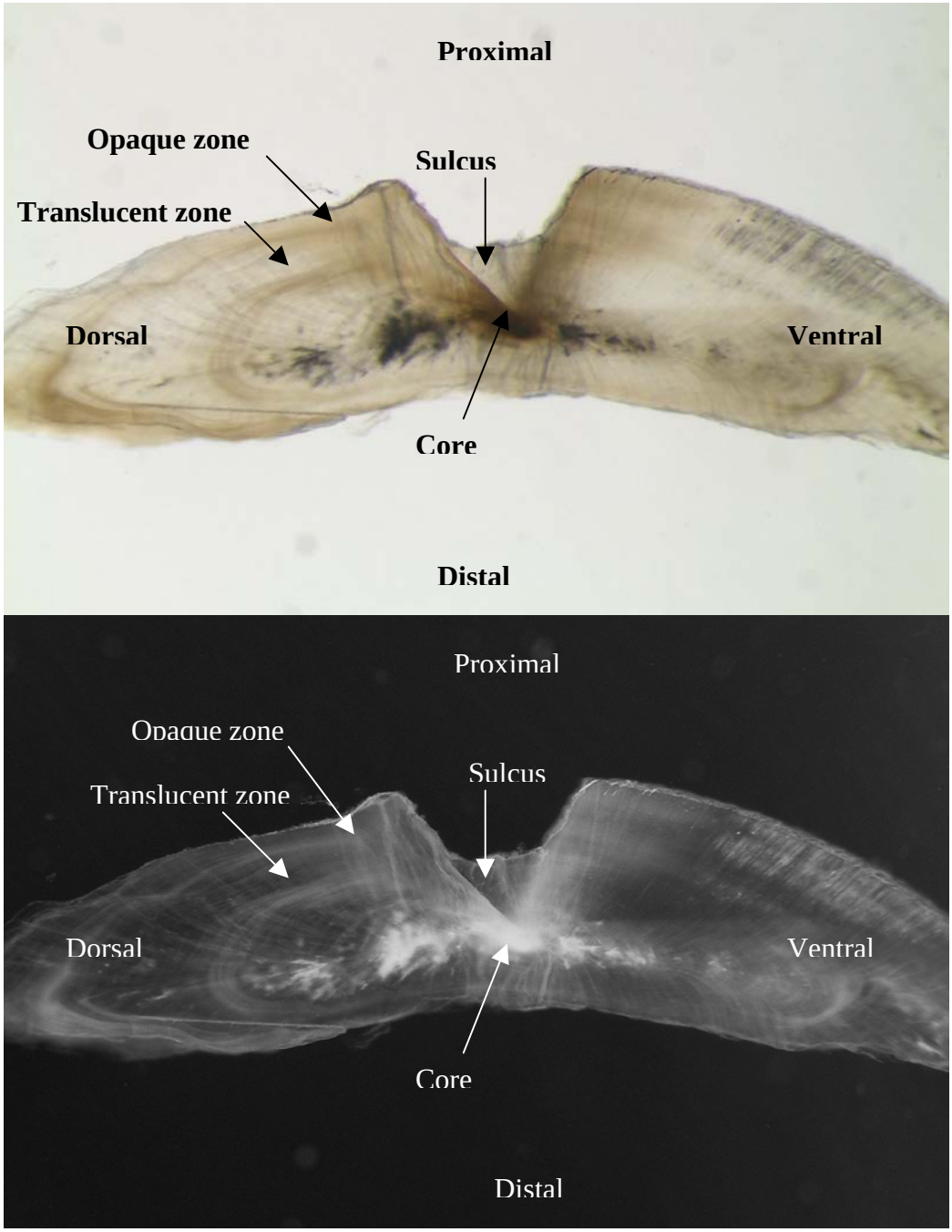

Figure 17. Transverse section through the core of the sagitta of a two-year-old *Ocyurus chrysurus* collected in September 1998. The top image was taken with transmitted light; the bottom image was taken with reflected light. 2.5x

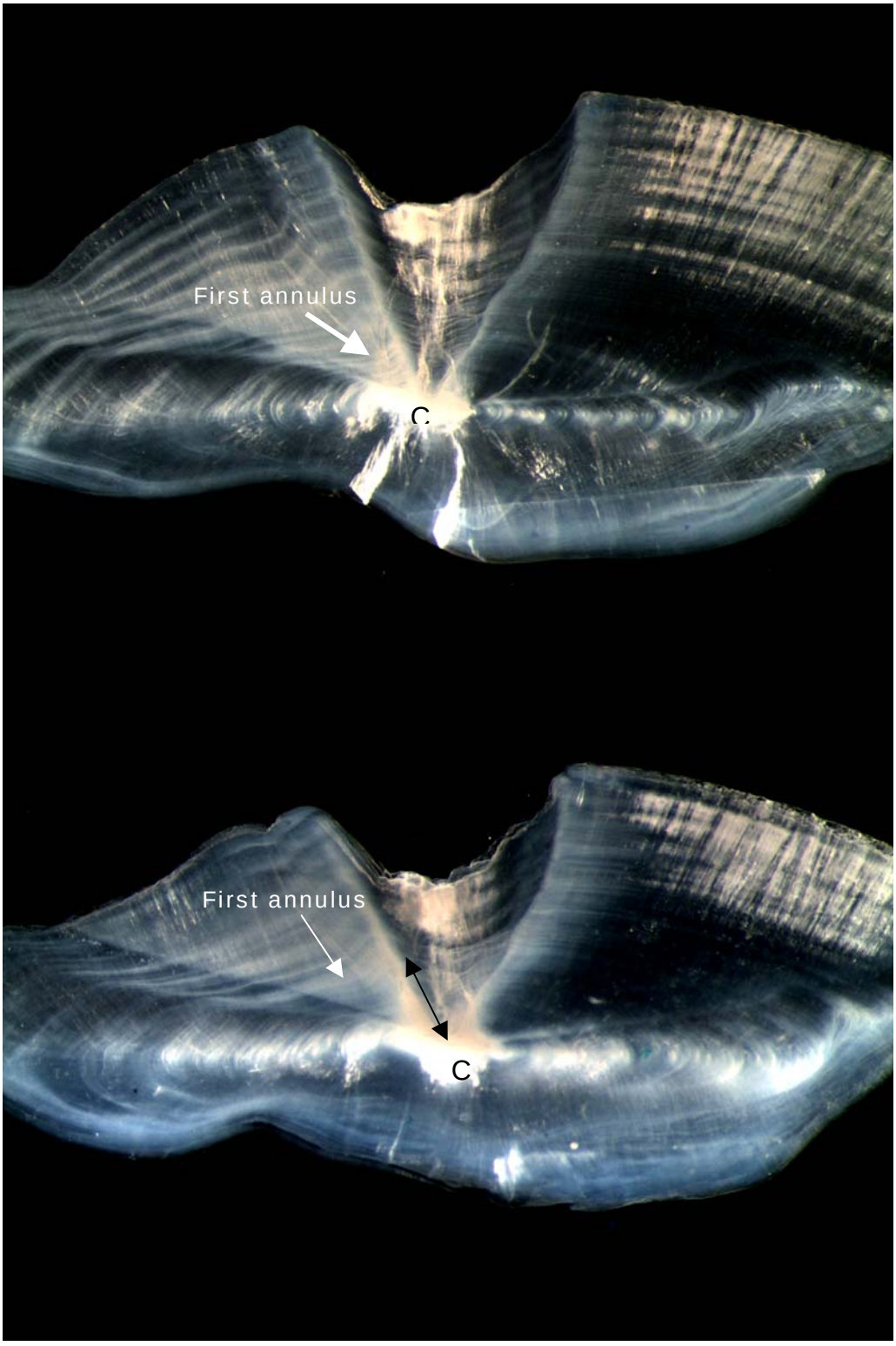

Figure 18. Examples of lane snapper (*Lutjanus synagris*) with the first annulus close to the core (top picture) and away from the core (bottom picture). The core is indicated by (C). Magnification 20x.

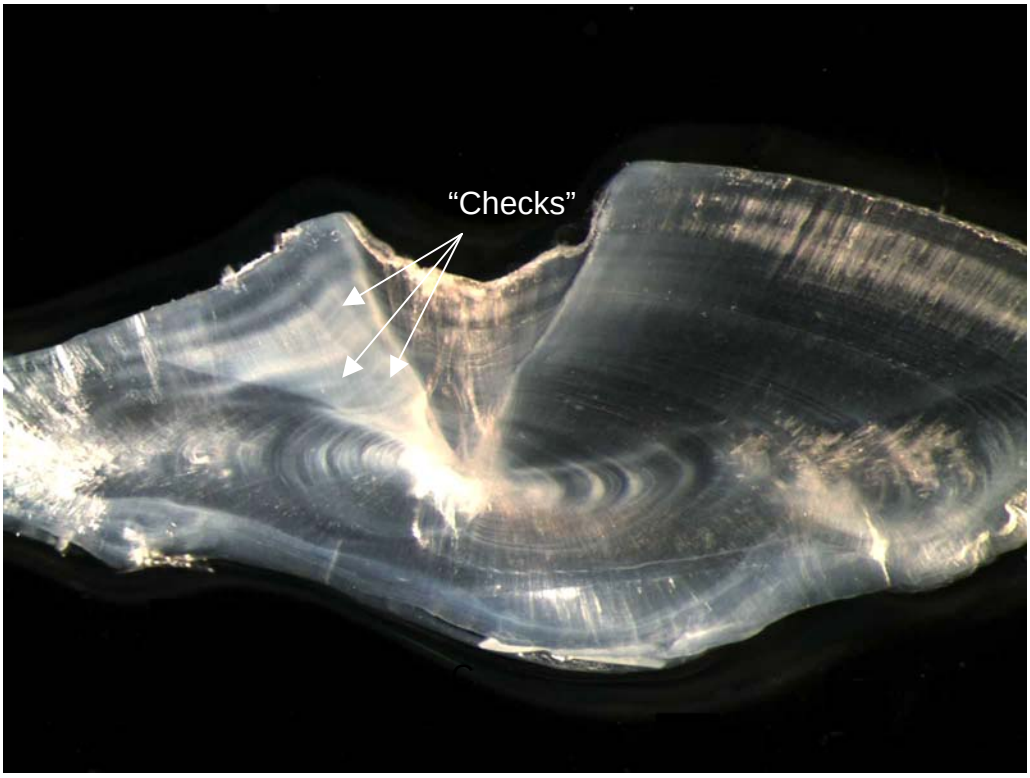

Figure 19. A five-year-old *Lutjanus synagris* collected in April 2001. “Checks” or false annuli occur frequently in lane snapper. The checks are thin and faint compared to the other annuli. Magnification 20x.

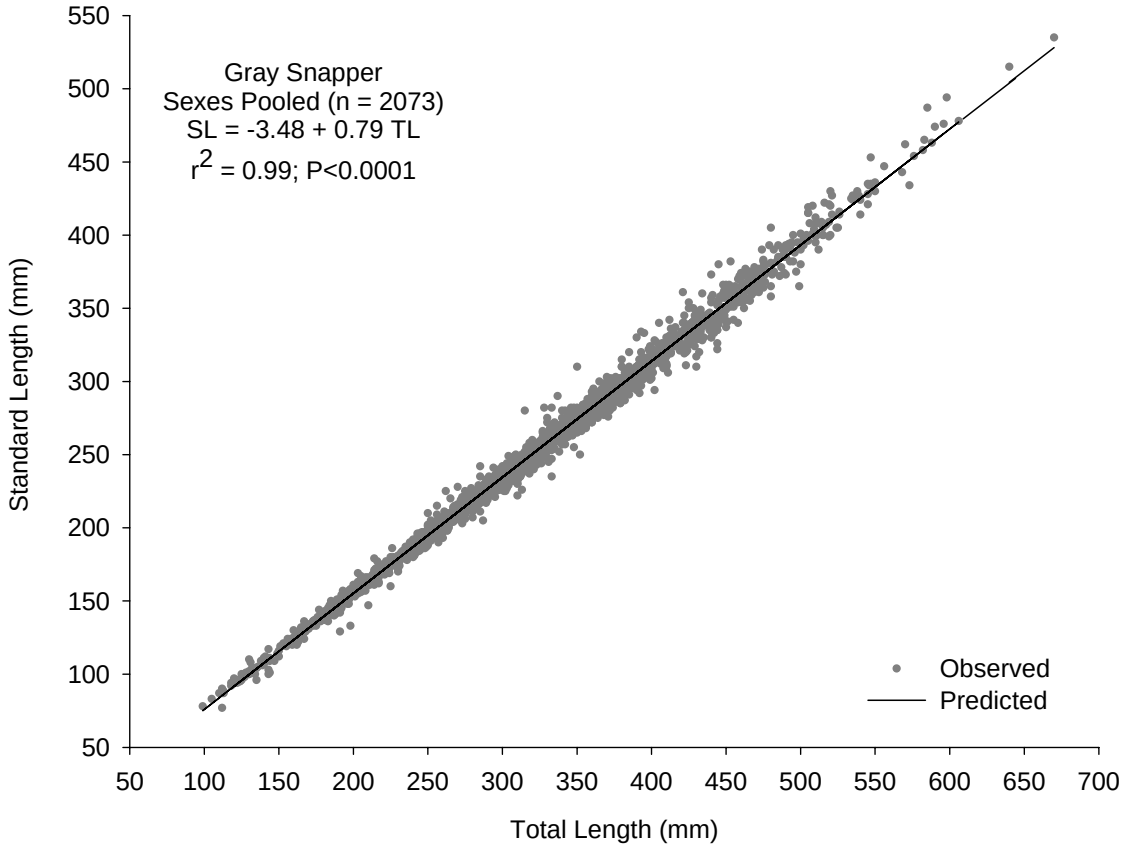

Figure 20. Total length (TL) and standard length (SL) relationship of gray snapper captured in southeast Florida and the Florida Keys.

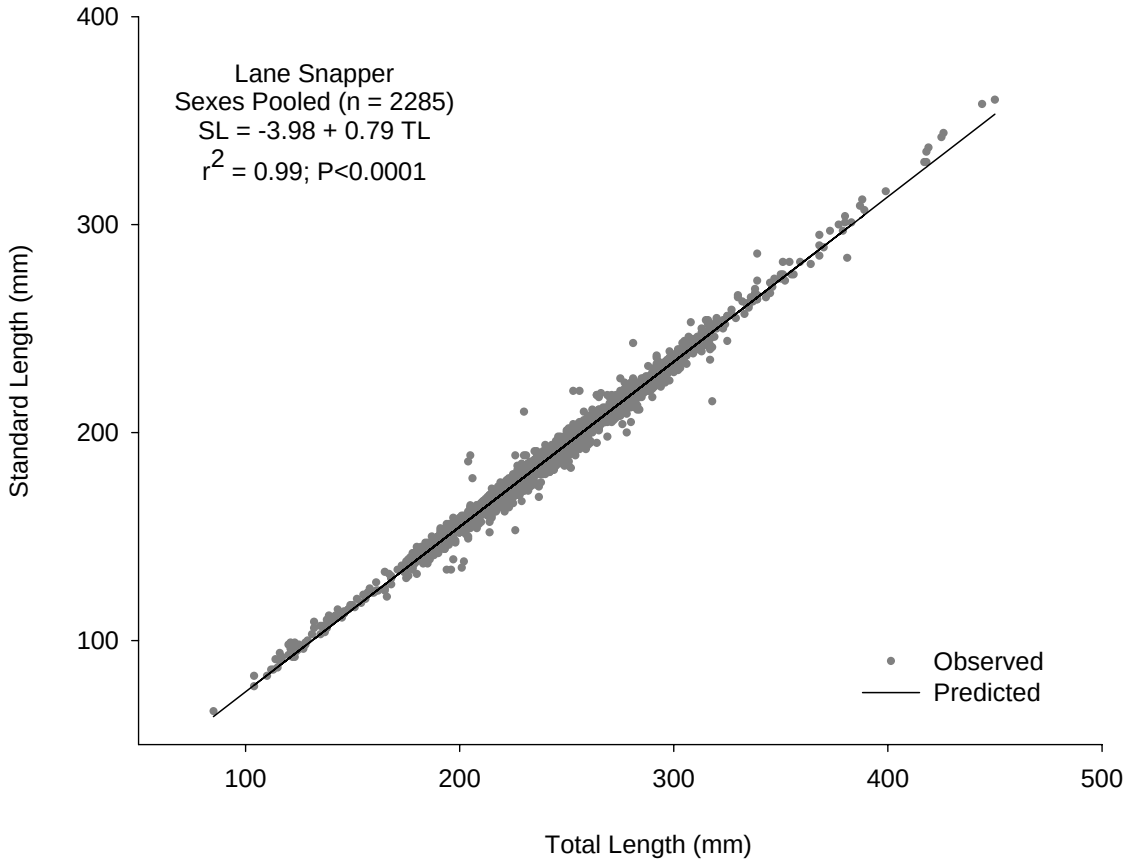

Figure 21. Total length (TL) and standard length (SL) relationship of lane snapper captured in southeast Florida and the Florida Keys.

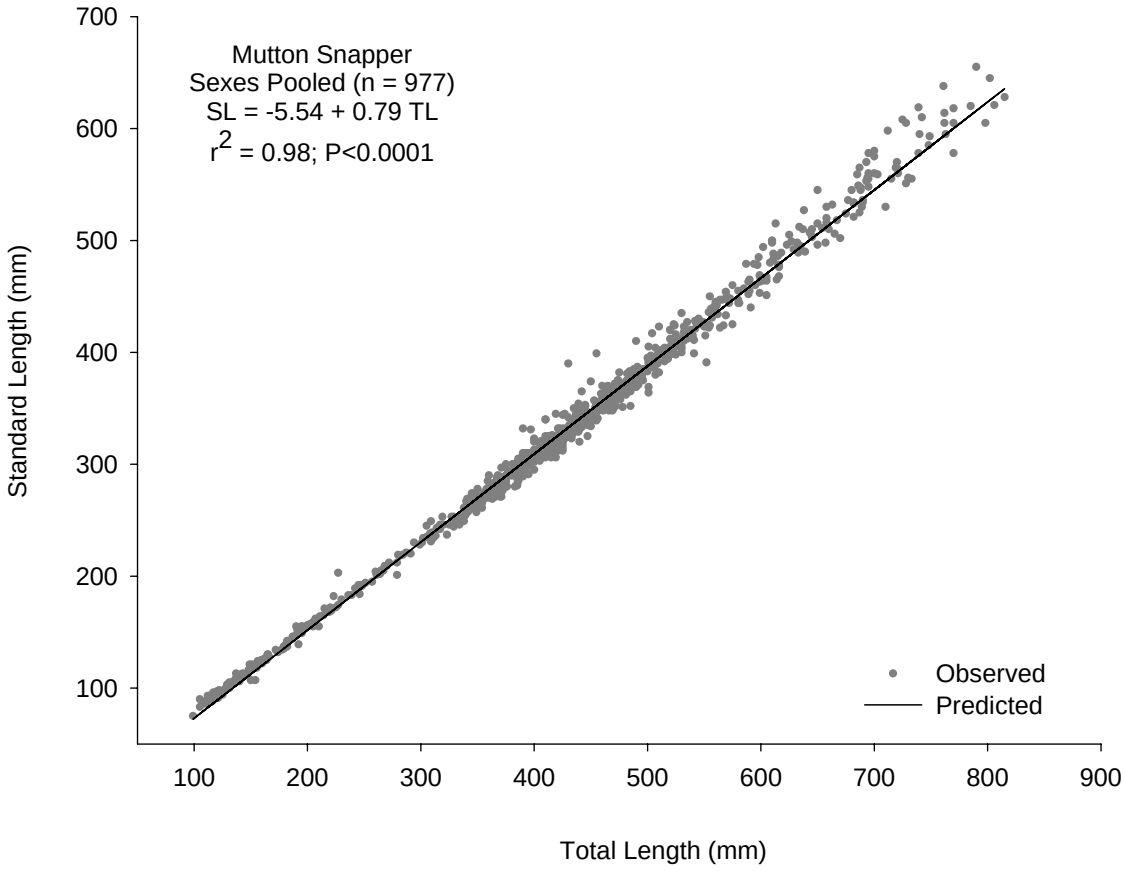

Figure 22. Total length (TL) and standard length (SL) relationship of mutton snapper captured in southeast Florida and the Florida Keys.

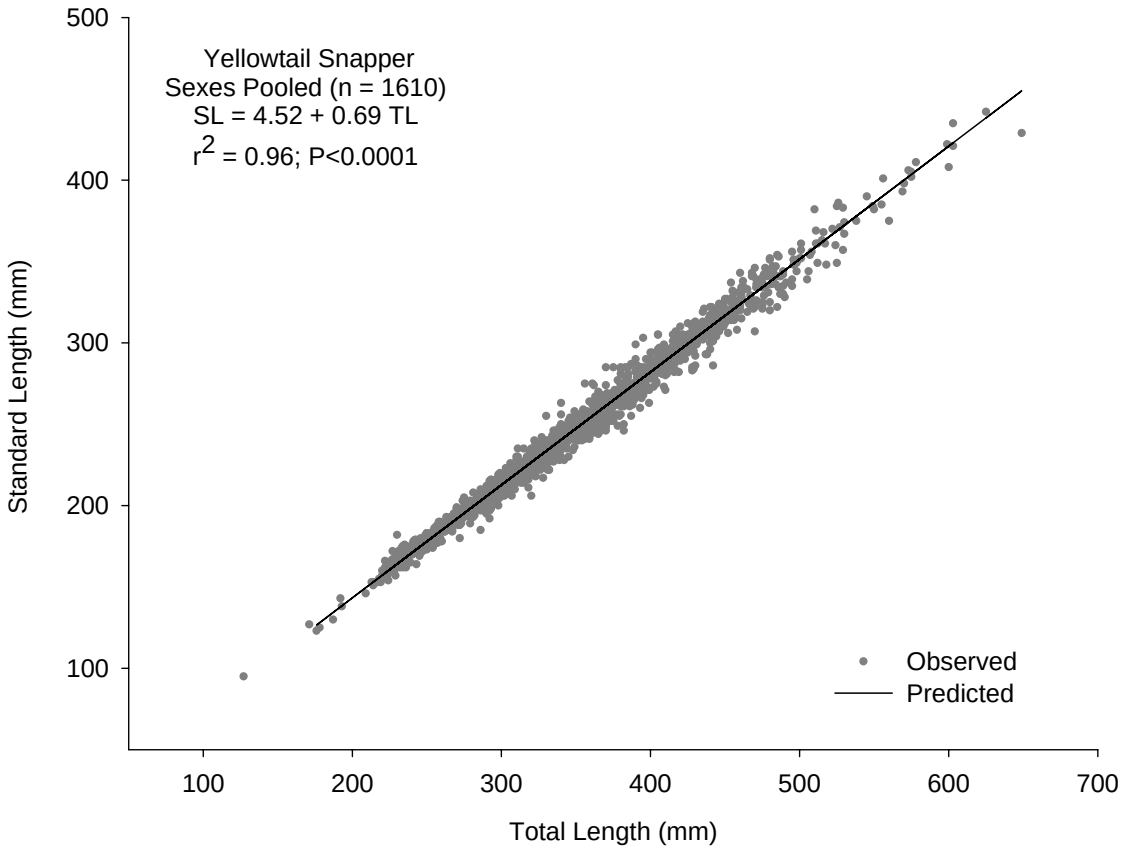

Figure 23. Total length (TL) and standard length (SL) relationship of yellowtail snapper captured in southeast Florida and the Florida Keys.

TL-TW relationships were better described by exponential regression models (Figures 24-28). With the exception of yellowtail snapper, no differences in TL-TW relationships were found between sexes. A summary of equation parameters and significance tests for each species is presented in Table 5.

Table 5. Total length (TL) to total weight (TW) relationships for snappers captured in southeast Florida and the Florida Keys. Sexes are pooled unless otherwise indicated.

Species	n	Equation	r^2	P-value
Gray	1536	$TW = 2.65 \times 10^{-5}\ TL^{2.88}$	0.98	P<0.0001
Lane	2144	$TW = 2.04 \times 10^{-5}\ TL^{2.93}$	0.98	P<0.0001
Mutton	810	$TW = 2.10 \times 10^{-5}\ TL^{2.92}$	0.99	P<0.0001
Yellowtail	1415	$TW = 2.95 \times 10^{-5}\ TL^{2.80}$	0.98	P<0.0001
Yellowtail (females)	690	$TW = 3.26 \times 10^{-5}\ TL^{2.78}$	0.97	P<0.0001
Yellowtail (males)	622	$TW = 3.01 \times 10^{-5}\ TL^{2.80}$	0.98	P<0.0001

Growth Parameter Estimates

Despite the high variability of lengths-at-age observed for all snapper species studied, observed total lengths showed a very good fit to the von Bertalanffy growth model (Figures 30-33). No differences in growth parameters between sexes were observed for any species [as tested by the method of Kimura (1980)], so parameter estimates were reported for pooled sexes. Estimated model parameters, asymptotic standard errors, and 95% confidence intervals for each snapper species are presented in Tables 6-9.

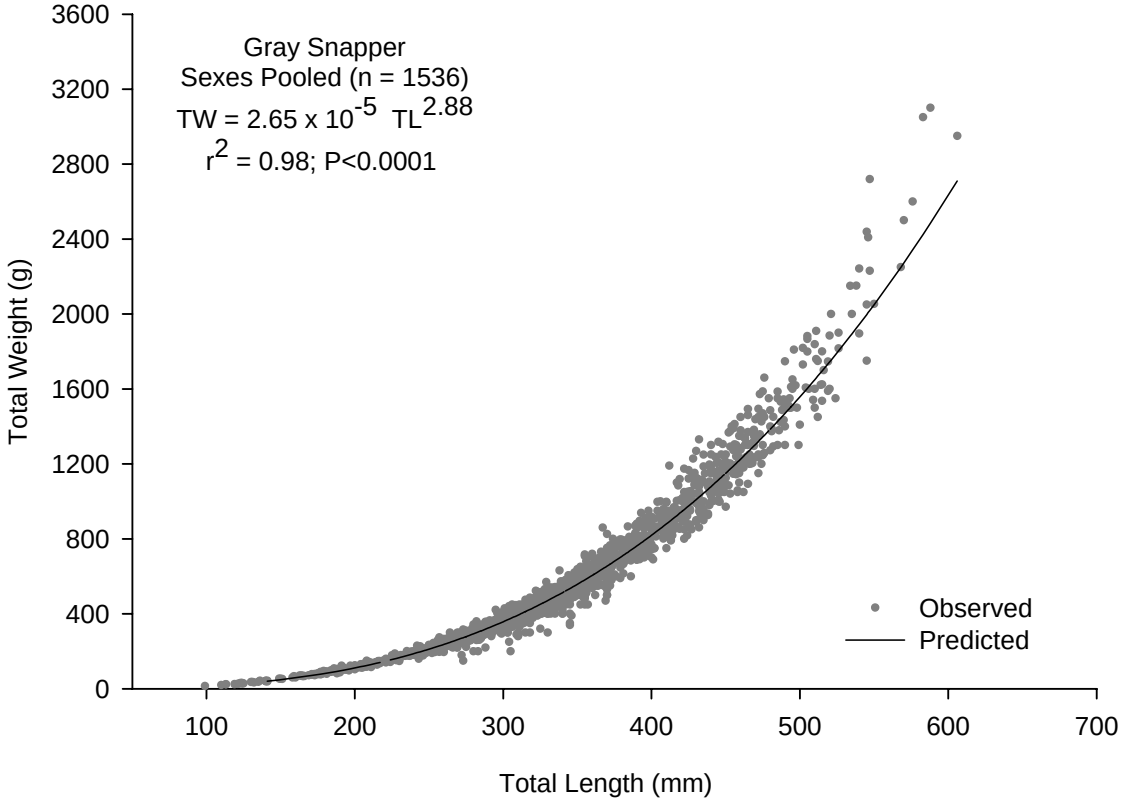

Figure 24. Total length (TL) and total weight (TW) relationship of gray snapper captured in southeast Florida and the Florida Keys.

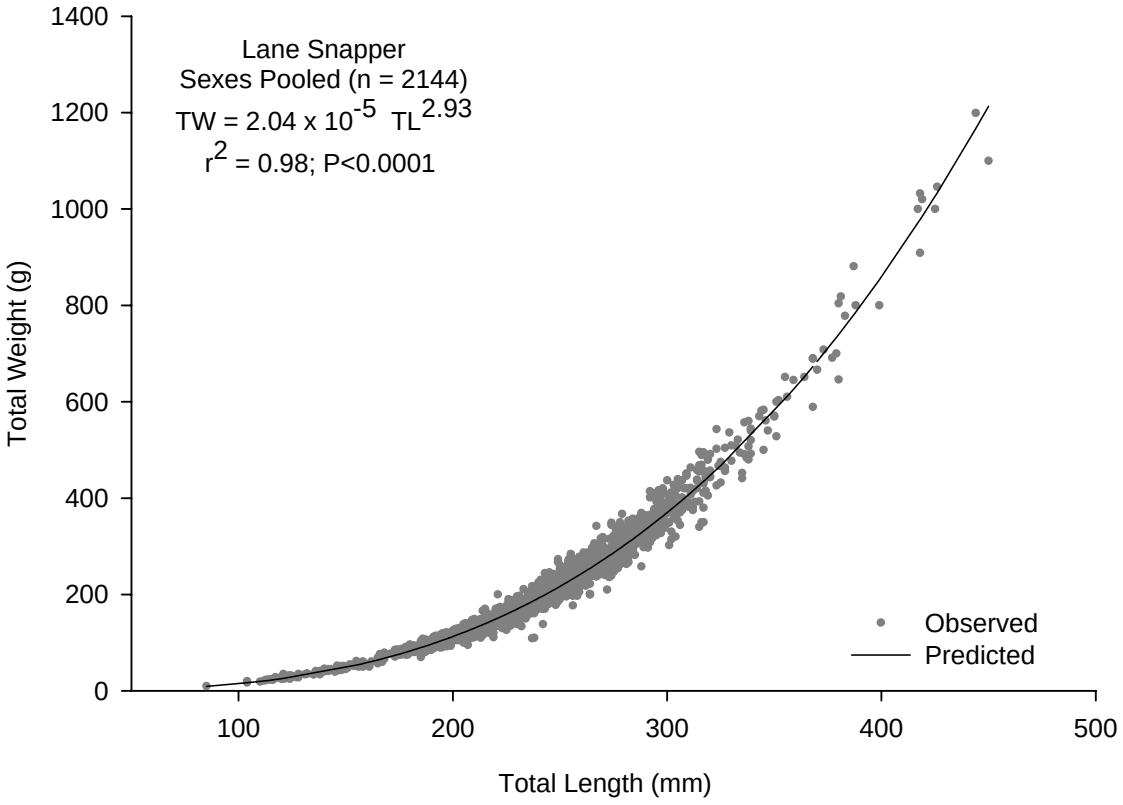

Figure 25. Total length (TL) and total weight (TW) relationship of lane snapper captured in southeast Florida and the Florida Keys.

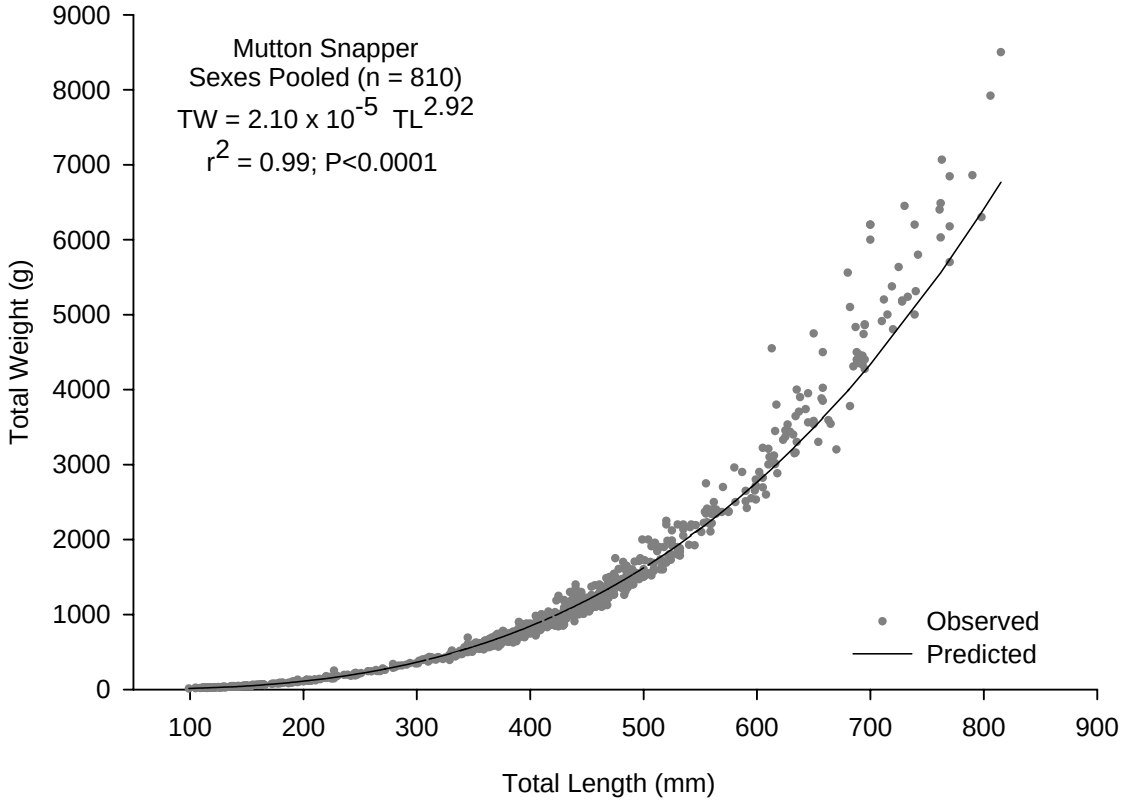

Figure 26. Total length (TL) and total weight (TW) relationship of mutton snapper captured in southeast Florida and the Florida Keys.

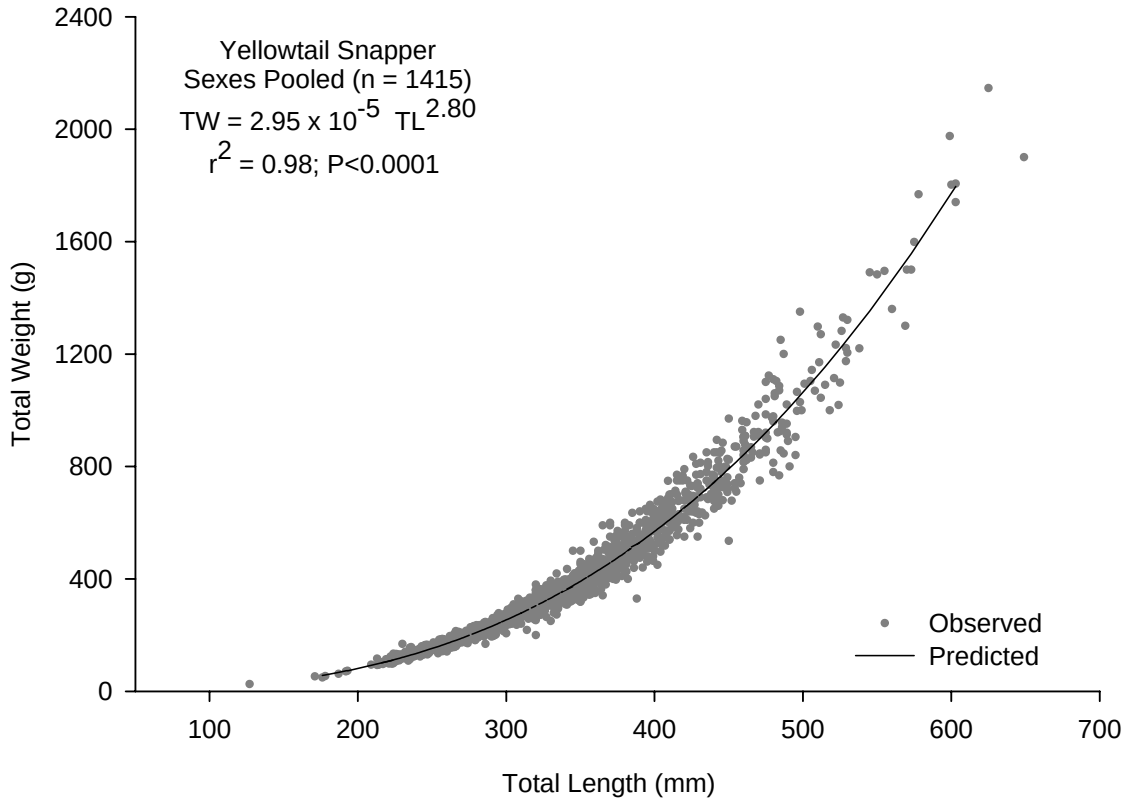

Figure 27. Total length (TL) and total weight (TW) relationship of yellowtail snapper captured in southeast Florida and the Florida Keys.

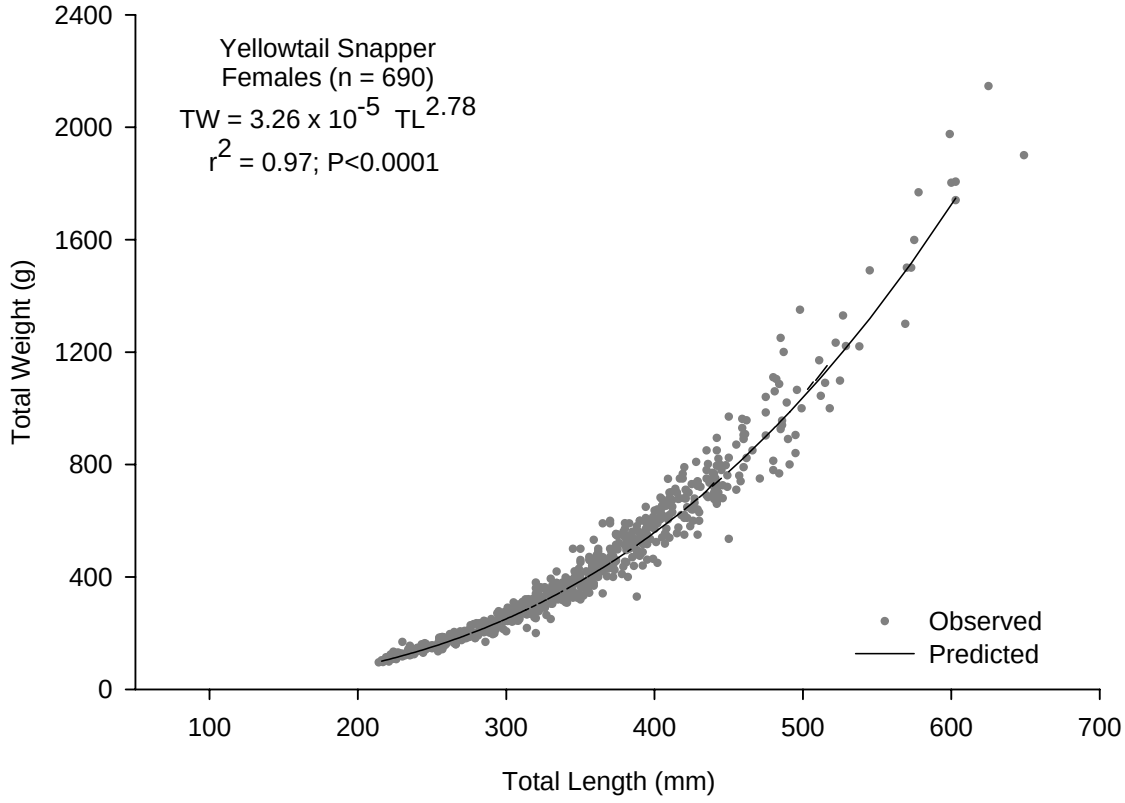

Figure 28. Total length (TL) and total weight (TW) relationship of yellowtail snapper females captured in southeast Florida and the Florida Keys.

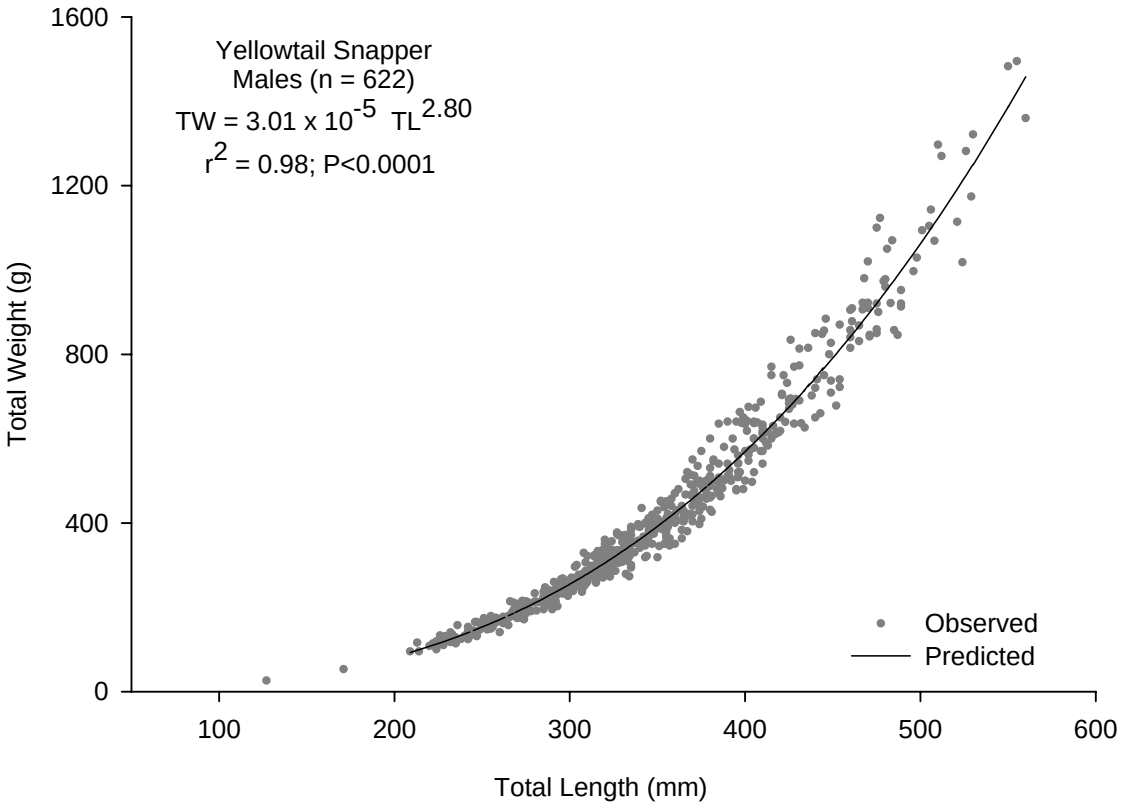

Figure 29. Total length (TL) and total weight (TW) relationship of yellowtail snapper males captured in southeast Florida and the Florida Keys.

Table 6. Parameter estimates, standard errors, and 95% confidence intervals for the von Bertalanffy growth model for lane snapper from southeast Florida(r^2 = 0.99, P<0.0001, n = 1,899).

Parameter	Estimate	Standard Error	95% Confidence Intervals	
			Lower	Upper
L_α (mm)	296.20	9.13	278.30	314.20
K (year $^{-1}$)	0.24	0.04	0.15	0.32
t_0	-4.52	0.79	-6.08	-2.97

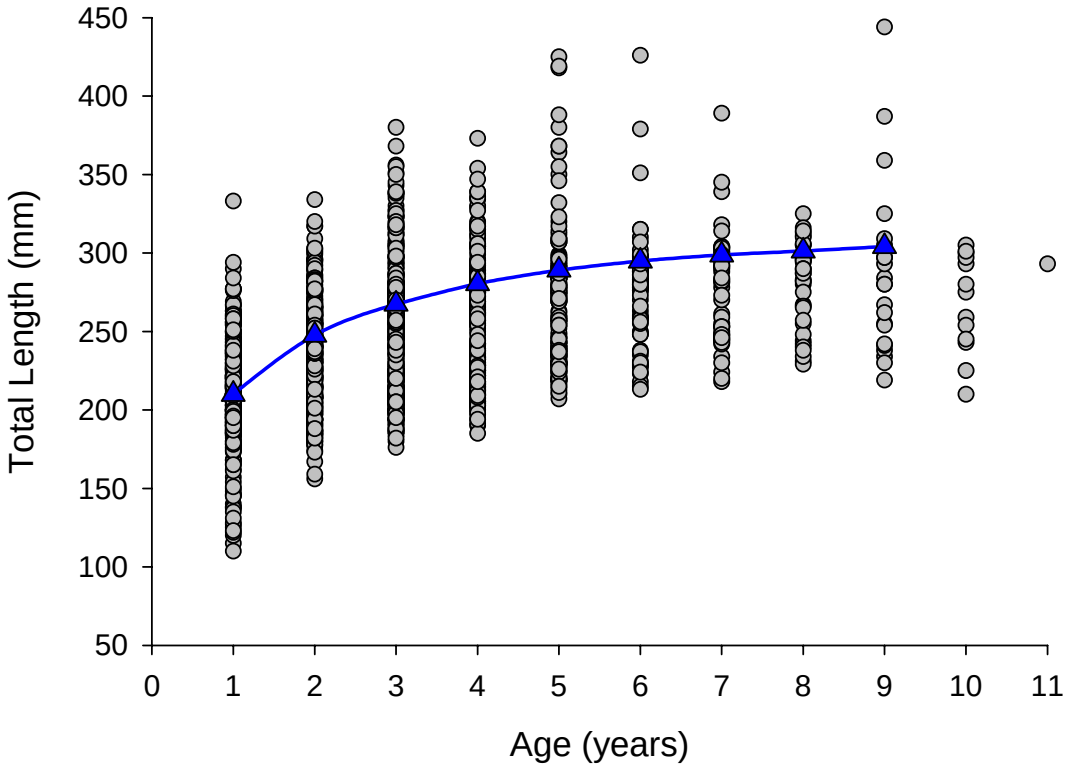

Figure 30. Observed lengths at age and fitted von Bertalanffy regression line for lane snapper from southeast Florida. Sample size and parameter estimates associated with these data are presented in Table 6.

Table 7. Parameter estimates, standard errors, and 95% confidence intervals for the von Bertalanffy growth model for mutton snapper from southeast Florida (r^2 = 0.99, P<0.0001, n =781).

Parameter	Estimate	Standard Error	95% Confidence Intervals	
			Lower	Upper
L_α (mm)	971.10	42.7	888.30	1,056.0
K (year $^{-1}$)	0.13	0.01	0.11	0.16
t_0	-1.43	0.16	-1.75	-1.10

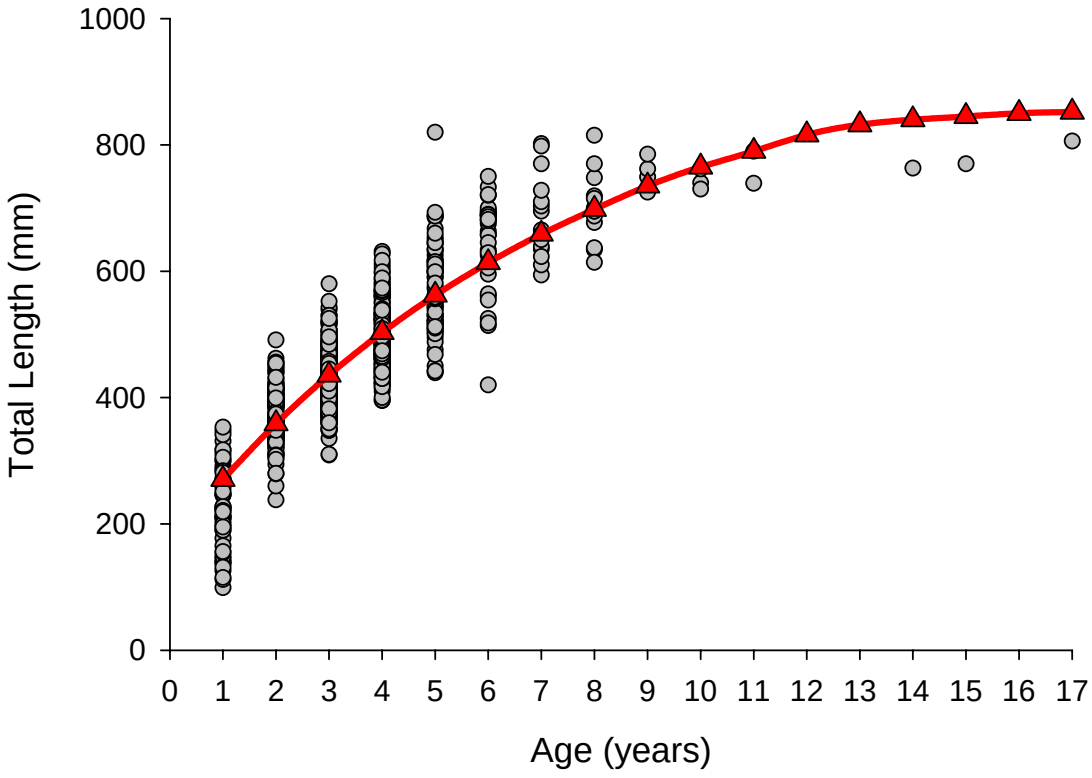

Figure 31. Observed lengths at age and fitted von Bertalanffy regression line for mutton snapper from southeast Florida. Sample size and parameter estimates associated with these data are presented in Table 7.

Table 8. Parameter estimates, standard errors, and 95% confidence intervals for the von Bertalanffy growth model for gray snapper from southeast Florida (r^2 = 0.99, P<0.0001, n =1,331).

Parameter	Estimate	Standard Error	95% Confidence Intervals	
			Lower	Upper
L_α (mm)	441.60	7.6	426.70	456.5
K (year $^{-1}$)	0.35	0.03	0.29	0.40
t_0	-0.41	0.17	-0.75	-0.07

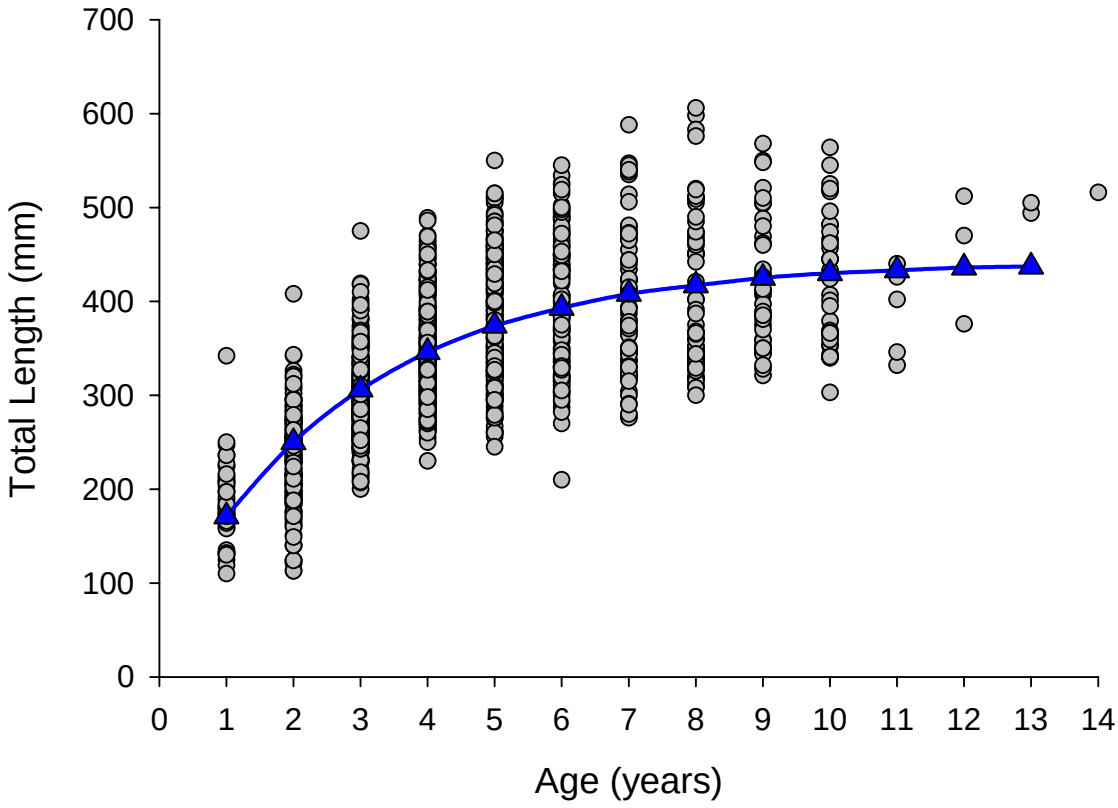

Figure 32. Observed lengths at age and fitted von Bertalanffy regression line for gray snapper from southeast Florida. Sample size and parameter estimates associated with these data are presented in Table 8.

Table 9. Parameter estimates, standard errors, and 95% confidence intervals for the von Bertalanffy growth model for yellowtail snapper from southeast Florida (r^2 = 0.99, P<0.0001, n = 1502).

		Standard	95% Confidence Intervals	
Parameter	Estimate	Error	Lower	Upper
L_α (mm)	301.70	4.37	293.10	310.30
K (year $^{-1}$)	0.47	0.05	0.38	0.57
t_0	-1.67	0.22	-2.10	-1.24

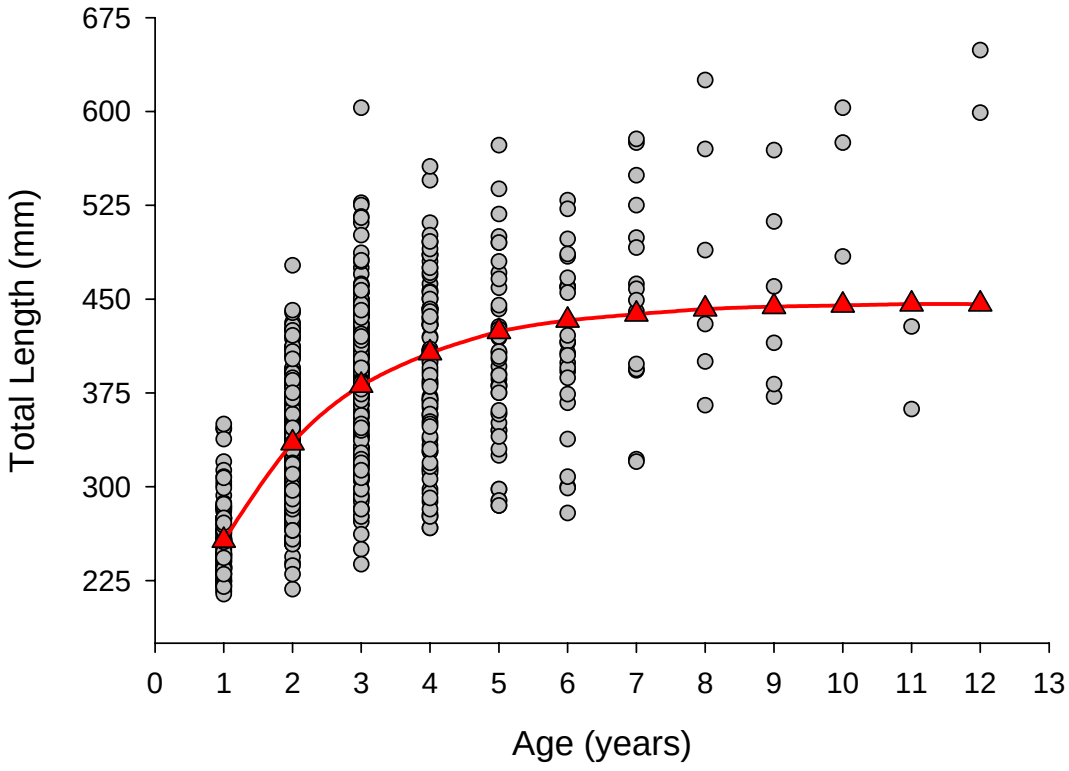

Figure 33. Observed lengths at age and fitted von Bertalanffy regression line for yellowtail snapper from southeast Florida. Sample size and parameter estimates associated with these data are presented in Table 9.

Maturity and Spawning

The monthly distribution of the gonadosomatic index (Figures 34-37) as well as the simultaneous occurrence of multiple oocyte stages in fully developed, vitellogenic females (Figures 38-41) indicate that all four snapper species studied during grant F-73 (i.e., lane snapper, gray snapper, mutton snapper, and yellowtail snapper) are multiple spawners with indeterminate fecundity.

All species showed a protracted spawning season, extending from spring to early fall, but concentrated in the summer months (Figures 34-37). Although adult, sexually mature fish were collected in both sampling areas (i.e., Tequesta and Florida Keys), spawning by mutton and yellowtail snappers was concentrated in the Florida Keys (Figures 36-37). Lane snapper showed spawning activity in both areas, but had higher GSI values in the Florida Keys (Figure 34). This pattern was consistent for both males and females and continued throughout the spawning season.

Lane snapper was the only species for which a large enough number of gravid (i.e., with hydrated but un-ovulated eggs) females were collected. Therefore, batch fecundity estimates and its relationship with fish size and age were reported only for lane snapper. Batch fecundity showed a linear relationship with both fish total weight and age (Figure 42). However, batch fecundity-at-age was highly variable and the relationship between batch fecundity and age showed a low r^2 value ($r^2 = 0.24$).

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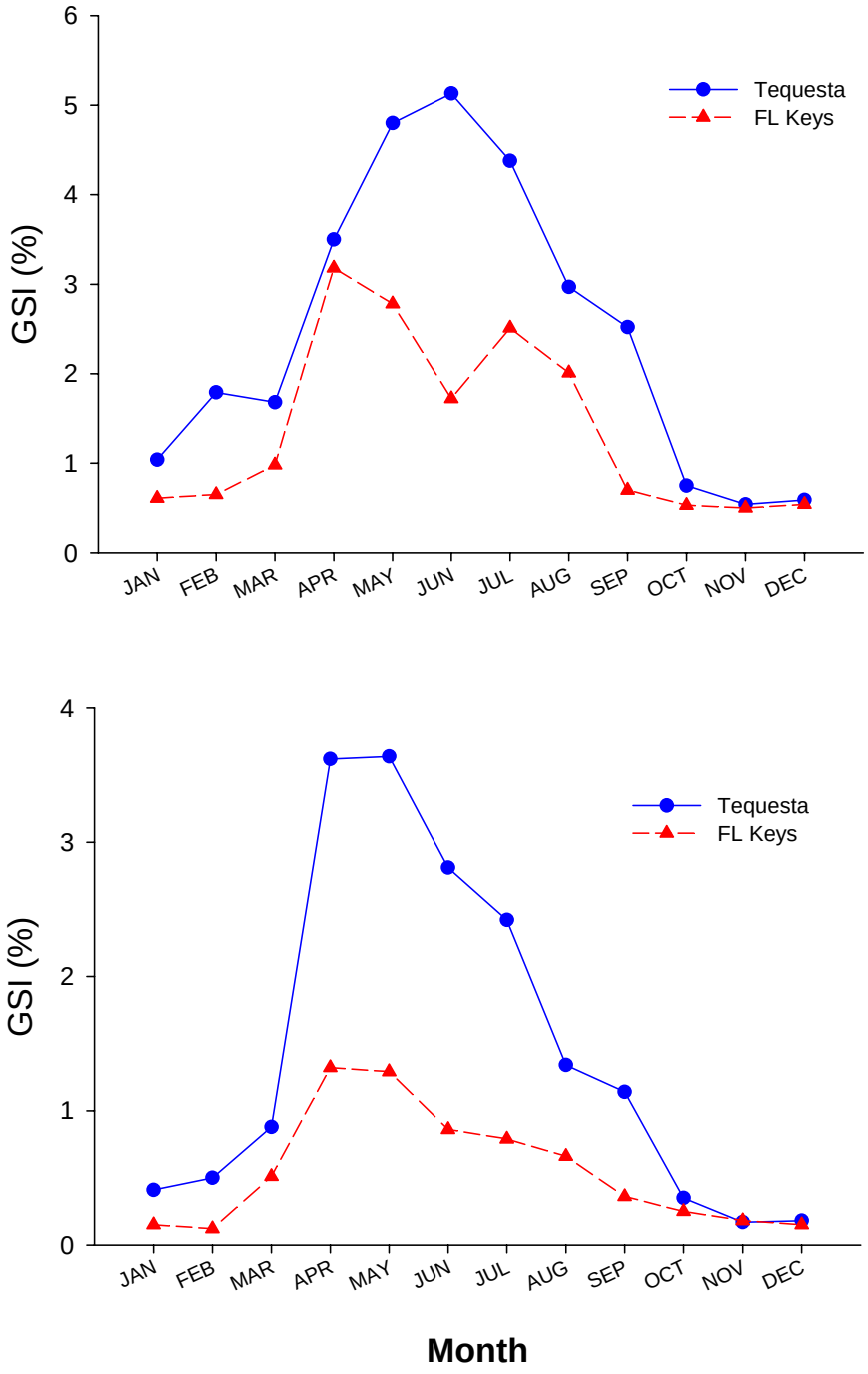

Figure 34. Monthly distribution of the gonadosomatic index for female (top) and male (bottom) lane snapper from southeast Florida.

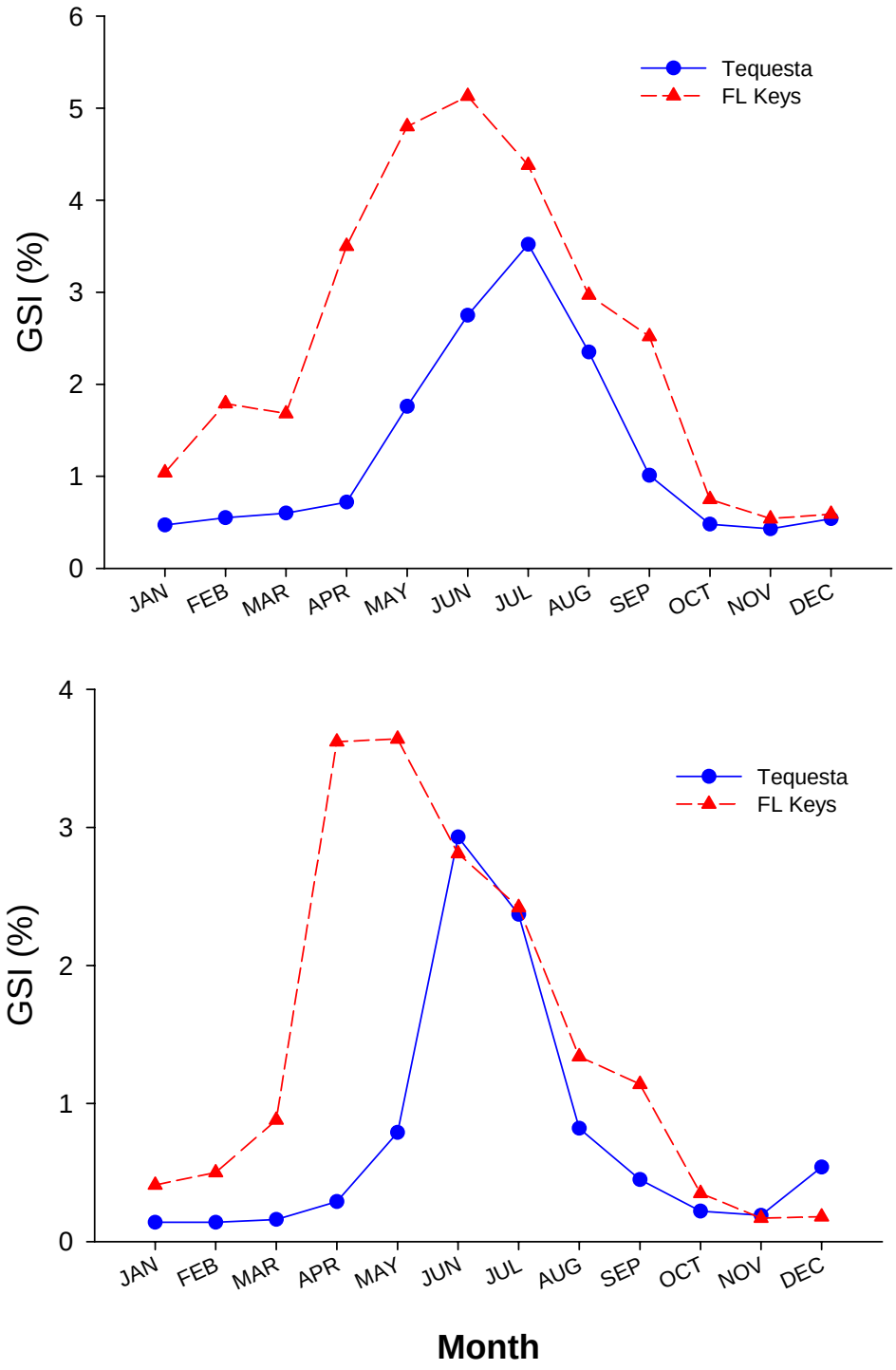

Figure 35. Monthly distribution of the gonadosomatic index for female (top) and male (bottom) gray snapper from southeast Florida.

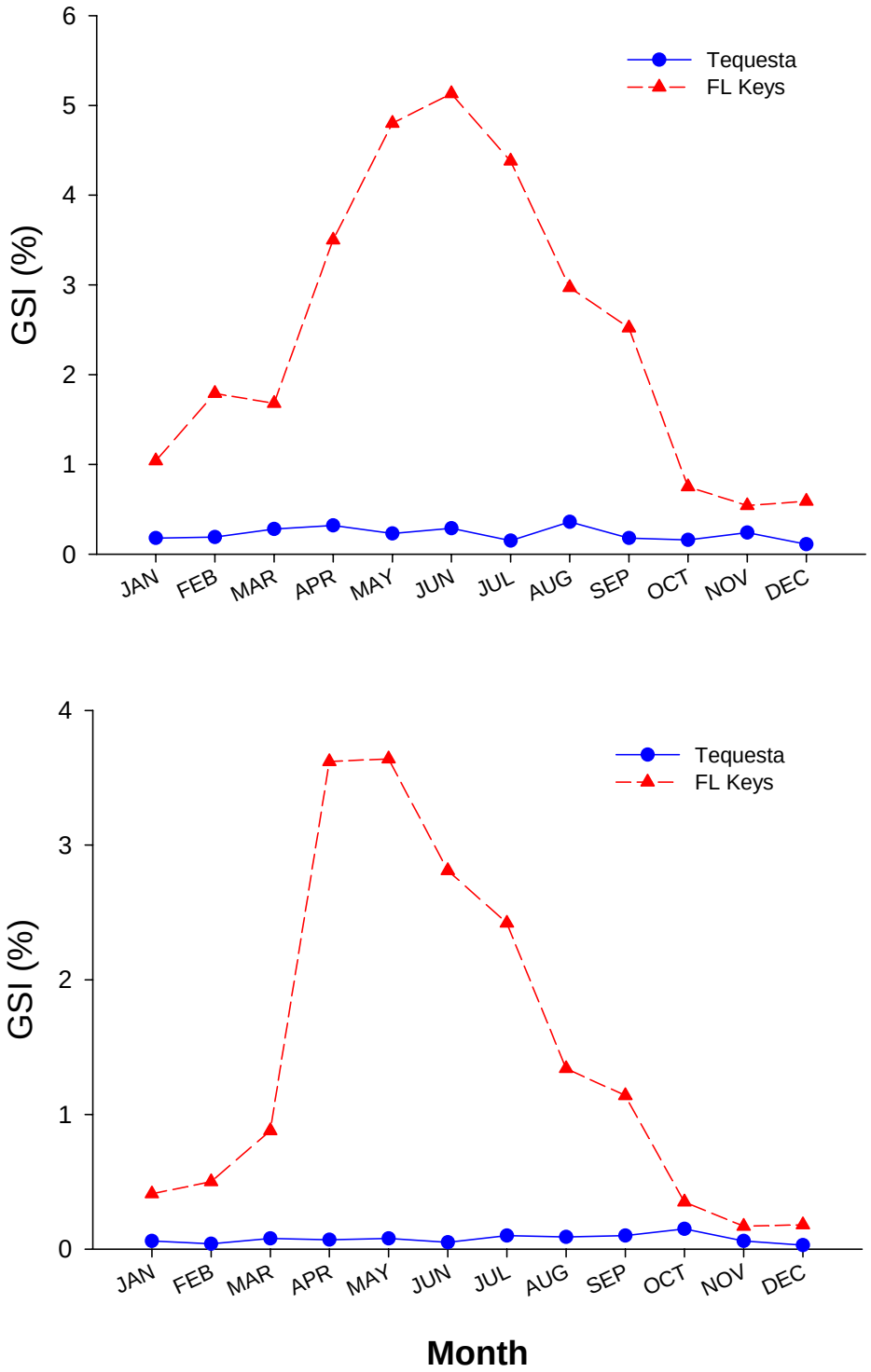

Figure 36. Monthly distribution of the gonadosomatic index for female (top) and male (bottom) mutton snapper from southeast Florida.

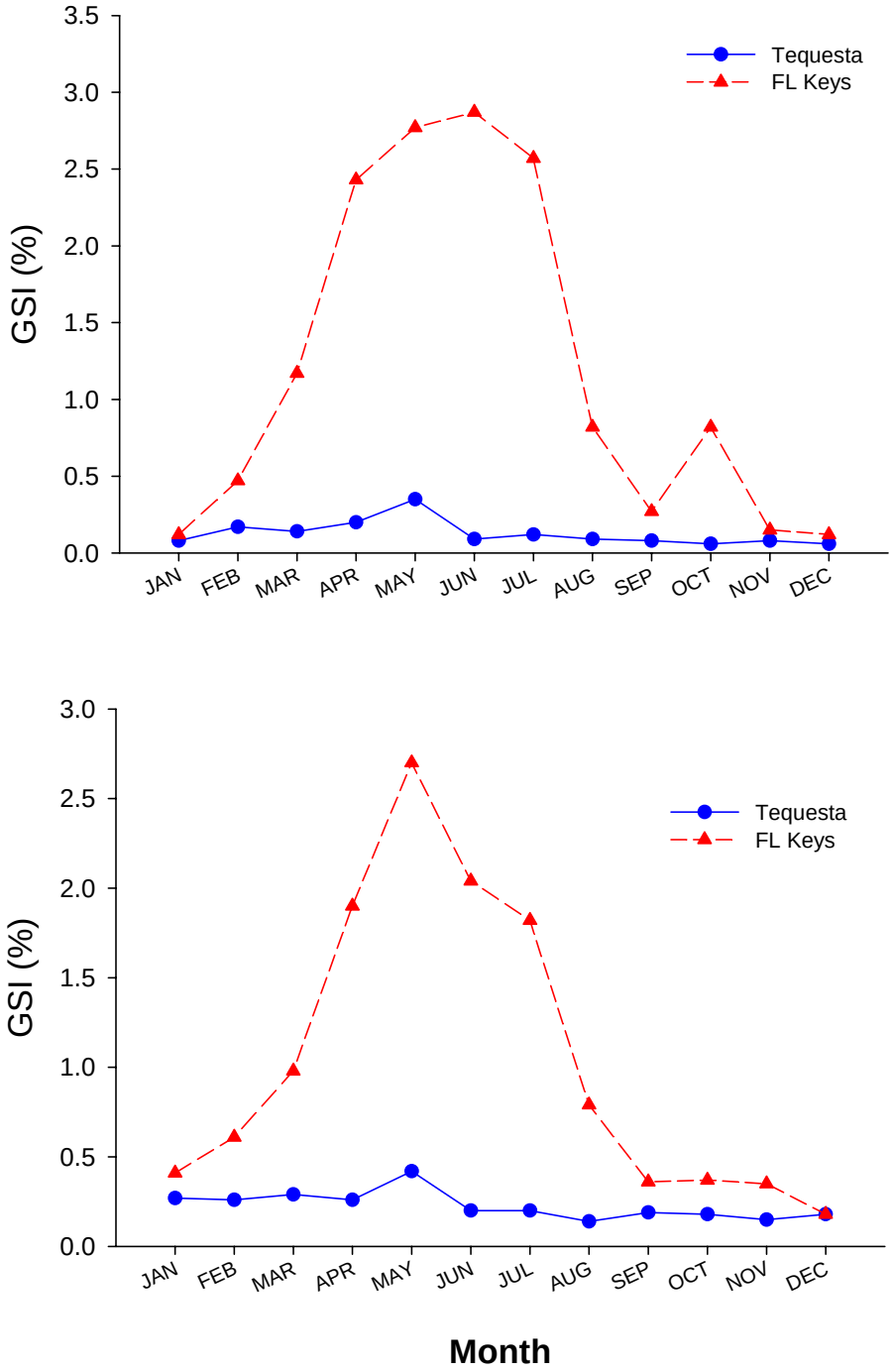

Figure 37. Monthly distribution of the gonadosomatic index for female (top) and male (bottom) yellowtail snapper from southeast Florida.

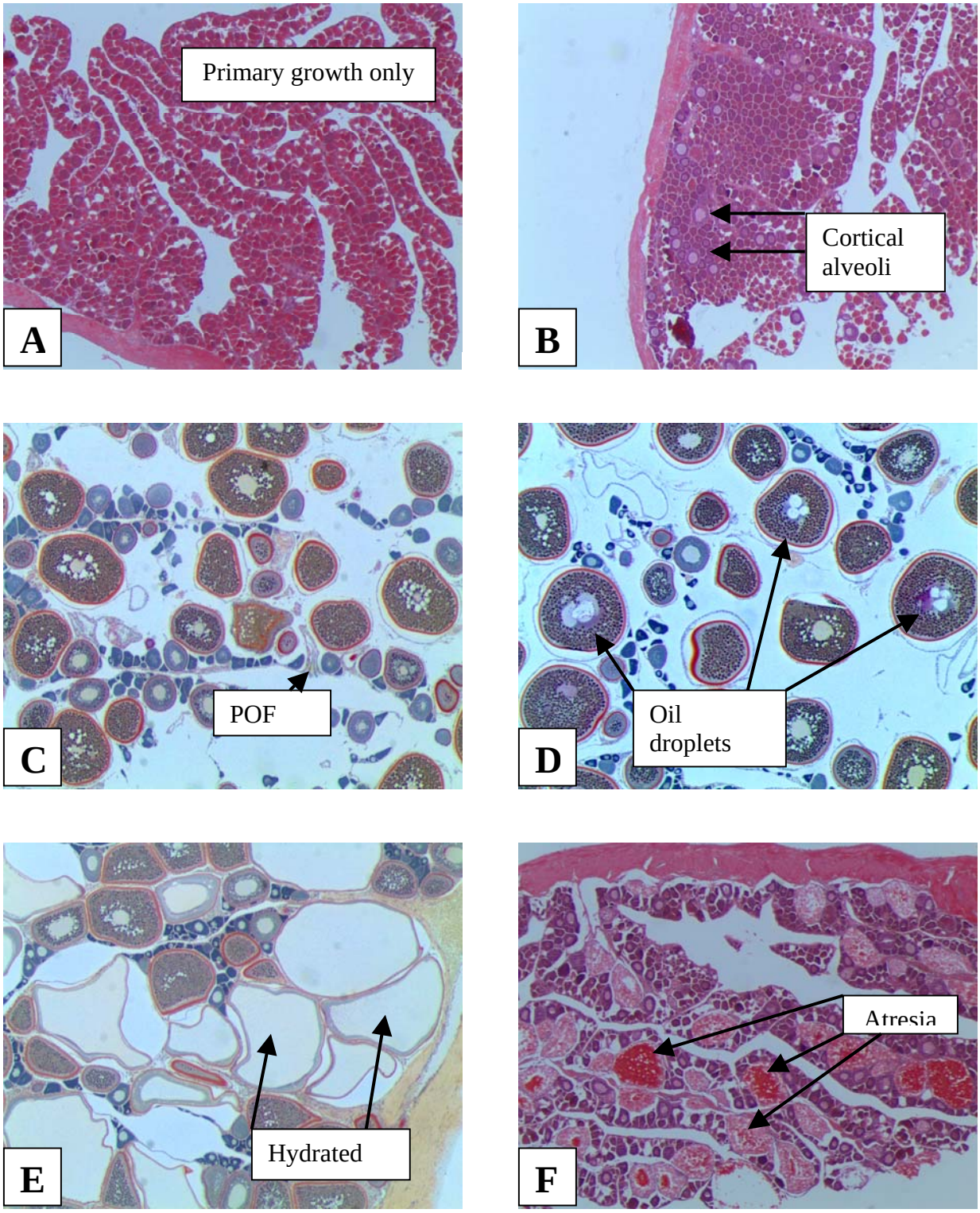

Figure 38. Histological sections of *Lutjanus synagris* ovary illustrating progression from immature to resting stages. A. Immature/resting. B. Developing. C. Partially spent. D. Gravid. E. Gravid. F. Regressing.

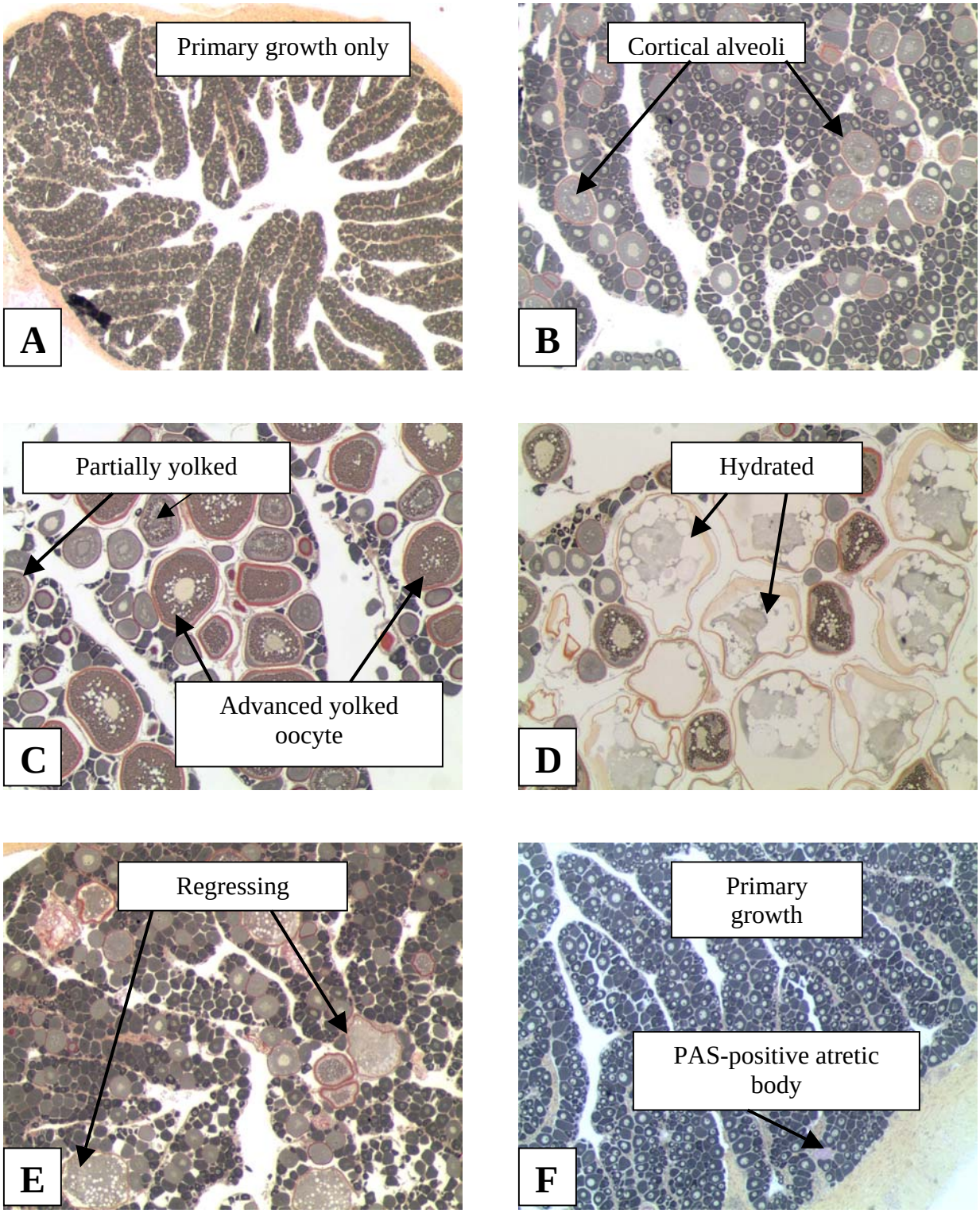

Figure 39. Histological sections of *Lutjanus griseus* ovary illustrating progression from immature to resting stages. A. Immature. B. Developing. C. Fully-developed. D. Gravid. E. Regressing. F. Resting.

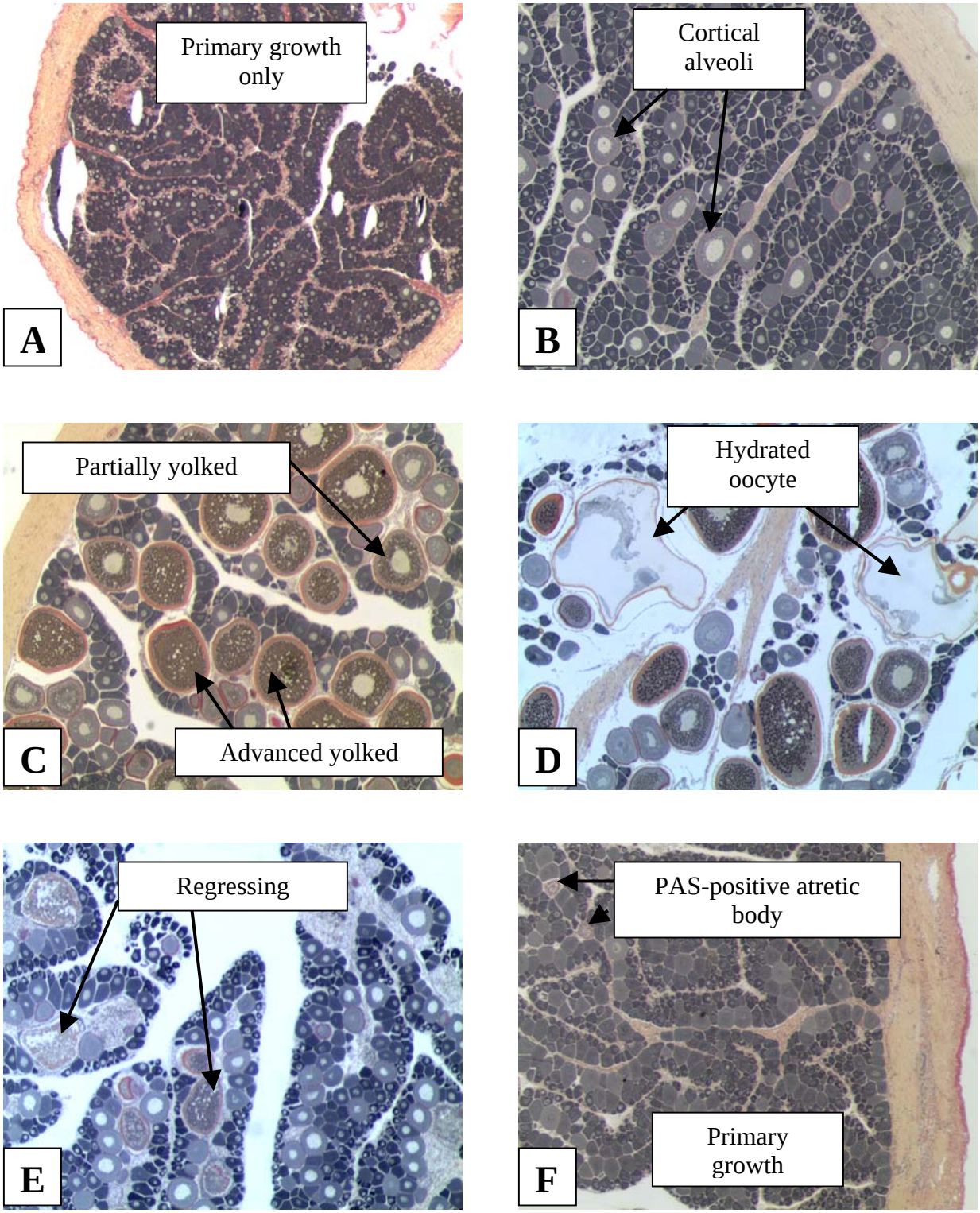

Figure 40. Histological sections of *Lutjanus analis* ovary illustrating progression from immature to resting stages. A. Immature. B. Developing. C. Fully-developed. D. Gravid. E. Regressing. F. Resting.

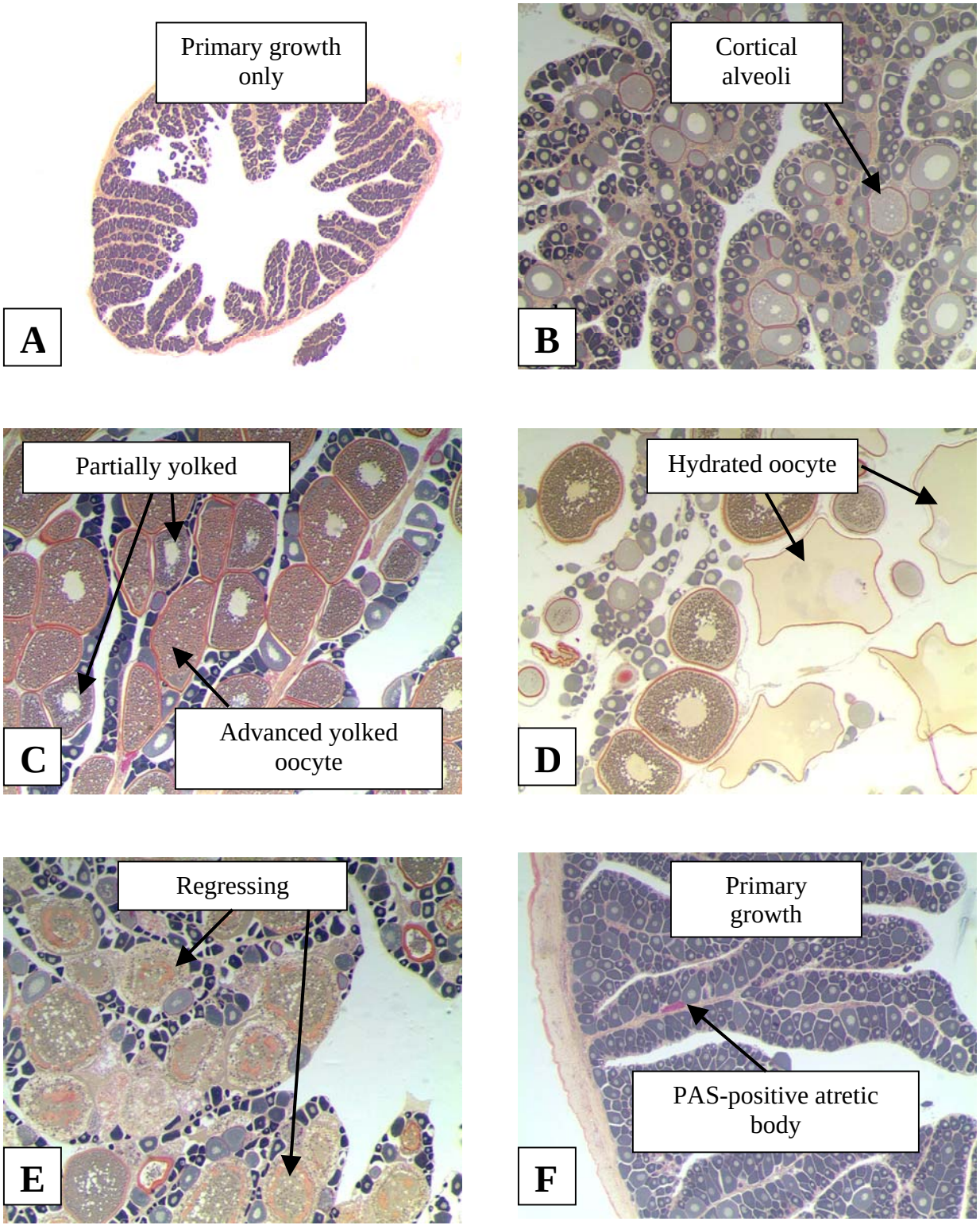

Figure 41. Histological sections of *Ocyurus chrysurus* ovary illustrating progression from immature to resting stages. A. Immature. B. Developing. C. Fully-developed. D. Gravid. E. Regressing. F. Resting.

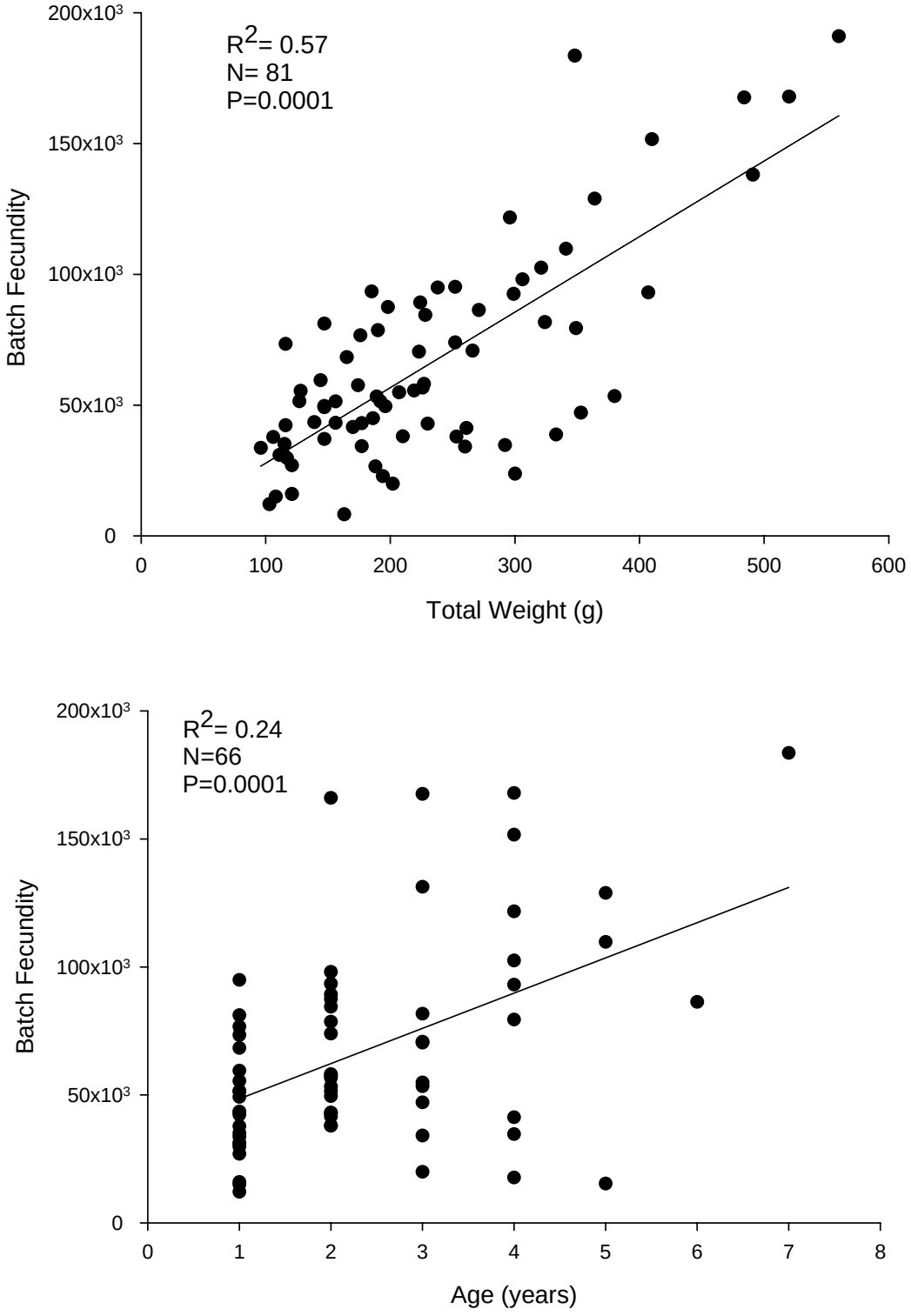

Figure 42. Plots of batch fecundity versus fish total weight (top) and batch fecundity versus fish age (bottom) for lane snapper from southeast Florida.

SECTION II – FEEDING ECOLOGY

FEEDING ECOLOGY OF FOUR SPECIES OF SNAPPERS (LUTJANIDAE) FROM SOUTHEAST FLORIDA WATERS

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INTRODUCTION

Snappers (Lutjanidae) represent an important family targeted by the recreational hook-and-line fishery in Florida, particularly in southern waters. Specific regional information is needed to identify essential fish habitat for four species: *Lutjanus analis* (mutton snapper), *L. synagris* (lane snapper), *L. griseus* (gray snapper) and *Ocyurus chrysurus* (yellowtail snapper). Information on the food habits for these species of snappers are entirely lacking for our study area in Florida, although it is available for some snapper species in other study areas, e.g. the West Indies (Randall, 1967), south Florida (Croker, 1962), Columbia (Duarte and Garcia, 1999a and b), and Cuba (Sierra, 1996-1997). Several of the snapper species are reported to be nocturnal feeders (Randall, 1967; Shipp, 1986), although recreational and commercial catch records clearly indicate snappers will take bait during daylight hours.

Published research suggests all four species spawn on reefs, or over sandy drop-offs near reefs (see review by Domeier and Colin, 1997). There are reported differences in interspecific spawning behavior. One species may aggregate to spawn in particular locations and at particular times year after year (*L. analis*), while another may be a simple

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migratory spawner on offshore reefs (*L. griseus*). The remaining two species may be non-migratory and non-aggregative spawners that can be observed on reef areas in fairly high densities even during non-spawning times (*L. synagris*, and *O. chrysurus*). Almost nothing is known about the feeding habits of these species during periods of active spawning. This study provides detailed feeding habits that can be used to characterize essential fish habitat used for feeding grounds, with particular interest in determining what foods are important just prior to and during reproductive seasons.

OBJECTIVES

(1) To describe the food habits of four snapper species. (2) To determine if foods of the four snapper species vary with season, and to identify the main foods used just prior to and during the spawning periods observed within the study area. (3) To determine the time of day when the most active feeding of snappers occurs. (4) To infer whether the main foods consumed during fat-buildup prior to spawning and during the spawning season are linked to specific habitat types (from what is known about the ecology of prey items consumed).

METHODS

Snappers were collected with both fishery-independent sampling and directed fishing. Specimens used for feeding habit research were collected between June 2000 and February 2002. From June 2000 through November 2001, we used fishery-independent methods, where systematic randomized sampling was employed using baited chevron traps paired with hook-and-line fishing (rods and reels, or limited "bandit" or electric reel rigs). We supplemented our catches during portions of the year (i.e., during reproductive periods) with additional hook-and-line fishing and spearfishing using SCUBA. Directed sampling was non-random and targeted locations where we had successfully captured fish during the randomized sampling or had observed abundant fish during reconnaissance SCUBA dives. Specific sampling protocols for specific gears are listed in separate subsections below.

-Chevron traps

For fishery-independent sampling, we randomly selected two locations each week to distribute sampling effort over all lunar phases. Locations were drawn from a pool of 1-minute cartographic grids from shore to approximately 60m of water depth, and bounded by 26° 51'N to 27° 05'N latitude and 79° 59'W longitude. By design, we sampled either in the morning (dawn to mid day) or the afternoon (mid day to evening); we sampled before sunrise or after sunset during a limited number of sampling trips. To select the trap location within the randomly selected "grid", which was approximately one square nautical mile in area, we used a pre-determined sampling protocol to locate

natural reef areas within the sampling unit. First, we traveled to the geographic center of the grid, and lowered a remote video unit to the bottom to determine the bottom type. If reef was present, we then flipped a coin to randomly select an east or west direction to search for a reef-to-sand margin. If no suitable reef margin was found within the sampling grid, we reversed direction and returned to the grid center and searched in the opposite direction to the edge of the grid. If this search pattern still did not locate a suitable trapping location, we then used an alternate grid selection strategy and repeated the process until a suitable sampling site was located. We deployed three traps in a cluster in the sand margin near reefs, using the remote video and color echosounder to pick specific drop sites. Care was taken to avoid dropping traps directly on exposed rock that would result in direct impact to epifauna on the hardbottom habitat. We baited each trap with six frozen sardines and one third of a box of commercially available frozen menhaden chum, which were placed in a small wire mesh box and suspended by a snap hook from the upper inside panel of the chevron trap. We typically deployed traps no closer than 30m to one another (usually ~100m), and pooled catches from the three samples as one replicate sampling unit. During the time when traps were soaking (a minimum of 90 minutes), we used line gears to sample additional fish which were also included as part of the random sample for this feeding study.

Locations, water depths, and times of deployment were recorded for each trap. After all tree traps were deployed, we also recorded temperature, salinity, and dissolved oxygen on both the surface and bottom using an electronic instrument (YSI-85). During periods when the YSI-85 malfunctioned, we recorded surface temperature and salinity using a mercury thermometer and refractometer.

-Hook-and-line gears

We used common bottom fishing techniques to capture snapper specimens, which typically consisted of a 20 to 35 lb line class fiberglass rod and open-faced bottom reel, spooled with either monofilament, or twisted/braided lines. We used 3-0 to 6-0 size hooks, typically connected in triples, and attached the hooks to a heavy monofilament leader approximately 1m in length, which was then attached to the line from the reel with a barrel swivel. Various sizes of lead weights were used depending on the current, and usually were between 2 and 6 ounces (e.g., egg sinker slipped on the reel line above the barrel swivel). A single dead Spanish sardine or round scad was hooked on the triple hook rigs and drifted over the bottom, typically where we observed fish in the water column using a color echo sounder. In higher current situations (1-2 kts) due to tidal movements, wind driven currents, or Florida Current effects, we often anchored and fished with bottom rigged gear, sometimes using commercially available electric bottom reels spooled with stainless steel wire. In this situation (electric reels), a large sinker was used (6 lb or more) and the length of the monofilament leader was increased to approximately 2 meters. Live bait, bycaught during the rod and reel activities, was sometimes used on the electric reel rigs. During a single set of the traps, 2-4 anglers fished within the selected cartographic grid, which typically amounted to 80 minutes of angler hours per angler.

-Spearfishing

We supplemented the random fish catches with directed spearfishing. In an attempt to minimize bias as a result of selection, divers collected snappers when encountered without regard to size of the individuals. The spear fisher's buddy, who also noted time and depth on waterproof paper, immediately placed fish on a stainless steel stringer. After the dive was completed, the locations of all speared fish were noted by the dive tender and the fish were individually labeled with collection information and bagged for laboratory examination. We immediately placed all collected fish on ice in the field and processed them within 24 hours. At this point, specimens were handled in a similar manner that is detailed below.

-Sample handling

Fish were processed in the laboratory to remove otoliths and gonads for a related life history study (see other sections of this report), at which time the stomachs from all fish were removed, wet weighed, and fixed in 10% formalin solution. Sex and macroscopic condition of gonads were also noted for each fish using methods similar to Barbieri et al. (1994). This allowed us to examine if certain feeding habits were associated with reproductive activities. Stomachs were later measured for stomach displacement, gross stomach weight, net stomach weight, and contents weight. In the first seven months of sampling, we returned the contents to 10% formalin solution prior to rough sorting using a dissecting microscope. These contents were then sieved in the lab as a separate step during the rough sorting process. Beginning in January 2001, we rough sorted stomach contents in batches on the same day that they were removed from the stomachs and weighed, which increased efficiency and allowed for a significant increase in laboratory processing efficiency. Each prey item was numbered and labeled sequentially, noted for its condition, given a separate sample container, weighed, and preserved in 70% ethanol solution. We identified prey to the lowest practical taxonomic level. This report provides summaries from the prey identifications and breaks the data into major taxonomic levels (family level or higher), although more specific identification information (in many cases to the species level) has been compiled in the database.

-Data management

All data are stored in a Microsoft Access relational database. Metadata for this data file have been prepared using Spatial Metadata Management Software (SMMS), and will be available in late 2003 upon request to the FWC-Florida Marine Research Institute metadata coordinator in St. Petersburg, Florida (currently Jill Trubey at (727) 896-8626 or jill.trubey@fwc.state.fl.us).

RESULTS

We found a fairly large percentage of three species of snappers held no prey in their stomachs (49% of gray snapper, 29% of lane snapper, 50% of mutton snapper, and 3% of yellowtail snapper). Regurgitation was also common, but easily identified by the

condition of the stomach that was either entirely or partially everted (Table 1). This was previously reported in other snapper diet studies (*e.g.*, DeMartini et al., 1996) All individuals showing evidence of eversion at the time of lab processing were rejected for diet analysis but still remained part of the life history study. Stomach eversion was particularly common for fish caught on hook and line, and lane snapper had a higher incidence of eversion than the other three species (Table 1). Although we excluded 260 fish due to evidence of regurgitation, we still had sufficient sample size for an evaluation of all four species, ranging from a low of 77 yellowtail snapper to a high of 469 lane snapper (Table 1).

Because of the large number of gray, lane, and mutton snappers that had no prey in their stomachs, we felt a need to evaluate whether our collection techniques using bait attracted fish that were more apt to be seeking food (*i.e.*, "hungry fish"). To do this, we employed directed spearfishing and compared the percentages of fish with empty stomachs collected using bait (by trap or hook and line) or without bait (by spear). Results of this evaluation showed no clear trends, with both speared lane (Fig. 1) and gray snappers (Fig. 2) having a prey masses consistent with those from fish collected using baited gears. The readers should note that the largest bars to the right of Figs. 1 and 2 are all the same magnitude for each gear type and correspond to fish with empty stomachs. Further examination using a gut fullness index showed similar results (see methods from Prejs and Colomine, 1981). It appears there may be a trend for prey masses from hook-and-line lane snapper tending to be larger on the opposite end of the distribution with respect to fish from other gears (Fig. 1). This corresponds well with the trend for sizes of hook-and-line catches of lane snapper, displaying a shift towards larger maximum size and mode when compared to speared and trapped fish (Fig. 3). This apparent gear-dependent difference in distribution of lane snapper catches was not apparent in gray snapper data (Fig. 4), although speared fish tended to have a lower central tendency (mode, median, or mean) with respect to the other two collection gears.

To examine if there were trends for diel changes in feeding activities (Objective 3), we plotted prey masses against time of day and also examined if there were times of the day when catches were higher. Since we fished with baited gears, this could be related to feeding activity if fish were more apt to respond to baits at daily times of naturally increased feeding (*e.g.*, crepuscular periods). Fish were caught with baits throughout the day, and a plot of prey mass to weight was also inconclusive (a scatter plot with no distinct pattern). We saw little relationship between observed prey mass and time of day or magnitude of catch and time of day. There was a tendency to pull traps more often at certain times of the day. This sampling artifact introduced a pattern to catches, but we do not believe this represented increased vulnerability or attraction to gears at any particular time of day.

Gray snapper consumed invertebrates, plants, fish and reptiles (Table 2). Bony fishes, various crabs, and shrimps were common prey and together composed the top four preys in numerical abundance (Table 1a). Sea turtle post-hatchlings ranked fifth in numerical abundance and first in mass for pooled stomach contents (Table 1a). For reproductively active females, sea turtles accounted for 4% of prey numbers and 57% of prey mass (Table 2b). Male gray snapper consumed a higher number of turtle post-hatchlings (n=10) than females (n=6). Gray snapper fed on two species of sea turtles,

primarily on loggerhead (*Caretta caretta*, Chelonidae), but one leatherback post hatchling (*Dermochelys coriacea*, Dermochelydae) was also recorded.

Lane snapper diet was moderately similar to that observed for gray snapper, with invertebrates and fish making up the top three prey types in terms of numerical abundance (Table 3a and b). The most striking difference between lane and gray snapper diets was a near complete lack of sea turtle hatchlings from lane snapper, although we did observe a fragment of one young loggerhead in a single stomach (Table 3a). In contrast, there was a distinct seasonal consumption of sea turtle hatchlings by gray snapper during summer to early fall (Table 2b). We found rock shrimp (Sicyonidae) to rank higher in numbers and mass for lane snappers overall (Table 3a), and particularly for females found in reproductive condition (Table 3b). Sicyonids were relatively unimportant in gray snapper diets (Table 2a and b). Mantis shrimps show promise in identifying specific habitats where lane snapper feed due to their particular niches; some stomatopod families are generally reef dwellers while others are sand dwellers and a good proportion of these prey were in condition suitable for keying to family level or lower. Preliminary results indicate lane snapper are feeding on sand habitat as well as on reef, more so than gray snapper, at least with respect to where they target stomatopod prey. Gray snapper consumed relatively more stomatopod in the Gonodactylidae (primarily reef dwelling, Dave Camp personal communication), while there was a more even split of stomatopods in the Gonodactylidae and Squillidae (typically sand dwelling) from lane snapper stomach contents. Swimming crabs (Portunidae) made the top 2-4 numerically dominant prey of lane and gray snapper (Tables 2 and 3). Crabs of the genus *Portunus* are very common prey of both lane and gray snapper, and we believe some of the species involved live on sandy bottoms but could move nocturnally to reef habitat.

Bony fish (Osteichthyes), swimming crabs (Portunidae), and mantis shrimps (Stomatopoda) were common prey of mutton snapper *(Lutjanus analis*). Bony fish made up 11.7% of prey numbers and 30.7% of prey mass, and is considered the dominant prey type (Table 4). Although mantis shrimps accounted for 13.3% of prey numbers, their low contribution to total prey mass (3.2%, Table 4) places them in a lower level of importance to other prey such as swimming crabs. Overall, crabs of many types were observed in mutton snapper stomachs, including spider crabs (Majidae), walking crabs (Xanthidae), and shame-faced crabs (Calappidae). This demonstrates a strong dependence of mutton snapper on benthic softbottom habitats (particularly sand plains) as feeding grounds. Shrimps of any type seemed less important in the diet of mutton snapper compared to the diet of either lane or gray snapper, at least with respect to the total prey mass consumed (Table 4).

The diet of yellowtail snapper (*Ocyurus* chrysurus) was much more dependent on water column feeding resources, in sharp contrast to the other three species that were more associated with benthic habitats (reef and sand bottoms). This species responded well to baits and chum, often gorging themselves on ground menhaden released as part of the sampling methods. Because of this, however, baited methods were not well suited for diet study because the chum and bait made separation of natural prey from stomach contents time consuming and tedious. For this reason we systematically subsampled the yellowtails stomachs due to the time necessary to pick out tiny prey from a 25-40g bait mass on the microscope. To eliminate bait contamination of prey items, we also tried

substituting a frozen-liquid chum (menhaden oil) for the ground menhaden chum, but discontinued this after a few weeks because it may have been less effective in attracting snappers. Although 40.5% of the prey mass of yellowtail snapper was composed of bony fishes (Osteichthyes), this prey type only accounted for 4.8% of prey numbers (Table 5). Despite a fairly large gape, we found a surprisingly large number of very small-bodied prey in the diet of yellowtail snappers, including calanoid and cyclopoid copepods, pelagic molluscs such as heteropods and pteropods, phyllosome larvae of spiny lobster, crab and shrimp larval forms, amphipods associated with gelatinous organisms (Hyperiidea), and arrow worms (Table 5). Presence of larval fish also leads us to believe that the common feeding location for yellowtail snapper in our study area is off the bottom. Yellowtail snapper consumed many types of shrimp, including penaeid shrimp, and hippolytid shrimp, which when combined with other types of shrimp approximated 19% of the total prey mass and 9% of prey numbers (Table 5). Segmented worms (Polychaeta), accounted for a small mass fraction (2.1%) but a fair proportion of prey numbers (14.7%). Many of the polychaetes were either larval forms or pelagic in habits, further linking yellowtail feeding to food in the water column.

DISCUSSION

This project yielded some interesting habitat use information for all species examined, and allows us to identify study-area specific food resources that are used by these important fishery species. Some of the information was not entirely new and followed along with information available in technical reports or published studies. For example, the diet of yellowtail snapper included pelagic foods such as plankton, which was in line with other published work (Randall, 1967). Some aspects are intriguing, however, from a feeding morphology and foraging theory perspective. The size range of prey consumed by yellowtail snapper encompassed a large range, from copepods to fairly large fish (15cm long or more), which demonstrates a generalist feeding habit that we did not expect.

Manuscripts published as a result of this project will further examine specific habitat that are essential for gray, lane, and mutton snapper. There was a fair amount of diet overlap for these three species, at least at higher levels of taxonomy. We plan detailed multivariate analysis for peer-reviewed manuscript that will yield additional characterizations of their diets (see methods of Clarke and Warwick, 1994) and will statistically examine feeding seasonality as it relates to reproductive periods. In general, mutton snapper diet indicates that this species is most closely tied to off-reef habitat for feeding grounds. This agrees well with our direct observations by SCUBA because we most often observed mutton snapper over sand habitat and broken reef bottom, but not typically over well developed reef ledges. Lane snappers utilize both on and off reef prey resources, which also agrees well with our field observations during spear collections. Lane snapper on some suspected spawning locations congregated in large schools over sandy drops in close proximity to large rock ledges, similar to what previously reported for some lutjanids (Domeier and Colin, 1997). Foods are taken both from reef and sand areas by lane snapper, while gray snapper tended to utilize a higher proportion of prey

directly from reefs. This also agreed well with our SCUBA observations, in that we often found gray snapper in large numbers near the edges of large reef ledges, particularly up on the terraces above steep drops to sandy bottom.

Of course, we feel it is important to note that we know very little about how these fish behave at night, and the well digested condition of the many of the prey fishes may indicate that nocturnal feeding occurs. Some snappers have been reported to have a fairly rapid rate of digestion for fish prey (Reshetnikov et al., 1974), and much of the digestion could have occurred during the time fish were stored on ice prior to processing. In contrast to some reports, the snappers in our study area were not primarily nocturnal feeders, which was clearly demonstrated by good condition of many of the prey, including arthropods and seaturtle post hatchlings.

Gray snapper also feed well above the bottom, in contrast to what we predicted (benthic-oriented habits). This can be inferred from the observations of young sea turtles found in their diets. In areas where we collected these fish, it was 20-22m deep and the turtles are not known to swim down from the surface for more than a few meters, mainly only in response to attacks by sea birds. This may be a seasonal feeding habit that only occurs during turtle emergence in summer to fall months, however, it was observed for two different years (five neonates were taken in the first year and 11 in the second year). Because we observed this habit in multiple years, we feel it is accurate to assign sea turtle hatchlings as having an important role as food targeted during the gray snapper spawning season (see other sections of this report). Our observations also included the first published record of natural fish predation on a leatherback post-hatchling (Vose and Shank, 2003), and offshore predation risk posed by reef fishes away from shore may be greater for sea turtle young than previously reported.

We were able to establish information regarding utilization of particular foods during reproductive seasons for only two of the four species of snapper (*L. griseus* and *L. synagris*). Our sampling did not record enough numbers of yellowtail or mutton snapper in spawning condition to evaluate whether certain prey are targeted during reproductive seasons. These fish may actually be spawning in our study area, but we were unable to detect this through a combination of randomized and directed sampling routines.

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Table 1: Summary of the numbers of snapper specimens collected as part of a 20-month study of the feeding habits of *Lutjanidae* in southeast Florida.

	# fish with prey	# with empty stomachs	# with regurgitation	totals	# used in this study
Gray snapper	138	68	40	246	206
Lane snapper	364	105	180	649	469
Mutton snapper	52	26	4	82	78
Yellowtail snapper	74	3	36	113	77
All species	628	202	260	1090	830

Table 2: A summary of the numbers of prey and prey masses of gray snapper, *Lutjanus griseus*, resulting from an examination of 206 stomachs (a) and from a subset of only females in active reproductive condition (b).

a.

Prey Category	%Abundance	% Mass
Shrimp, other	20.07	2.519
Portunidae	17.11	16.919
Osteicthyes	17.11	26.219
Brachyura, other	9.44	1.339
Testudines	5.26	41.0345
Calappidae	2.96	1.591
Gastropoda	2.63	1.899
Crustacean, other	2.3	0.325
Stomatopoda	2.3	0.3869
Cirripedia	1.97	0.052
Majidae	1.97	0.6114
Xanthidae	1.97	0.695
Spec. unid	1.97	0.0437
Algae	1.64	0.008
Plant material	1.64	0.21
Sicyonidae	1.64	0.0725
Penaeidae	1.32	0.256
Decapod, other	0.99	0.1425
Echinoida	0.99	5.011
Bivalvia	0.99	0.1365
Alpheidae	0.66	0.0289
Caridea	0.66	0.0036
Albunidae	0.33	0.12
Anomura	0.33	0.087
Decapod larvae	0.33	0.0002
Leucosiidae	0.33	0.0144
Paguridae	0.33	0.0063
Polychaeta	0.33	0.0241
29 prey types	**100%**	**100%**

b.

Prey Category	%Abundance	% Mass
Shrimp, other	23.36	3.72
Osteicthyes	14.60	19.10
Portunidae	13.87	7.02
Brachyura, other	5.84	1.42
Cirripedia	4.38	0.18
Calappidae	4.38	2.81
Stomatopoda	4.38	1.18
Testudines	4.38	57.45
Algae	2.92	0.02
Majidae	2.19	0.72
Bivalvia	2.19	0.49
Penaeidae	2.19	0.18
Spec. unid	2.19	0.09
Xanthidae	1.46	0.94
Decapod, other	1.46	0.46
Gastropoda	1.46	3.25
Plant material	1.46	0.03
Alpheidae	1.46	0.10
Sicyonidae	1.46	0.16
Decapod larvae	0.73	0.00
Leucosiidae	0.73	0.05
Crustacean, other	0.73	0.01
Bothidae	0.73	0.60
Caridea	0.73	0.00
Crustacean, larva	0.73	0.01
Gastropoda	1.46	3.25
27 prey types	**100%**	**100%**

Table 3: A summary of prey numbers and prey masses from lane snapper, *Lutjanus synagris*, resulting from the examination of 469 stomachs (a), and from a subset of only females in active reproductive condition (b).

a.

Prey Category	%Abundance	%Mass
Shrimp, other	44.36	14.95
Portunidae	9.80	22.81
Osteichthyes	8.11	19.42
Penaeidae	5.48	2.05
Stomatopoda	4.43	7.88
Sicyonidae	3.69	4.08
Brachyura	3.48	3.62
Majidae	2.11	2.81
Crustacea, other	1.79	1.40
Specimen unknown	1.77	1.16
Calappidae	1.37	4.68
Xanthidae	1.37	1.12
Shrimp, larval	1.05	0.03
Alpheidae	0.95	0.62
Caridea	0.95	0.24
Polychaeta	0.84	0.82
Algae	0.74	0.10
Processidae	0.74	0.06
Decapoda, other	0.73	0.09
Amphipoda	0.53	0.01
Echinoida	0.53	1.13
Albunidae	0.42	4.12
Isopoda	0.42	0.05
Bivalvia	0.42	0.15
Gastropoda	0.42	1.57
Plant material	0.42	0.09
Anomura	0.32	1.25
Raninidae	0.32	0.79
Mollusca	0.32	0.13
Cephalopoda	0.32	0.87
Scyllaridae	0.32	0.68
Stomatopoda, larval	0.32	0.03
Bryozoa	0.21	0.06
Leucosiidae	0.21	0.10
Pasipheidae	0.21	0.04
Shrimp, planktonic	0.21	0.00
Chaetognatha	0.11	0.00
Cnidaria	0.11	0.90
Calanoida	0.11	0.00
Paguridae	0.01	0.78

b.

Prey Category	%Abundance	%Mass
Shrimp, other	37.06	13.19
Portunidae	11.42	15.45
Osteichthyes	9.64	18.56
Sicyonidae	6.35	8.31
Stomatopoda	5.58	12.71
Majidae	4.06	5.82
Brachyura	3.30	2.94
Penaeidae	3.05	0.47
Xanthidae	2.03	1.26
Calappidae	1.52	3.35
Specimen unknown	1.27	1.64
Amphipoda	1.02	0.01
Crustacea, other	1.02	0.03
Polychaeta	1.02	0.92
Shrimp, larval	1.02	0.03
Algae	0.76	0.17
Echinoida	0.76	0.02
Alpheidae	0.76	1.18
Albunidae	0.51	6.41
Leucosiidae	0.51	0.02
Decapoda, other	0.51	0.09
Gastropoda	0.51	0.19
Plant material	0.51	0.18
Caridea	0.51	0.30
Shrimp, planktonic	0.51	0.00
Stomatopoda, larval	0.51	0.07
Chlorophyta	0.25	0.01
Rhodophyta	0.25	0.00
Anomura	0.25	0.66
Chaetognatah	0.25	0.02
Cnidaria	0.25	2.09
Calanoida	0.25	0.00
Paguridae	0.25	1.84
Pinnotheridae	0.25	0.09
Decapod, larval	0.25	0.00
Fish egg	0.25	0.00
Holothuroidea	0.25	0.74
Isopoda	0.25	0.05
Mollusca, other	0.25	0.04
Bivalvia	0.25	0.05

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Table 3: Lane snapper, *Lutjanus synagris* (continued).

Pinnotheridae	0.11	0.04	Scyllaridae	0.25	0.62
Fish egg	0.11	0.00	Ogyrididae	0.25	0.07
Holothuroidea	0.11	0.32	Solenoceridae	0.25	0.39
Ogyiridae	0.11	0.03			
Palaemonidae	0.11	0.01			
Solenoceridae	0.11	0.17			
Taniadacea	0.11	0.03			
Thalassinidea	0.11	0.03			
Testudines	0.11	0.06			
51 prey types	100%	100%	**44 prey types**	100%	100%

Table 4: A summary of prey numbers and prey masses from mutton snapper, *Lutjanus analis,* resulting from the examination of 78 stomachs.

Prey Category	%Abundance	%Mass
Stomatopoda	13.33	3.22
Osteichthyes	11.67	30.70
Brachyura, other	11.11	1.42
Portunidae	10.56	23.71
Shrimp, other	10.00	0.87
Calappidae	9.44	13.08
Majidae	6.67	2.88
Algae	2.78	0.35
Xanthidae	2.78	3.34
Crustacea, other	2.22	6.40
Decapoda, other	2.22	0.40
Alpheidae	2.22	0.16
Albunidae	1.11	1.09
Raninidae	1.11	0.20
Fish scales	1.11	0.00
Syngnathidae	1.11	0.05
Penaeidae	1.11	0.07
Specimen unknown	1.11	0.01
Amphipoda	0.56	0.01
Bryozoa	0.56	0.00
Anomura	0.56	0.76
Palinuridae	0.56	1.82
Gobiidae	0.56	0.01
Ophichthidae	0.56	1.38
Isopoda	0.56	0.02
Cephalopoda	0.56	0.14
Gastropoda	0.56	0.01
Nematoda	0.56	0.00
Plant material	0.56	0.03
Polychaeta	0.56	0.71
Callianassidae	0.56	6.76
Caridea	0.56	0.04
Sicyonidae	0.56	0.35
33 prey types	**100%**	**100%**

Table 5: Summary of prey numbers and prey masses from yellowtail snapper, *Ocyurus chrysurus,* resulting from the examination of 77 stomachs.

Prey Category	%Abundance	%Mass
Copepoda	14.72	1.00
Polychaeta	14.72	2.14
Shrimp, other	9.06	18.94
Chaetognatha	8.25	0.33
Calanoida	5.50	0.14
Heteropoda	5.02	1.69
Osteichthyes	4.85	40.48
Crustacea, other	4.69	1.52
Cyclopoida	4.53	0.09
Amphipoda	4.37	0.14
Pteropoda	2.91	0.19
Specimen unknown	2.75	1.15
Gammaridea	1.46	0.10
Osteichthyes, larval	1.46	0.12
Mollusca, unknown	1.46	0.26
Decapoda, other	1.29	0.11
Isopoda	1.29	0.34
Stomatopoda	1.29	7.65
Palinuridae, phyllosoma	1.13	0.31
Megalopa	0.97	0.07
Portunidae	0.97	10.80
Algae	0.81	0.10
Cephalopoda	0.65	2.81
Shrimp, planktonic	0.65	0.03
Cnidaria	0.49	0.12
Brachyura, other	0.49	1.71
Shrimp, larval	0.49	0.05
Hyperidea	0.32	0.01
Majidae	0.32	2.11
Mysidacea	0.32	0.00
Ostracoda	0.32	0.01
Plankton, unknown	0.32	0.37
Siphonophora	0.32	0.02
Caprellidea	0.16	0.01
Cladocera	0.16	0.00
Calappidae	0.16	1.42
Xanthidae	0.16	0.13
Echinoida	0.16	0.00
Egg mass	0.16	0.04
Fish egg	0.16	0.03
Gastropoda	0.16	0.02
Hippolytidae	0.16	1.66
Penaeidae	0.16	1.59
Stomatopoda, larval	0.16	0.17
44 prey types	**100%**	**100%**

Figure 1: Prey masses found in *Lutjanus synagris* stomachs by gear type. Front panel of bars represent log transformed data from fish collected by spear, center panel from fish collected by hook and line, and the rear panel from fish collected by trap.

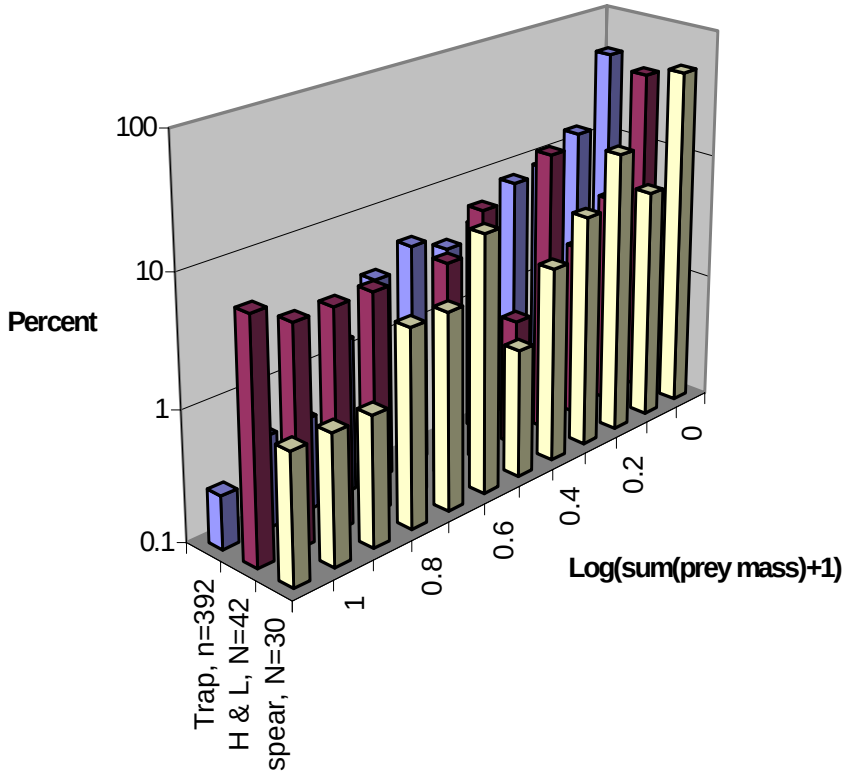


Figure 2: Prey masses found in *Lutjanus griseus* stomachs by gear type. Front panel of bars represent log transformed data from fish collected by spear, center panel from fish collected by hook and line, and the rear panel from fish collected by trap.

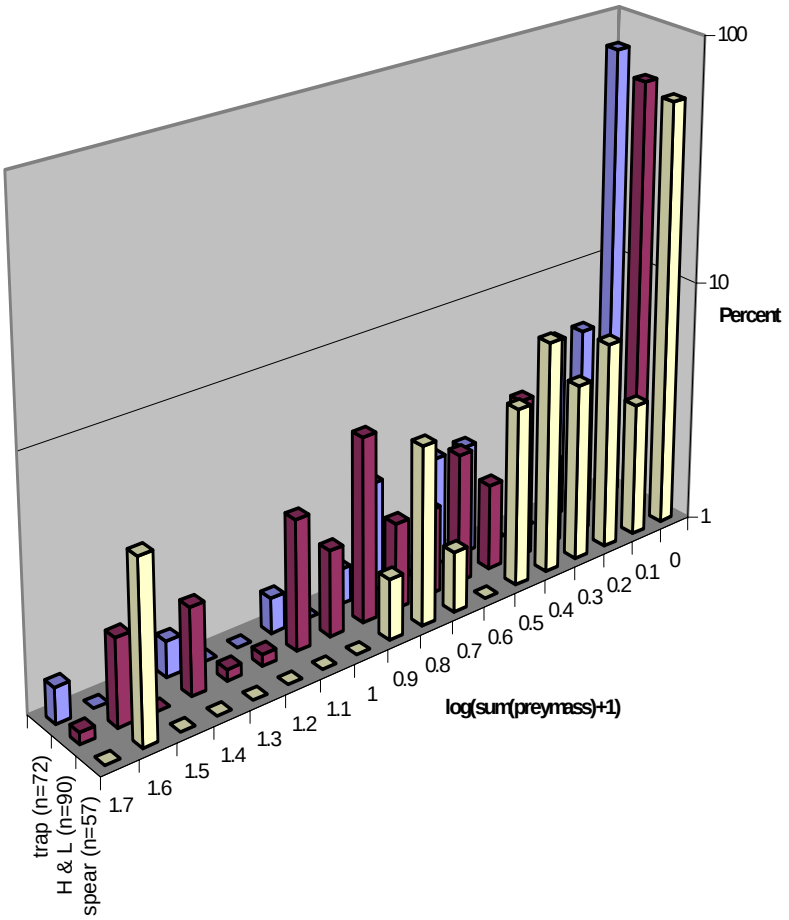
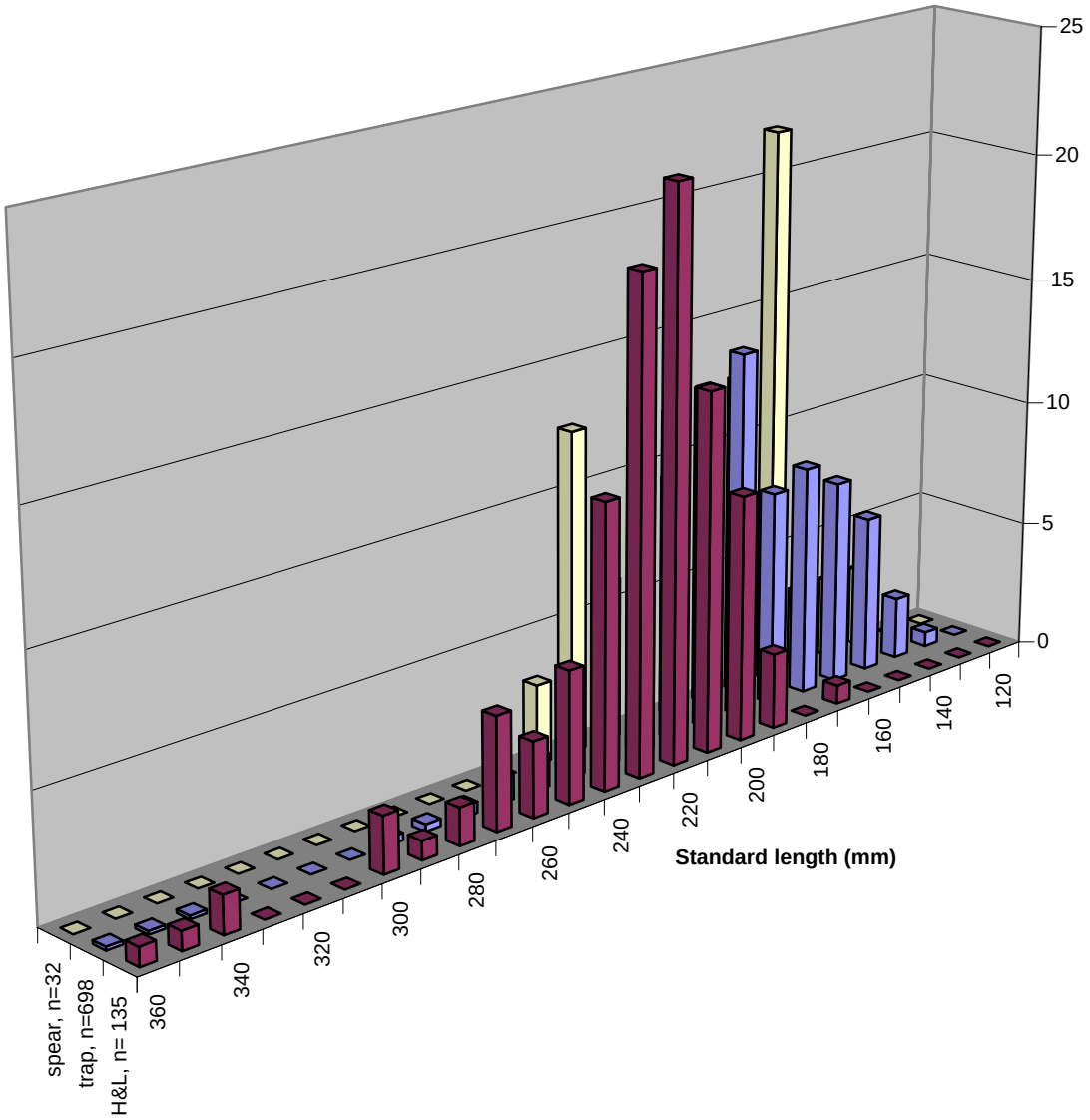


Figure 3: Distribution of *Lutjanus synagris* standard length by gear type



PREDATION ON LOGGERHEAD AND LEATHERBACK POST-HATCHLINGS IN OFFSHORE WATERS BY GRAY SNAPPER

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Sharks and finfishes have been documented as a significant source of mortality for hatchling sea turtles entering the ocean from rookery beaches and during the swim-frenzy period en route to nursery habitats (Witham 1974; Woodard 1980a; 1980b; 1980c; Witzell 1981; Stancyk 1982; Carr 1986; Witherington & Salmon 1992; Gyuris 1994; Wyneken & Salmon 1994). The aforementioned studies report snappers (*Lutjanus* sp.), tarpon (*Megalops atlanticus*), sea bass (*Centropristis striata*), grouper (*Epinephelus* spp., *Promicrops* sp.), moray eels (Muraenidae), barracuda (Sphyraenidae), jacks (*Caranx* spp.), wrasses (Labridae), parrotfish (Scaridae), dolphin (*Coryphaena hippurus*) and catfish (*Arius* sp.) as predators of loggerhead (*Caretta caretta*), green (*Chelonia mydas*), Kemp's ridley (*Lepidochelys kempi*) and hawksbill (*Eretmochelys imbricata*) turtles. Unfortunately, these studies provide little or no qualitative or quantitative data regarding the predatory fishes involved, and predominately studied predation occurring directly adjacent to the nesting beaches. Fish predation on post-hatchlings (hereafter defined as neonates no longer in frenzied-swimming mode, Wyneken & Salmon 1992) in the western Atlantic has had limited study, particularly in continental-shelf waters away from nesting beaches. Here we present data on the frequency of occurrence of loggerhead (*Caretta caretta)* and leatherback (*Dermochelys coriacea*) post- hatchlings in the stomach contents of gray snappers (*Lutjanus griseus*) collected over offshore reef areas well to the east (2.5-11.5km) of high-density nesting beaches in southeastern Florida (study area bounded by 27º 05'N, 79º 59'W; 27º 05'N, 80º 08'W; 26º 51'N, 79º 59'W; 26º51' N, 80º 03'W). Additionally, we provide data on the physical characteristics of predatory snappers in relation to the size and condition of the post-hatchling turtles consumed.

Fish were collected as part of a study that is examining the feeding ecology of gray (*Lutjanus griseus*), lane (L. synagris), *mutton (L. analis*), and yellowtail (*Ocyurus chrysurus*) snappers, which focuses on identifying the principal prey that snappers consume just prior to and during the their spawning season. We collected fish specimens from June through November 2000, a period spanning the sea turtle hatching season in our study area. The sampling area is a coastal section of southeast Florida extending from navigable, nearshore waters out to a depth of 60 m. Sampling sites were randomly drawn from a pool of one-minute cartographic grids, and sampling locations within grids were selected using a sampling protocol for identifying reef structure within each grid (approximately 1 square nautical mile). At each sampling site, we collected fish with wire fish traps containing bait and with bottom-rigged hook-and-line gear. We sampled

two sites per week, setting three traps adjacent to hard bottom at each site. Collected specimens were immediately placed on ice for later processing in the laboratory. Processing of specimens included measuring the fish lengths and weights, removing and weighing gonads, macroscopically assessing reproductive state, removing and weighing stomachs, and fixing stomachs and all their contents in a 10% formalin solution. Contents were later extracted from the stomach, individually identified, counted, and weighed.

A total of 111 gray snapper were collected during the sampling period, 22 of which were excluded from stomach-content analysis because they had partially or fully everted stomachs. A total of 99 prey items were extracted from the remaining 89 specimens, including seven turtle post-hatchlings from the stomachs of five fish. All of the fish with turtles in their stomachs in our study samples were captured on two dates and at three locations (Table 1). These fish were captured between 1531 and 2105 hrs. in depths of 21-22 m. Of the 5 snapper that had post-hatchlings in their stomachs, one fish contained a whole leatherback hatchling weighing 39.4g (specimen 1, Table 1). The remaining four fish contained loggerhead post-hatchlings: specimen 2 had a slightly damaged hatchling and fragments of a second, specimen 3 had fragments of a post-hatchling, specimen 4 had two whole post-hatchlings, and specimen 5 had a single whole post-hatchling (Table 1). Pooling all prey items found in all gray snapper stomachs, sea turtle post-hatchlings represented 7.1% of prey items and 55.3% of identifiable prey by weight, excluding our bait and any unidentifiable material in an advanced state of digestion. When we included this unidentified material but excluded our bait, sea turtle prey composed 47.6% of all the stomach contents. Although one of us (FEV) had previously observed gray snappers surface feeding in 10-13 m depths in the Florida Keys, we did not expect to record predation of surface-dwelling prey in the deeper water areas (21-22 m) of this study. We had presumed gray snapper would not be found to feed on surface prey because they are typically caught with bottom-fishing rigs. It is possible, though unlikely, that some of the neonate turtles were consumed nearer shore the day before, and the fish subsequently moved 5-7.5km east to the collection sites. Since gray snapper may enter offshore waters in July in the southernmost portions of Florida (Domeier et al. 1996), and the consumed turtles had not grown beyond the size of a typical neonate, (Witherington 1994), we believe that the gray snapper consumed the prey in the immediate vicinity of our study area. Only one of the turtle prey showed evidence of advanced digestion, and carapace scutes, which readily detach during digestion, were very well attached in two other loggerhead specimens. Based on the rapid prey digestion reported for several snapper species including *L. griseus*, with advanced digestion (90-97%) of prey in 14-22 hrs. when water temperatures were 28-29º C (Reshetnikov et al. 1974), it is unlikely that the turtles were taken far from the immediate collection locations. We conclude that the gray snapper consumed at least some of the post-hatchlings on site and near the surface, given the reported feeding and diving behavior of early hatchlings (Bjorndal 1997, Musick & Limpus 1997, Witherington 1995), the buoyant nature of the hatchlings due to their lipid reserves (Carr 1982), and the condition of the hatchling prey.

There was little evidence that other species of snappers examined as part of this study consumed turtle neonates. We did observe one fragment of an appendage from what appeared to be a loggerhead post-hatchling in the stomach of a single lane snapper (*L. synagris*), but did not observe turtle prey in the diet of any mutton (*L. analis*), or

yellowtail (*Ocyurus chrysurus*) snappers examined. We would have expected yellowtail snapper, which were observed to feed higher in the water column, as more likely to feed on surface prey than the other three species. Mouth gape may play an important role in determining which individuals within a species are capable to prey on neonate turtles, particularly with respect to larger leatherback young. Gray snapper are the most common snapper species at 3 of 4 sites where turtles were taken. Surface observations of currents in the majority of these locations may also support downwelling along a Florida Current front as one possible reason (Witherington 2002) why these particular reef areas are unique compared to the larger sample area. These fronts, evidenced by distinct color and surface disturbances, may cause a concentration of turtle prey to occur regularly over certain reefs during the hatching season.

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Table 1: Data regarding fish which had consumed turtle post-hatchlings including description of stomach contents and turtle morphometrics (SCL: Straight Carapace Length; CCL Curved Carapace Length, SCW: Straight Carapace Width; CCL Curved Carapace Width)

a. Fish specimen #	**1**	**2**	**2**	**3**	**4**	**4**	**5**
Collection Location	27 00.493N 80 01.086W	27 02.462N 80 03.065W	27 02.462N 80 03.065W	27 00.483N 80 01.092W	27 00.341N 80 01.077W	27 00.341N 80 01.077W	27 00.341N 80 01.077W
Depth (m)	22	21	21	22	22	22	22
Date	7/10/2000	7/10/2000	7/10/2000	7/10/2000	8/28/2000	8/28/2000	8/28/2000
Time	1718	2105	2105	1733	1531	1531	1551
Standard Length (mm)	319	381	381	293	293	293	322
Total Length (mm)	402	480	480	360	369	369	401
Fish Weight (g)	907	1486	1486	605	643	643	853
Gonad Weight (g)	13.3	56.0	56.0	14.5	29.0	29.0	17
Sex	Male	Male	Male	Female	Female	Female	Male
Gear	Trap	Trap	Trap	Trap	Hook & line	Hook & line	Hook & line
b. Turtle specimen #	1	2	3	4	5	6	7
Prey Weight (g)	39.4	16.4	4.5	2.07	16.0	15.8	16.6
SCL/CCL (cm)	6.0/6.6	4.0/4.5	NA	NA	4.5/4.9	4.3/4.6	4.2/4.6
SCW/CCW (cm)	3.2/5.2	NA	NA	NA	3.0/4.1	3.2/4.2	3.2/4.2
Prey Species	Leatherback	Loggerhead	Loggerhead	Loggerhead	Loggerhead	Loggerhead	Loggerhead
Note/Prey condition	Whole	Carapace damaged	Fragments	Fragments	Whole	Whole	Whole

SECTION III – ARTIFICIAL REEF MONITORING

COMPARISON OF FISH ASSEMBLAGES ON ARTIFICIAL AND NATURAL REEFS OFF SOUTHEAST FLORIDA

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Abstract

Fish assemblages were monitored for species composition, abundance, and fish size on artificial reefs constructed of three different materials from December 1998 to March 2001. During the final 13 months of this period, adjacent natural reefs were also monitored and compared to the artificial reefs. We censused a total of 157 species and 45,297 fishes on artificial reefs and 123 species (4,922 fishes) on natural reefs. Artificial reefs supported considerably higher numbers of fish than natural reefs, especially species of economic importance (32 species and 64% of individuals), and lutjanids were over ten times more abundant there. On the other hand species diversity was highest on natural reefs, as was the ratio of juvenile to adults, and both parameters were positively correlated with vertical relief. In contrast, high relief among artificial reefs was associated with high fish abundance, especially for several species of lutjanids. Fish assemblages on a low relief limestone boulder artificial reef were the most similar to those found on the adjacent natural reef, while those on a high relief barge were the most dissimilar. Latitudinal variation was evident among fish assemblages for both artificial and natural reefs, and this variation was positively correlated with geographic distance. Colonization occurred rapidly on a recently deployed artificial reef; carangids were initially the most abundant taxa followed by scarids between the first and second years post-deployment.

Introduction

The deployment of artificial reefs has become widespread during the past 35 years, in part due to the desire to partially compensate for human impacts to natural reef systems. This practice is especially common in Florida, where approximately 350 reefs have been created during this period (Pybas, 1997; Grossman et al., 1997). Despite the enormous popularity and interest in artificial reef construction, the influence of these structures on local fish assemblages is still not well understood (Bohnsack et al., 1994; Bohnsack and Sutherland, 1985; Seaman and Sprague, 1991), and the relative effects of different construction materials on these assemblages has seldom been evaluated.

Despite frequent claims that artificial reefs enhance fish populations by providing additional habitat, one of the main criticisms against their use is that observations of high abundances on these structures may simply represent a redistribution of individuals rather than an actual increase in fish production (Bohnsack, 1989). Most reef fish are characterized by a bi-partite life history consisting of a planktonic stage, during which eggs and larval fish are dispersed from a spawning area, and a subsequent benthic stage. Since most reef fish populations ultimately depend on settlement of larval fishes from planktonic sources, these populations may be more influenced by variations in larval supply than by the amount of available habitat (Doherty and Williams, 1988; Richards and Lindeman 1987). Therefore, deployment of additional habitat may be of little consequence in increasing local fish populations, and may even prove deleterious if fish are attracted to these structures, and thus become more susceptible to overfishing (Bohnsack and Sutherland 1985: Bohnsack 1989). Furthermore, reef fish often have specific habitat requirements at the time of settlement from the plankton (Ross and Moser, 1995; Light and Jones, 1997) and therefore many habitats will not provide adequate levels of food and shelter for these early life-stages. Thus, an important management question concerns whether artificial reefs can be designed which function to enhance populations of economically valuable fish while also providing suitable habitat for newly settled and juvenile fish.

The goal of this study was to characterize fish assemblages found on artificial reefs offshore southeastern Florida, to better understand their effectiveness as a reef fish management tool. Specific objectives were to: 1) evaluate the effectiveness of artificial reefs in enhancing numbers of economically important species, 2) evaluate the effectiveness of artificial reefs in enhancing numbers of juvenile and newly-settled individuals, and 3) compare fish assemblages on artificial reefs constructed of different materials with those occurring on natural reefs. We also investigated whether species composition responded to variations in vertical relief and geographical position, and examined changes that occurred in the assemblage composition with respect to the age of the reef and colonization stage.

Materials and Methods

Description of monitoring sites

Artificial and natural study sites were located in mid-shelf waters off southeastern Florida where the continental shelf is between 3 and 6 km wide (Figure 1). This area is predominantly influenced by the Gulf Stream Current which delivers warm, clear water in a northerly direction during much of the year (Lee et al., 1986). Variations in this current along the outer shelf can cause reversals from the normal northward flow and result in cold-water upwellings even during warmer summer months (Smith, 1983).

Three artificial reefs (MG-111, Tri-County Reef, and Boynton Corridors) placed as part of the Palm Beach County's Department of Environmental Resources Management's Artificial Reef program were selected for detailed study. Natural hardbottom study sites consisting of lithified Pleistocene beach ridges and oriented roughly parallel to the present day shoreline (Lovejoy, 1987) were selected near artificial reef sites. Specific descriptions of these sites are provided below.

Artificial reefs

MG-111 is a 60 m hopper barge with approximately 914 metric tons of concrete and was scuttled in 1995. It is located in 18 m of water, about 3 km northeast of the Jupiter Inlet (26^{0}56.6'N, 80^{0}04.3'W) and approximately 5 km offshore. MG-111 has a maximum vertical profile of 5 m, and is approximately 60 m from the nearest natural reef.

Tri-County Reef was built between 1989 and 1992, and is made up of approximately 6,096 metric tons of concrete placed in 18 to 20 m of water. It is located approximately one mile south of the Palm Beach Inlet (26^{0}46.3', 80^{0}00.6') and approximately 300 m northwest of the closest natural reef. This reef is the largest artificial reef monitored during this study, with an areal extent of approximately 1.6 hectares. It has a vertical profile of up to 3 m.

Boynton Beach Corridor consists of approximately 3,048 metric tons of natural limestone rock, roughly 0.3 to 1.0 m in diameter, placed in 24 to 25 m of water, 6 km south of the Palm Beach Inlet (26^{0}32.7'N, 80^{0}02.5'W), at a distance of approximately 300 m from the nearest natural reef. This reef was built in 1998, has an average vertical profile of 1 m., and is linearly configured (approximately 3 m. wide by 300 m. long). Genesis Reef is adjacent to the southern end of Boynton Beach Corridor and is composed of approximately 1,020 tons of concrete with maximum vertical relief of 3 m.

Natural Reefs

Jupiter Reef is located approximately 60 m east of MG-111, and is between 17 and 18 m in depth. Vertical relief is relatively low (approximately 0.5 to 0.75 m). Hard bottom is patchy, and the reef top is relatively flat, with occasional cracks and crevices.

Cross Current Reef is located approximately 300 m southeast of the Tri-County, and is about 18 m deep. This area consists of relatively low (0.5 to 0.75 m) relief natural hardbottom.

Delray Ledge is located approximately 300 m south of the Genesis Reef/Boynton Beach Corridors complex, approximately one mile from shore. Depth ranges from 14 to 17 m. The area selected for sampling is characterized by relatively high relief (approximately 1 to 1.5 m).

Survey Methods

Fishes were censused at four stations on each reef that were selected to maximize coverage of habitat types and areal extent. At each station, both stationary samples and roving samples were taken. The stationary sampling method used was a modification of Bohnsack and Bannerot (1986) and consisted of counts of all fish observed during a ten minute count within a 15 m diameter cylinder (estimated using a tape measure) centered on a specified location on the bottom. Surveys were restricted to days when visibility was in excess of 15 m. All novice divers were trained in underwater fish identification by conducting fish counts in tandem with an experienced observer and comparing results. A species list was compiled during the first three minutes of each count, after which individuals for each species were counted and assigned to size classes, starting from the bottom of the list and working upwards. Any additional species that were observed during the remainder of the count were also counted and assigned to size classes, but care was taken to count fish only once. Fish were assigned to one of six size classes based on total length; 1 = 0 - 1.9 cm, 2 = 2.0 - 5.9 cm, 3 = 6.0 - 10.9 cm, 4 = 11.0 - 20.9 cm, 5 = 21.0 - 30 cm, 6 = 30+ cm (divers were trained in underwater length estimation prior to the start of the sampling program). These size classes were used to assign a subset of individuals to life-stage categories (see below). Roving samples were compiled by listing all fish species encountered during a haphazardly oriented ten minute swim in the vicinity of each stationary sample. Surveys took place at approximately monthly intervals from December 1, 1998 to March 27, 2001. During the final period of the project (March 7, 2000 to March 27, 2001) the sampling protocol was modified to include one natural reef in the vicinity of each artificial reef. In addition, sampling at Genesis Reef was discontinued during this period, because it is contiguous with another monitoring reef.

Data analyses

Stationary samples consisted of 1 to 6 (usually 4) stationary fish counts made on a given date and reef, which were converted to average abundance (average number of individuals per stationary count). Roving samples consisted of a list of all species observed during roving surveys on a given date and reef; these were subsequently used to construct presence/absence data sets.

The Bray-Curtis similarity index (Bray and Curtis, 1957) was used on untransformed abundance data (data sets were clear and interpretable without transformation) to

generate sample similarity matrices. Sorenson's binary index (Legendre and Legendre, 1998) was used to generate sample similarity matrices for presence/absence data. These similarity matrices provided the foundation for several descriptive multivariate techniques: Multidimensional Scaling (MDS), analysis of similarities (ANOSIM), and similarity percentages (SIMPER) (Clarke, 1993). The MDS produced a picture of the relationships among individual samples in ordination space (normal analysis). All MDS results are given as two-dimensional ordinations with a stress value indicating how well the two dimensional ordination represents the actual spatial arrangement of samples in the ordination. The lower the stress value the better the representation, and stress values higher than 0.20 should be interpreted with caution (Clarke, 1993). The ANOSIM was used to test hypotheses about differences in assemblage composition for samples from different categories (e.g., artificial vs. natural) designated *a priori* (Clarke, 1993). Statistical significance of ANOSIM tests was determined using 999 permutations of the original data sets. A significance level of $P > 0.05$ was used to confirm differences between *a priori* categories (Table 1). In addition, an R statistic was calculated for all comparisons. ANOSIM breaks down the Bray Curtis similarity matrix by comparing the rank order of similarities among groups of samples from categorically different sampling locations (e.g. artificial or natural). This comparison is achieved by computing a statistic, R, that reflects differences between locations contrasted with differences among replicates within locations. R generally ranges from 1 (all replicates within a location are more similar to each other than to any replicates from different locations) to 0 (similarities between location and within locations are the same on average); however, negative values are possible. The R statistic is valuable in interpreting the outcome of ANOSIM tests, particularly in pairwise comparisons among locations (Clarke, 1993).

One-way ANOSIM's were conducted separately for artificial reefs, natural reefs, artificial versus natural reefs, categorical relief (high, medium,low), and reef material type (natural limestone, quarried limestone, concrete, ship), and life-stage (adult versus juvenile). Stationary and roving data sets were tested separately. SIMPER analysis was used to determine the primary typifying or discriminating species responsible for significant differences between sample categories used in ANOSIM or groups of samples identified by MDS.

Individuals from all species within six selected families: grunts (Haemulidae), snappers (Lutjanidae), wrasses (Labridae), damselfishes (Pomacentridae), surgeonfishes (Acanthuridae), and butterflyfishes (Chaetodontidae) were assigned as either juveniles or adults, based on published life-stage characteristics and ontogenetic color pattern changes, (Humann and DeLoach, 2002). We then designated juvenile and adult stages as separate taxa for specific analyses of the inverse taxa by taxa matrix. Inverse analysis of the life-stage data matrix using life-stage as a factor (juvenile or adult) was then used to provide a test for differences in life-stage distribution among samples. Following the inverse analysis, SIMPER was used to determine the samples which were most important in discriminating between species categories (i. e., juvenile vs. adult). All analyses were performed with the program Primer (Plymouth Routines in Multivariate Ecological Research.

Results

Overall assemblage structure

509 surveys were conducted on artificial and natural reefs during the 28 month period of the study (244 roving surveys and 265 stationary counts, Table 1). A total of 180 species were recorded, representing 50 families. A total of 207 stationary counts, recording 157 species and 45,297 fishes were taken on artificial reefs during 56 sampling days between December 1, 1998 and March 27, 2001. Tri-County Reef had the greatest species richness among artificial reefs with 127 species, followed by Boynton Corridors with 126. MG-111 had the greatest average abundance of fish (424.0). Genesis Reef had the lowest overall number of species (116) and abundance (111.6) among artificial reefs. On natural reefs, 123 species (4,922 fishes) were censused in 59 counts between March 7, 2000 and March 27, 2001 (Table 2).

ANOSIM found significant differences between fish assemblages on almost all reefs compared (Table 3), and R values were generally greater than 0.5. The exceptions were for comparisons between Delray Ledges and Jupiter Reef stationary count (R = 0.069) and life-stage (R = 0.006) data. Similarly, almost all comparisons of assemblages on reefs characterized by different materials and relief categories (Table 4) showed significant differences and relatively high R values. The exceptions were for roving survey data comparing quarried limestone vs. natural reefs (R = 0.150), and concrete vs. natural reefs (R = 0.173).

Comparisons among artificial reefs

Of the 145 species observed on artificial reefs during the final 13 months of this study, 32 (22.1%, Table 2) were economically important species (South Atlantic Fishery Management Council, 1983). In addition, 5 of the top 10 most abundant species were members of this group, which collectively represented 63.6% of the total individuals recorded. The three most abundant species were tomtate (*Haemulon aurolineatum*, 52.5%), followed by bluehead wrasse (*Thalassoma bifasciatum*, (5.1%), and gray snapper (*Lutjanus griseus*, 4.2%). Individuals of *L. griseus* on artificial reefs comprised 558 of 590 (Table 2) of the total number recorded on all reefs. MDS ordination of the artificial reef data from stationary counts for the entire 28 month project (Figure 2) indicated that fish assemblages at MG-111 and Tri-County Reefs were generally distinct from those on other reefs. On the other hand, assemblages at Boynton Corridors and Genesis Reef were quite similar to each other. This is not surprising, given the close proximity of the two reefs, and was the primary reason for dropping Genesis Reef from the final 13 months of the sampling program. MDS ordination of both the stationary count and roving survey data for this final period (Figure 3) grouped samples into clusters that closely corresponded to individual reefs, although the relative positions of the Tri-County and Boynton Corridor clusters are reversed in the stationary count and roving survey analyses. This reversal probably results from the much higher abundances of *H. aurolineatum* occurring on Tri-County Reef.

Comparisons among natural reefs (March 2000 – March 2001)

Of the 123 species observed on natural reefs, 20 (16.3 %) were economically important species (Table 2). Only 1 of the top 10 most abundant species (*Haemulon aurolineatum*) was a member of this group, which collectively represented 17.3% of the assemblage. The three most abundant species were bi-color damselfish (*Stegastes partitus*, 15.0%) followed by *Thalassoma bifasciatum*, (13.8%), and *Haemulon aurolineatum*, (11.7%). Ordination of both stationary count and roving survey data indicated clear differences in species composition among samples from individual reef sites (Figure 3).

Comparisons between artificial and natural reefs

During the final period of the study, there were notable differences in species composition between artificial and natural reefs; for example, lutjanids comprised 12.6% of the assemblages on artificial reefs, but only 2.2% on natural reefs. Other species were comparatively common on natural reefs (i. e. bigeye (*Priacanthus arenatus*), green razorfish (*Hemipteronotus splendens*), and tobaccofish (*Serranus tabacarius*).

In general, average fish abundance was greater (261.7) on artificial than on natural reefs (82.8). On the other hand, the number of species was higher on natural reefs; despite fewer surveys, more species were observed on natural reefs (123 species in 59 surveys) than on artificial reefs (120 species in 76 surveys). Ordination of stationary count and roving survey data (Figure 4) showed some separation into artificial and natural reef groupings. SIMPER analysis of the stationary count data (Table 5) determined that the main species contributing to the dissimilarity were: *Haemulon aurolineatum, Stegastes partitus, Thalassoma bifasciatum, Lutjanus griseus,* and smallmouth grunt (*Haemulon chrysargyreum).* Ordination of roving survey data for the final 13 months of the study (Figure 5), agreed with findings obtained using stationary count abundance data. Reefs were separated into clusters corresponding to artificial and natural reefs, and were also clustered according to material. Furthermore, there was a latitudinal gradient that was consistent for both reef types.

Relative abundances of the most abundant families (Figure 6) varied among reefs (since numbers of fish at all artificial reefs were dominated by *Haemulon aurolineatum,* they were removed from the analysis to facilitate graphical comparison). The most notable difference between artificial and natural reefs was the high relative abundance of lutjanids on artificial reefs (20.0%) versus natural reefs (2.6%). Conversely, assemblages on natural reefs were dominated primarily by smaller and/or herbivorous species. On natural reefs, the combined numbers of pomacentrids and labrids comprised 54.9% of the total numbers of fishes, while these same families comprised 30.5% of the total numbers on artificial reefs. In addition, scarids were among the top six most abundant species on all natural reefs, but were not a dominant family on any artificial reef. Numbers of serranids were relatively low at all reefs, ranging from 1 - 7%, with the highest abundances recorded at Cross Current Natural Reef and Delray Ledges Natural Reef.

Although most of these serranids consisted of small serranine species such as harlequin bass (*Serranus tigrinus*), there were some exceptions. Red grouper (*Epinephelus morio*) were in low abundance (9 individuals) at Delray Ledges Natural Reef. Goliath grouper (*Epinephelus itajara*) were regularly recorded at MG-111 (three individuals during a survey in August, 2000).

Life-stage data

The ratio of juvenile to adults on natural reefs was considerably greater (0.81) than on the adjacent artificial reefs (0.09). Ratios varied among individual natural reefs; the J/A ratios on the low relief reefs (Cross-Current and Jupiter Reefs) were nearly identical (0.65 and 0.64), but the ratio was greater (1.37) on the high relief reef at Delray Ledges. Ratios were considerably lower and varied less among individual artificial reefs; Tri-County (0.14), Boynton Corridors (0.10), and MG-111 (0.07).

Ordination of life-stage coded abundance data (Figure 7) yielded results similar to those from the overall data; surveys separated into artificial and natural reef groupings. SIMPER analysis (Table 6) indicated this grouping was primarily influenced by the numbers of *Haemulon aurolineatum* among adults, and *Thalassoma bifasciatum* among juveniles.

Inverse SIMPER analysis (Table 7) identified the three top discriminating samples contributing to differences between juvenile vs. adult distributions as Tri-County (6/17/00), Jupiter Reef (July 19, 2000), and Delray Ledges (August 1, 2000).

Discussion

Abundances of economically important species

Artificial reefs monitored during this study supported fish assemblages that differed significantly from those on nearby natural reefs. The most salient difference between the two reef types from a reef fish management perspective was the greater number of economically important species recorded on artificial reefs; these fish comprised 32 species and 64% of individuals, although most individuals were grunts with relatively low economic value. Of those with higher value, some were found almost exclusively on artificial reefs (e.g. lutjanids were over ten times more abundant on artificial reefs).

The high abundance of lutjanids on artificial reefs may be due to several factors. Snappers are active predators that are reputed to feed primarily at night, and availability of adequate shelter spaces providing refuge from predation is probably important to these species during daytime periods of reduced activity (Alevizon et al. 1985). As a result, they may seek out and occupy artificial reefs in the day, using them as bases from which to forage during the night. Another possibility suggests that high vertical relief of some artificial reefs may allow them to serve as focal points for aggregation behavior. Monthly abundance data seemed to indicate seasonal components for a number of

species, (e.g. *Lutjanus synagris*, most of which were recorded on MG-111 during sampling events in April and November 2000). On natural reefs, fish occasionally aggregate at sites of promontories, outcroppings, or other conspicuous reef features, and in some cases these aggregations may be correlated with reproductive behavior (Johannes, 1978; Domeier and Colin, 1997). High relief artificial reefs such as MG-111 may serve equivalent functions in areas where prominent natural features are either lacking or have been historically targeted by fishers. A third possibility is that lutjanids and other large predatory fish are attracted to artificial reefs due to the presence of abundant food resources there. A comparison of each artificial reef with its adjacent natural reef indicated that smaller species, especially labrids and pomacentrids, were considerably less abundant on artificial reefs. The scarcity of these smaller individuals may have been due to elevated predation levels. A negative relationship has often been found between the number of piscivorous fish on a reef and the maximum number of co-occurring prey fishes (Schulman 1984, 1985; Hixon and Beets 1989). In addition, there may be an indirect interaction between large shelter and small fishes; increase in shelter size causes an increase in the numbers of large piscivorous fish, which in turn results in a decrease in the numbers of small prey species (Randall, 1963; Hixon and Beets, 1989). Shelter scaling, the tendency for fish size to be correlated with the dimensions of available shelter space on a reef, may also be responsible for differences in overall species composition among artificial reefs. These reefs represented a broad range of shelter size, from large dimensioned shelter spaces within the hull of MG-111, to medium sized shelter spaces within the concrete culverts at Tri-County and Genesis Reefs, to relatively small shelter spaces within the cracks and crevices in limestone boulders at Boynton Corridor. MG-111 consistently supported the highest numbers of snappers and grunts, and was also inhabited by several species of large predatory fish (goliath grouper, *Epinephelus itajara*; nurse shark, *Ginglymostoma cirratum*), Tri-County had the greatest abundances of medium sized carangids (blue runner, *Caranx crysos*) while Boynton Corridor typically supported the greatest numbers of labrids.

Despite the predominance of economically important species on artificial reefs, few of these species settled directly onto these reefs; most were either transients or individuals that had moved onto the reefs after having settled on alternate habitats. A considerable body of literature indicates that adult abundance of many reef fishes is more likely to be limited by recruitment variability than by habitat availability (Doherty and Williams, 1988, Doherty and Fowler, 1994). Economically important species such as most groupers (Moe, 1969; Keener et al., 1988; Koenig and Coleman, 1998; Lindeman et al, 2000) and snappers (Starck, 1970; Lindeman et al., 2000; Nagelkerken et al., 2000) first settle to inshore habitats such as sea grass beds before migrating offshore. These heavily exploited species are more likely to be limited by the amount of sea grass or other nearshore habitats than by offshore hardbottom habitats (Bohnsack et al.,1994).

Juvenile abundance

While adults of many species were relatively abundant on artificial reefs, juveniles were more common on natural reefs. We propose two hypotheses to explain this pattern.

Firstly, the artificial reefs may have provided sub-optimal habitat quality for early life-stages. Most fish have specific habitat requirements at the time of settlement (Sale et al., 1984; Eckert, 1985; Light and Jones, 1997) and may subsequently undergo ontogenetic shifts in habitat use, shifting habitats to match shelter size to body size, or to exploit different food sources (Werner and Gilliam, 1984; Beets and Hixon, 1994; Ross and Moser, 1995; Light, 1995; Lindeman et al., 2000). The differential pattern of juvenile abundance may therefore result from settlement to specific substrata prior to movement to alternate habitats, including artificial reefs. Under this scenario, artificial reefs could function to augment growth and survival of older life-stages after recruitment to adjacent natural habitats. Alternatively, juveniles may have been less abundant on artificial reefs as a result of predation on early life-stages. Shelter spaces on natural reefs were smaller and more varied in shape than on artificial reefs, and consequently may have provided a more optimal fit for juveniles seeking shelter from predation. According to this hypothesis, juveniles may be attracted to these habitats only to suffer increased mortality, resulting in a decrease in local abundance.

The importance of recruitment processes to juvenile distribution patterns was underscored by identification of surveys that contributed most to this pattern. Surveys on natural reefs during summer months were most important in discriminating between artificial and natural reefs based on the predominance of juveniles. Although recruitment of juveniles to benthic habitats could be expected to peak during summer, this phenomenon was not observed on artificial reefs, despite close proximity to adjacent natural habitats. This may be because turnover due to predation is high; thus juveniles may recruit, but are not ultimately successful in settling on reefs due to the "wall of mouths" phenomenon (Hamner et al., 1988). Predation on newly settled fishes could greatly influence observed assemblage structure in the region as has been demonstrated for small artificial reefs by Eklund (1997).

Assemblage structure

Fish assemblage structure on artificial reefs was influenced by construction material, vertical relief, and latitudinal position. Relief and material type appeared to be the primary determinants of fish assemblage structure among artificial reefs. The low relief limestone boulder artificial reef (Boynton Corridor) most closely approximated natural reefs in terms of species composition, while assemblages on the relatively high profile scuttled barge (MG-111) were the most divergent. On natural reefs, fish assemblages also appeared to be influenced by relief. MDS ordination and R values indicated that assemblages at Cross Current and Jupiter Reefs (both low relief) were extremely similar in terms of species composition and distribution of life stages; the ratios of juveniles to adults on these two reefs were nearly identical. On the other hand, Delray Ledges (high relief) supported a significantly different fish assemblage from the other natural reefs, and had the highest species diversity and ratio of juveniles to adults among all natural reefs.

Some studies comparing fish assemblages on natural and artificial reefs have shown that artificial reefs supported higher numbers of individuals and species than adjacent natural

reefs (e.g., Rilov and Benayahu, 2000). Whereas other studies indicated that artificial reefs supported fewer or equivalent numbers of species and individuals than adjacent natural reefs (Tupper and Hunte, 1998; Randall, 1963). Clearly there are multiple factors influencing these observations and each example will vary with respect to geographic location, reef area, reef size and relief, distance to natural reefs (isolation), and a suite of biotic factors. Rilov and Benayahu (2000) have pointed out that comparing assemblages on relatively discrete artificial reefs with selected sites on continuous natural hard bottom, as we have done, will skew the results towards the artificial reefs.

Assemblage structures of both artificial and natural reefs also varied with latitude. MDS ordination plots indicated differences between northern, middle, and southern pairs of artificial and natural reefs. The most extreme differences in species composition were found between the northern and southern reef pairs. These results agree with descriptions of large-scale geographic changes in fish assemblage structure along the Eastern Florida shelf (Gilmore, 1995). MG-111 and Jupiter Reef lie close to the northern distributional limits of many stenothermic tropical species, thus it would be expected that such species would begin to drop out in a northerly direction along this portion of the Florida coast. Samples from our southern reef sites included tropical species such as *Inermia vittata*, *Microspathodon chrysurus*, *Melichthys niger*, and *Centropygge argi*. It appears that the Jupiter area may represent the southern portion of a biogeographical transitional zone that extends to at least Cape Canaveral on Florida's east coast (Gilmore, 1995; Smith-Vaniz, 1999). Alternatively, the north-south pattern in assemblage composition we observed may simply indicate that the repeated samples from individual reefs were more similar to one another than they were to adjacent reefs and by chance formed a north-south image in the ordination. Nevertheless, because there was no replication of reefs within latitudinal blocks our interpretation is largely speculative; a properly designed gradient analysis that includes a larger spatial separation among sampling sites and replication within sites would be needed to accurately quantify latitudinal patterns.

Artificial Reef Colonization

An important consideration in reef design is the length of time required for artificial reef colonization (Carr and Hixon, 1997). Because of variability associated with settling of fishes from the plankton and immigration of older juveniles and adults from adjacent habitats, each reef is expected to exhibit differing colonization trajectories. Boynton Corridor represented the closest approximation to a newly-deployed reef; construction was completed about 6 months prior to the start of systematic monitoring, thus providing a nearly complete time series documenting initial colonization of a limestone boulder reef. Adult fish were well established at the time of the first survey in January 1999, and relative abundances of most families showed little change over the course of the study. However, there were two exceptions: jacks (Carangidae) were relatively common during the first year of the study but were not a major component of the assemblage during the second year, and parrotfishes (Scaridae) were not among the most abundant families in the first year but were relatively common in the second year. The change in the numbers of jacks is not surprising, given their mobility and the ephemeral nature of their prey. Parrotfishes, on the other hand tend to be more site-attached, and their presence tends to

be correlated with abundant food resources (i. e., algae and other epibiota). The increased numbers of scarids may indicate that epibiotic colonization had reached a stage at which this reef is capable of sustaining these herbivorous fish.

The results of this study provide a framework for evaluating the performance of artificial reef in enhancing recreational reef fishing opportunities. Additional studies focusing on specific construction materials and using replicated reefs to address questions regarding recruitment, predation, and movement patterns may help to clarify some of the controversies surrounding the use of artificial reefs. Future studies on the southeastern Florida shelf should also consider a range of natural hardbottom habitat types in comparisons with artificial reefs and take into account the continuous aspect of these natural features during the design phase.

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Table 1. Physical characteristics, sampling effort, and summary statistics for natural (N) and artificial (A) reefs. Note: average abundance = average number of individuals counted per stationary count.

Reef	Type	Material	Relief	Relative Geographic Position	Surveys (Total)	Roving surveys (RS)	Stationary counts (SC)	# Species (RS &SC Combined)	#Species (SC)	Average abundance
Jupiter Reef	N	Natural limestone	Low	North	44	20	24	101	76	114.2
Cross Current	N	Natural limestone	Low	Mid	26	14	11	85	70	82.7
Delray Ledges	N	Natural limestone	High	South	47	24	23	104	86	73.0
MG-111	A	Ship+concrete	High	North	100	44	56	121	95	424.0
Tri-County	A	Concrete	Med	Mid	101	48	53	127	109	163.9
Boynton Corridor	A	Limestone boulders	Low	South	110	52	58	126	107	143.4
Genesis	A	Concrete	Med	South	82	42	40	116	92	111.6
TOTALS					509	244	265	180	161	190.7

Table 2. Total numbers and relative abundances of species counted during stationary counts on artificial reefs (left) between December 1998 and March 2001 and natural reefs between March 1999 and March 2000 (right). Economically important species in bold, * indicates species which are not officially listed within the SAFMC snapper-grouper complex, but which also represent recreationally or commercially important species. (Note: Goliath grouper Epinephelus itajara is in the SAFMC complex but is now a protected species; all values in relative abundance column below triple lines represent values < 0.1%).

	Artificial Reefs			Natural Reefs		
	Species	**Total number**	**%**	**Species**	**Total number**	**%**
1	*Haemulon aurolineatum*	23733	52.5	*Stegastes partitus*	750	15.0
2	*Thalassoma bifasciatum*	2327	5.2	*Thalassoma bifasciatum*	678	13.8
3	*Lutjanus griseus*	1919	4.2	*Haemulon aurolineatum*	574	11.7
4	*Haemulon chrysargyreum*	1327	2.9	*Halichoeres garnoti*	288	5.8
5	*Anisotremus virginicus*	1075	2.4	*Halichoeres bivittatus*	241	4.9
6	*Mulloidichthys martinicus*	1030	2.3	*Haemulon chrysargyreum*	200	4.1
7	*Abudefduf saxatilis*	988	2.2	*Acanthurus bahianus*	179	3.6
8	*Lutjanus synagris*	819	1.8	*Sparisoma aurofrenatum*	115	2.3
9	*Ocyurus chrysurus*	799	1.8	*Elagatis bipinnulata*	101	2.1
10	*Stegastes partitus*	788	1.7	*Kyphosus sectatrix*	94	1.9
11	*Caranx ruber*	685	1.5	*Chromis cyanea*	87	1.8
12	*Haemulon flavolineatum*	541	1.2	*Chaetodon sedentarius*	76	1.5
13	*Pseudupeneus maculatus*	473	1.1	*Halichoeres maculipinna*	67	1.4
14	*Halichoeres garnoti*	435	1.0	*Stegastes variabilis*	63	1.3
15	*Acanthurus bahianus*	434	1.0	*Anisotremus virginicus*	63	1.3
16	*Sparisoma aurofrenatum*	371	0.8	*Acanthurus coeruleus*	52	1.1
17	*Decapterus punctatus*	365	0.8	*Sparisoma viride*	51	1.0
18	*Clepticus parrae*	349	0.8	*Acanthurus chirurgus*	50	1.0
19	*Chromis scotti*	343	0.8	*Priacanthus arenatus*	47	1.0
20	*Inermia vittata*	340	0.8	*Coryphopterus hyalinus*	44	0.9
21	*Caranx crysos*	328	0.7	*Chaetodon ocellatus*	43	0.9
22	*Acanthurus coeruleus*	323	0.7	*Serranus tigrinus*	41	0.8
23	*Kyphosus sectatrix*	305	0.7	*Haemulon flavolineatum*	40	0.8
24	*Sphyraena barracuda**	291	0.6	*Chromis scotti*	40	0.8
25	*Lutjanus mahogoni*	268	0.6	*Canthigaster rostrata*	37	0.8
26	*Canthigaster rostrata*	242	0.5	*Lutjanus griseus*	35	0.7
27	*Stegastes adustus*	231	0.5	*Serranus subligaruis*	34	0.7
28	*Chaetodon sedentarius*	231	0.5	*Balistes capriscus*	32	0.6
29	*Haemulon melanurum*	220	0.5	*Lutjanus synagris*	32	0.6
30	*Chromis cyanea*	213	0.5	*Bodianus rufus*	32	0.6
31	*Acanthurus chirurgus*	167	0.4	*Scarus taeniopterus*	31	0.6
32	*Chromis multilineata*	148	0.3	*Pseudupeneus maculatus*	31	0.6
33	*Bodianus rufus*	139	0.3	*Ocyurus chrysurus*	30	0.6
34	*Haemulon plumierii*	132	0.3	*Chromis enchrysurus*	28	0.6
35	*Sparisoma viride*	127	0.3	*Abudefduf saxatilis*	27	0.6

36	*Scarus taeniopterus*	120	0.3	*Haemulon plumierii*	27	0.6
37	*Scarus iseri*	111	0.3	*Caranx ruber*	25	0.5
38	*Stegastes leucostictus*	104	0.2	*Cephalopholis cruentata*	24	0.5
39	*Elagatis bipinnulata*	103	0.2	*Holocentrus adscensionis*	24	0.5
40	*Haemulon parra*	95	0.2	*Epinephelus morio*	22	0.5
41	*Chromis insolata*	95	0.2	*Haemulon macrostomum*	22	0.5
42	*Chaetodon ocellatus*	93	0.2	*Scarus iseri*	22	0.5
43	*Lutjanus apodus*	88	0.2	*Chaetodon capistratus*	21	0.4
44	*Halichoeres bivittatus*	88	0.2	*Hemipteronotus splendens*	20	0.4
45	*Hypoplectrus unicolor*	81	0.2	*Chromis insolata*	20	0.4
46	*Coryphopterus personatus*	77	0.2	*Hypoplectrus unicolor*	18	0.4
47	*Pomacanthus paru*	65	0.1	*Stegastes leucostictus*	16	0.3
48	*Haemulon sciurus*	62	0.1	*Pomacanthus arcuatus*	15	0.3
49	*Pomacanthus arcuatus*	60	0.1	*Coryphopterus personatus*	13	0.3
50	*Aluterus scriptus*	59	0.1	*Sphyraena barracuda*	12	0.2
51	*Stegastes variabilis*	56	0.1	*Sparisoma atomarium*	12	0.2
52	*Lutjanus buccanella*	55	0.1	*Holacanthus ciliaris*	12	0.2
53	*Balistes capriscus*	55	0.1	*Caranx bartholomaei*	12	0.2
54	*Aulostomus maculatus*	53	0.1	*Myripristis jacobus*	11	0.2
55	*Anisotremus surinamensis*	51	0.1	*Holacanthus tricolor*	11	0.2
56	*Chromis enchrysurus*	51	0.1	*Aulostomus maculatus*	11	0.2
57	*Parques umbrosus*	45	0.1	*Rachycentron canadum**	10	0.2
58	*Cephalopholis cruentata*	44	0.1	*Stegastes adustus*	10	0.2
59	*Scarus coeruleus*	42	0.1	*Lutjanus analis*	10	0.2
60	*Bodianus pulchellus*	40	0.1	*Serranus tabacarius*	10	0.2
61	*Mycteroperca phenax*	36	0.1	*Chaetodon striatus*	8	0.2
62	*Mycteroperca microlepis*	33	0.1	*Holacanthus bermudensis*	8	0.2
63	*Caranx bartholomaei*	33	0.1	*Clepticus parrae*	8	0.2
64	*Holacanthus ciliaris*	31	0.1	*Lactophrys triqueter*	8	0.2
65	*Haemulon striatum*	31	0.1	*Pomacanthus paru*	7	0.1
66	*Lutjanus analis*	29	0.1	*Halichoeres poeyi*	6	0.1
67	*Haemulon macrostomum*	28	0.1	*Cantherhines pullus*	6	0.1
68	*Coryphopterus hyalinus*	26	0.1	*Stephanolepis hispidus*	6	0.1
69	*Halichoeres radiatus*	26	0.1	*Haemulon parra*	6	0.1
70	*Serranus tigrinus*	25	0.1	*Aluterus scriptus*	6	0.1
71	*Calamus penna*	25	0.1	*Anisotremus surinamensis*	5	0.1
72	*Seriola dumerili*	23	0.1	*Scorpaena plumieri*	5	0.1
73	*Lactophrys triqueter*	23	0.1	*Haemulon sciurus*	4	0.1
74	*Caranx latus*	22	0.1	*Coryphopterus glaucofraenum*	4	0.1
75	*Epinephelus morio*	21	0.1	*Lachnolaimus maximus*	4	0.1
76	*Diplodus holbrookii*	20		*Calamus calamus*	4	0.1
77	*Caranx hippos*	19		*Lutjanus apodus*	4	0.1
78	*Acanthostracion polygonia*	18		*Opistognathus aurifrons*	4	0.1
79	*Holacanthus bermudensis*	17		*Melichthys niger*	3	0.1
80	*Halichoeres maculipinna*	17		*Haemulon melanurum*	3	0.1
81	*Epinephelus itajara*	17		*Acanthostracion polygonia*	3	0.1
82	*Haemulon album*	17		*Serranus baldwini*	3	0.1
83	*Holacanthus tricolor*	17		*Scarus vetula*	3	0.1
84	*Acanthostracion quadricornis*	16		*Acanthostracion quadricornis*	3	0.1

85	*Gymnothorax vicinus*	15	*Calamus penna*	3	0.1
86	*Coryphopterus glaucofraenum*	14	*Gymnothorax moringa*	3	0.1
87	*Chaetodipterus faber*	13	*Haemulon striatum*	3	0.1
88	*Hypoplectrus puella*	13	*Cantherhines macrocerus*	3	0.1
89	*Haemulon carbonarium*	13	*Mycteroperca bonaci*	2	
90	*Calamus calamus*	13	*Scomberomorus regalis**	2	
91	*Stegastes planifrons*	13	*Pareques umbrosus*	2	
92	*Diodon hystrix*	12	*Labrisomus nuchipinnis*	2	
93	*Pempheris schomburgkii*	11	*Calamus proridens*	2	
94	*Pareques acuminatus*	11	*Scarus coelestinus*	2	
95	*Archosargus probatocephalus*	11	*Xyrichtys novacula*	2	
96	*Lachnolaimus maximus*	10	*Parablennius marmoreus*	2	
97	*Gobiosoma oceanops*	10	*Scaridae*	2	
98	*Diplodus argenteus*	10	*Mulloidichthys martinicus*	2	
99	*Scorpaena plumieri*	10	*Urobatis jamaicensis*	2	
100	*Cantherhines macrocerus*	10	*Diodon holocanthus*	1	
101	*Chaetodon striatus*	9	*Hypoplectrus puella*	1	
102	*Cantherhines pullus*	9	*Lutjanus buccanella*	1	
103	*Seriola rivoliana*	7	*Fistularia tabacaria*	1	
104	*Mycteroperca bonaci*	7	*Hypoplectrus gemma*	1	
105	*Dasyatis americana*	7	*Scarus coeruleus*	1	
106	*Rachycentron canadum**	6	*Centropyge argi*	1	
107	*Stephanolepis hispidus*	6	*Mycteroperca microlepsis*	1	
108	*Sparisoma rubripinne*	6	*Heteropriacanthus cruentatus*	1	
109	*Archosargus rhomboidalis*	6	*Pempheris schomburgki*	1	
110	*Calamus proridens*	5	*Gymnothorax funebris*	1	
111	*Stegastes diencaeus*	5	*Elacanthinus oceanops*	1	
112	*Odontoscion dentex*	5	*Ogcocephalus cubifrons*	1	
113	*Gymnothorax funebris*	4	*Diodon hystrix*	1	
114	*Scarus guacamaia*	4	*Epinephelus adscensionis*	1	
115	*Epinephelus adscensionis*	4	*Mycteroperca phenax*	1	
116	*Synodus intermedius*	4	*Diplodus argenteus*	1	
117	*Rypticus saponaceus*	4	*Rypticus saponaceus*	1	
118	*Mycteroperca interstitialis*	4	*Dasyatis americana*	1	
119	*Serranus baldwini*	3	*Bodianus pulchellus*	1	
120	*Ginglymostoma cirratum*	3	*Lactophrys bicaudalis*	1	
121	*Lagodon rhomboides*	3	*Halichoeres cyanocephalus*	1	
122	*Epinephelus guttatus*	3	*Mycteroperca venenosa*	1	
123	*Serranus subligarius*	2	*Mycteroperca interstitialis*	1	
124	*Labrisomus nuchipinnis*	2	Total	4922	
125	*Scarus coelestinus*	2			
126	*Aluterus schoepfii*	2			
127	*Malacoctenus triangulatus*	2			
128	*Malacanthus plumieri*	2			
129	*Lactophrys bicaudalis*	2			
130	*Holocentrus adscensionis*	2			
131	*Microspathodon chrysurus*	2			
132	*Strongylura marina*	1			
133	*Myripristis jacobus*	1			

134	*Pterelotris calliurus*	1
135	*Hypoplectrus gemma*	1
136	*Cephalopholis fulva*	1
137	*Sparisoma atomarium*	1
138	*Canthidermis sufflamen*	1
139	*Sparisoma chrysopterum*	1
140	*Aetobatus narinari*	1
141	*Gymnothorax moringa*	1
142	*Serranus tabacarius*	1
143	*Opistognathus aurifrons*	1
	Total	45215

Table 3. *Results of ANOSIM test from the multivariate analyses: values of the R statistic in overall (Global) and pair-wise comparisons between fish assemblages on reefs sampled between March 2000 and March 2001. Reef differences were significant at P< 0.05, except where marked by (*).*

Reefs Compared	Stationary	Roving	Life-stage
Artificial (3/7/00-3/27/01)			
Overall	0.638	0.529	0.618
(MG-111, Tri-County)	0.845	0.606	0.882
(Boynton Corridor, MG-111)	0.734	0.742	0.598
(Boynton Corridor, Tri-County)	0.496	0.368	0.535
Natural (3/7/00-3/27/01)			
Overall	0.442	0.903	0.248
(Cross Current, Jupiter Reef)	0.069*	0.959	0.006*
(Cross Current, Boynton Corridor)	0.484	0.748	0.306
(Delray Ledges, Jupiter Reef)	0.739	1.000	0.341
Artificial vs. Natural (3/7/00-3/27/01)			
Overall	0.564	0.438	0.601
(Boynton Corridor, Cross Current)	0.981	0.848	0.992
(Boynton Corridor, Delray Ledges)	0.827	0.579	0.706
(Boynton Corridor, Jupiter Reef)	0.735	0.998	0.691
(Cross Current, MG-111)	1.000	0.798	1.000
(Cross Current, Tri-County)	0.437	0.944	0.46
(Delray Ledges, MG-111)	1.000	0.926	0.956
(Delray Ledges, Tri-County)	0.570	0.869	0.483
(Jupiter Reef, MG-111)	0.908	0.992	0.908
(Jupiter Reef, Tri-County)	0.589	1.000	0.555
Artificial (12/1/98-3/27/01)			
Overall	0.369		
(Boynton Corridor, Genesis)	0.114		
(Boynton Corridor, MG-111)	0.447		
(Boynton Corridor, Tri-County)	0.269		
(Genesis, MG-111)	0.521		
(Genesis, Tri-County)	0.197		
(MG-111, Tri-County)	0.497		

Table 4. *Results of ANOSIM test from the multivariate analyses: values of the R statistic in overall (Global) and pair-wise comparisons between factors on reefs sampled with stationary counts between March 2000 and March 2001. In all cases factor differences were significant at P < 0.05 Material categories: QL = quarried limestone, NL = natural limestone, SC = ship + concrete, C = concrete. Reef differences were significant at P< 0.05, except where marked by (*).*

Factor	Stationary Counts	Roving Surveys
Relief (Artificial Reefs, 3/7/00-3/27/01)		
Overall	0.638	0.529
(high, low)	0.734	0.742
(high, medium)	0.845	0.368
(medium, low)	0.496	0.606
Relief (Natural Reefs, 3/7/00-3/27/01)		
Overall (high, low)	0.641	0.567
Material (Artificial and Natural Reefs)		
Overall	0.607	0.279
(QL, NL)	0.510	0.150*
(QL, SC)	0.734	0.742
(QL, C)	0.496	0.368
(NL, SC)	0.883	0.583
(NL, C)	0.569	0.173*
(SC, C)	0.845	0.606
Life-stage		
Overall (adult vs. juvenile)	0.120	N/A

Table 5. Results of SIMPER analysis of abundance data for artificial and natural reefs sampled between March 7, 2000 and March 27, 2001, showing breakdown of average dissimilarity between reef types into contributions from each species. Top ten discriminating species are ordered in decreasing contribution.

Species	Average Abundance Artificial Reefs	Average Abundance Natural Reefs	Average Dissimilarity
Haemulon aurolineatum	112.04	8.57	23.42
Stegastes partitus	4.02	12.70	4.48
Thalassoma bifasciatum	11.01	12.61	4.09
Lutjanus griseus	8.74	0.65	3.54
Haemulon chrysargyreum	5.44	4.44	2.94
Mulloidichthys martinicus	4.64	0.02	2.11
Ocyurus chrysurus	4.45	0.40	1.99
Abudefduf saxatilis	4.64	0.73	1.87
Halichoeres garnoti	1.96	4.92	1.82
Anisotremus virginicus	5.23	1.14	1.72

Average dissimilarity = 78.52

Table 6. Results of SIMPER analysis of life-stage coded abundance data for artificial and natural reefs sampled between March 7, 2000 and March 27, 2001, showing breakdown of average dissimilarity between reef types into contributions from each species. Top ten discriminating species are ordered in decreasing contribution; juveniles in bold.

Species	**Average Abundance Artificial Reefs**	**Average Abundance Natural Reefs**	**Average Dissimilarity**
Haemulon aurolineatum	140.18	5.46	37.72
Haemulon chrysargyreum	13.59	0.00	4.56
Stegastes partitus	4.77	11.49	3.85
Thalassoma bifasciatum	10.69	8.85	3.70
Lutjanus griseus	9.01	0.65	3.13
Haemulon aurolineatum	0.01	9.91	2.51
Lutjanus synagris	6.24	0.35	1.97
Chromis cyanea	2.35	1.31	1.77
Clepticus parrae	2.47	0.44	1.58
Abudefduf saxatilis	4.15	0.71	1.56

Average dissimilarity = 83.24

Table 7. Results of SIMPER analysis of the inverse life-stage data set, showing the ten most important discriminating samples responsible for distribution of adults and juveniles among different reefs.

Sample	Average Abundance Adults	Average Abundance Juveniles	Average Dissimilarity
Tri-county (6/17/00)	5.96	0.66	6.52
Jupiter Reef (7/19/00)	0.91	3.21	6.47
Delray Ledges 8/01/00	0.40	4.87	6.32
Boynton Corridor (8/01/00)	4.14	1.01	4.30
MG-111 (5/9/00)	12.15	0.79	4.26
MG-111 (7/19/00)	6.45	1.30	4.12
Jupiter Reef (2/1/01)	2.56	1.28	4.05
Cross Current (7/25/00)	1.32	0.77	3.97
Tri-county (4/28/00)	2.57	0.30	3.71
Boynton Corridor (1/17/01)	5.23	0.56	3.58

Average dissimilarity = 94.19

Figure 1. Map of Palm Beach County, Florida, showing locations of artificial and natural reefs. Study is centered on 26.76º N., 80.03º W.

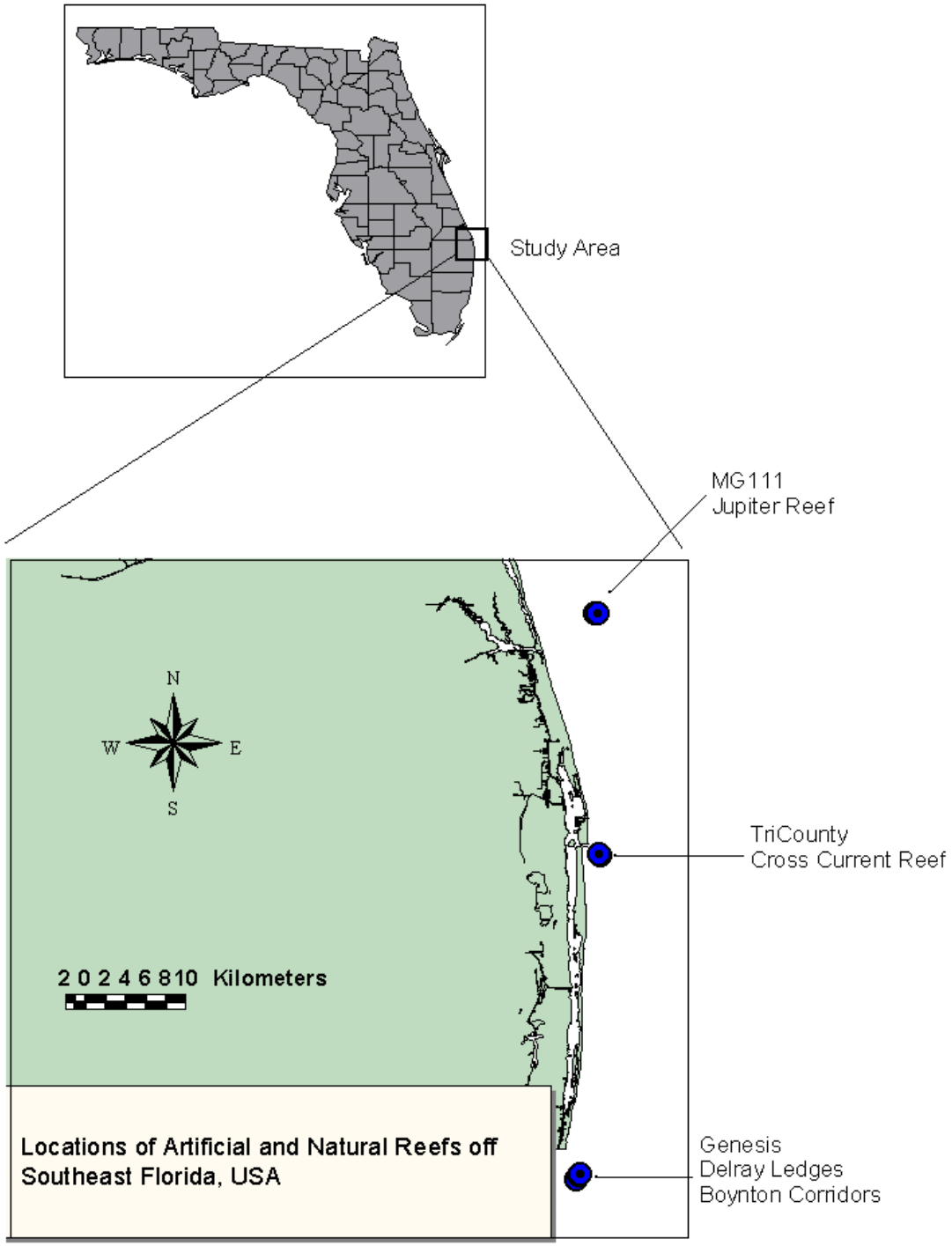

Figure 2. Ordination of abundance data for artificial reefs sampled between December 1998 and March 2001. (note: sampling on Genesis Reef was discontinued in March 2000).

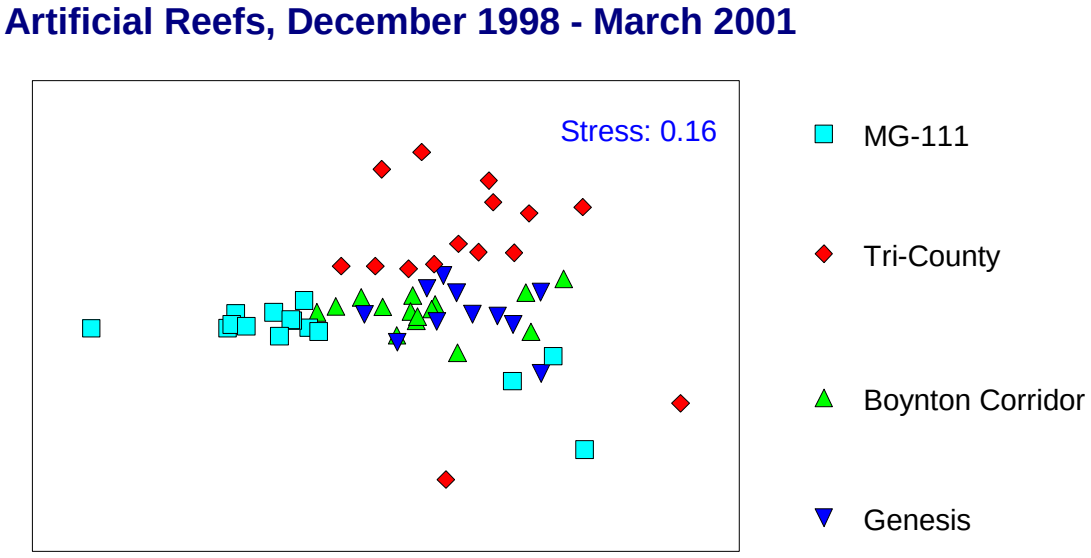

Figure 3. Ordination of abundance data for artificial (top left) and natural reefs (top right), and for species composition data for artificial (bottom left) and natural reef data (bottom right). All reefs were surveyed between March 2000 and March 2001.

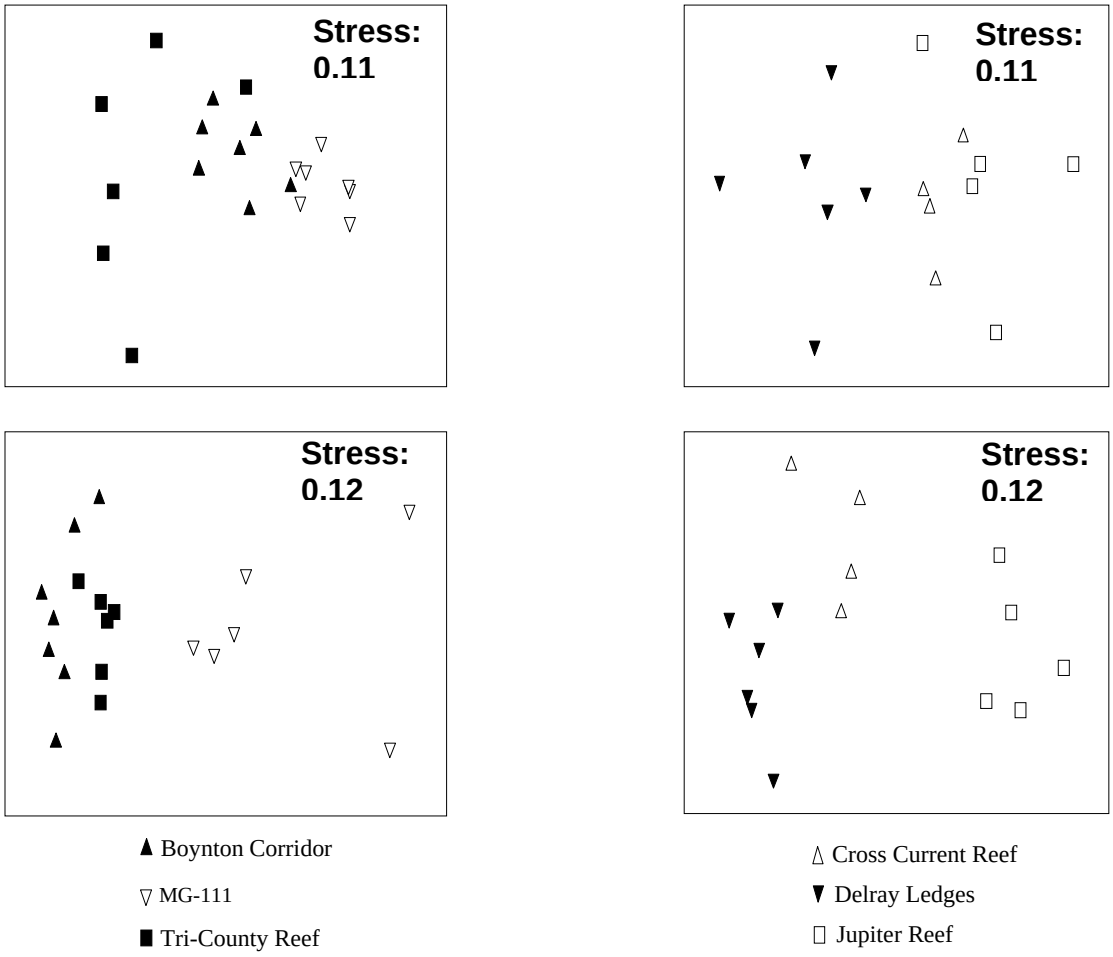

Figure 4. Ordination of stationary count (top) and roving survey (bottom) data for artificial and natural reefs surveyed between March 2000 and March 2001.

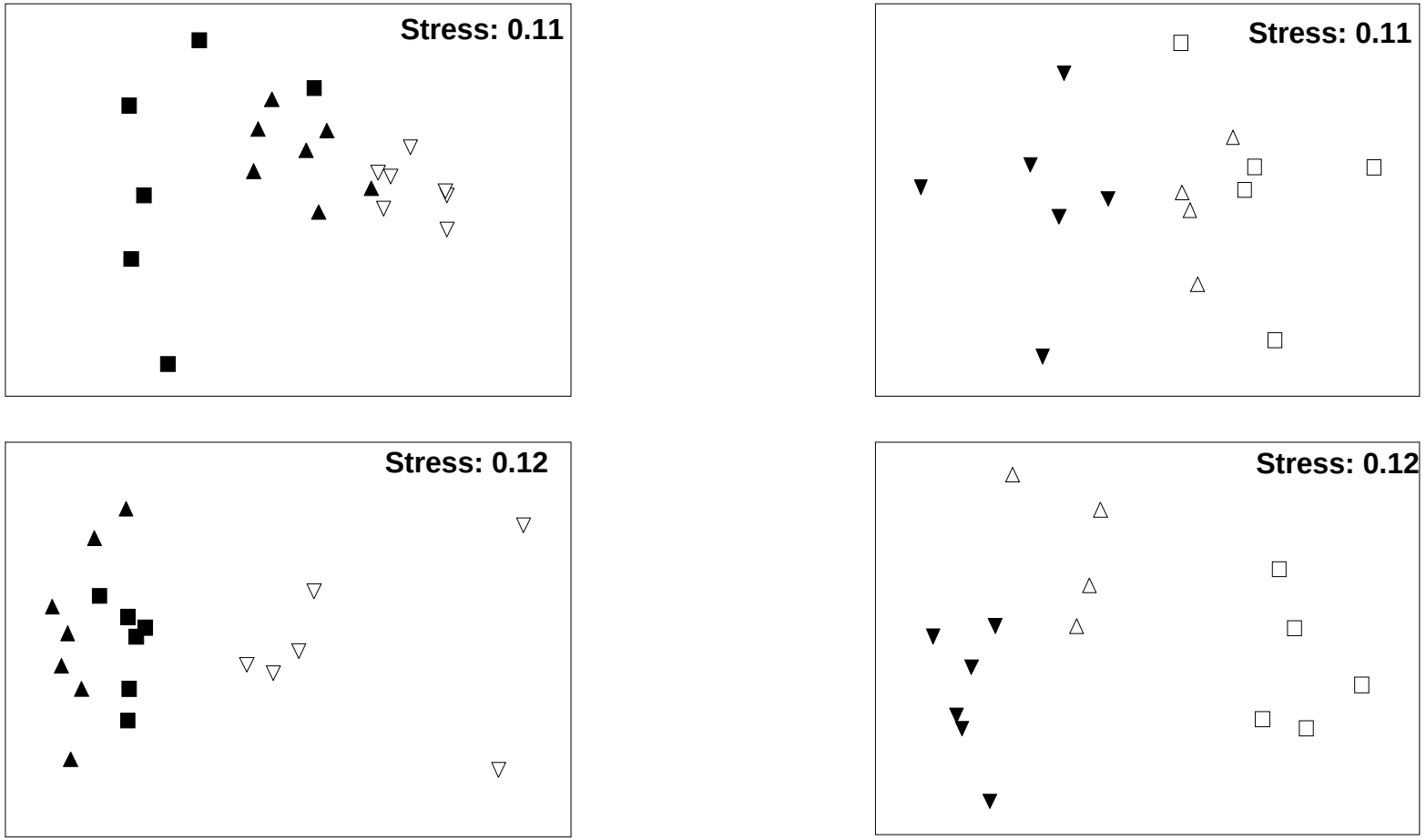

Figure 5. Ordination of roving survey data for artificial and natural reefs surveyed between March 2000 and March 2001, showing composition material of reefs. Transverse lines divide reefs into northern, middle, and southern sections of Palm Beach County.

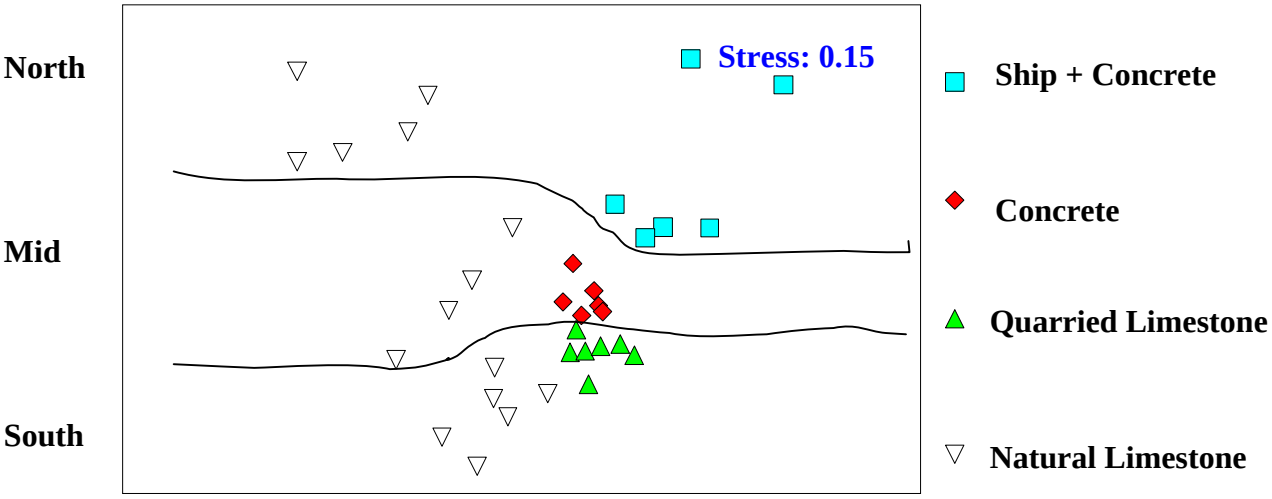

Figure 6. Relative abundances of six most abundant families from stationary counts on artificial and natural reefs surveyed between March 2000 and March 2001 (*Haemulon aurolineatum* are removed from this figure).

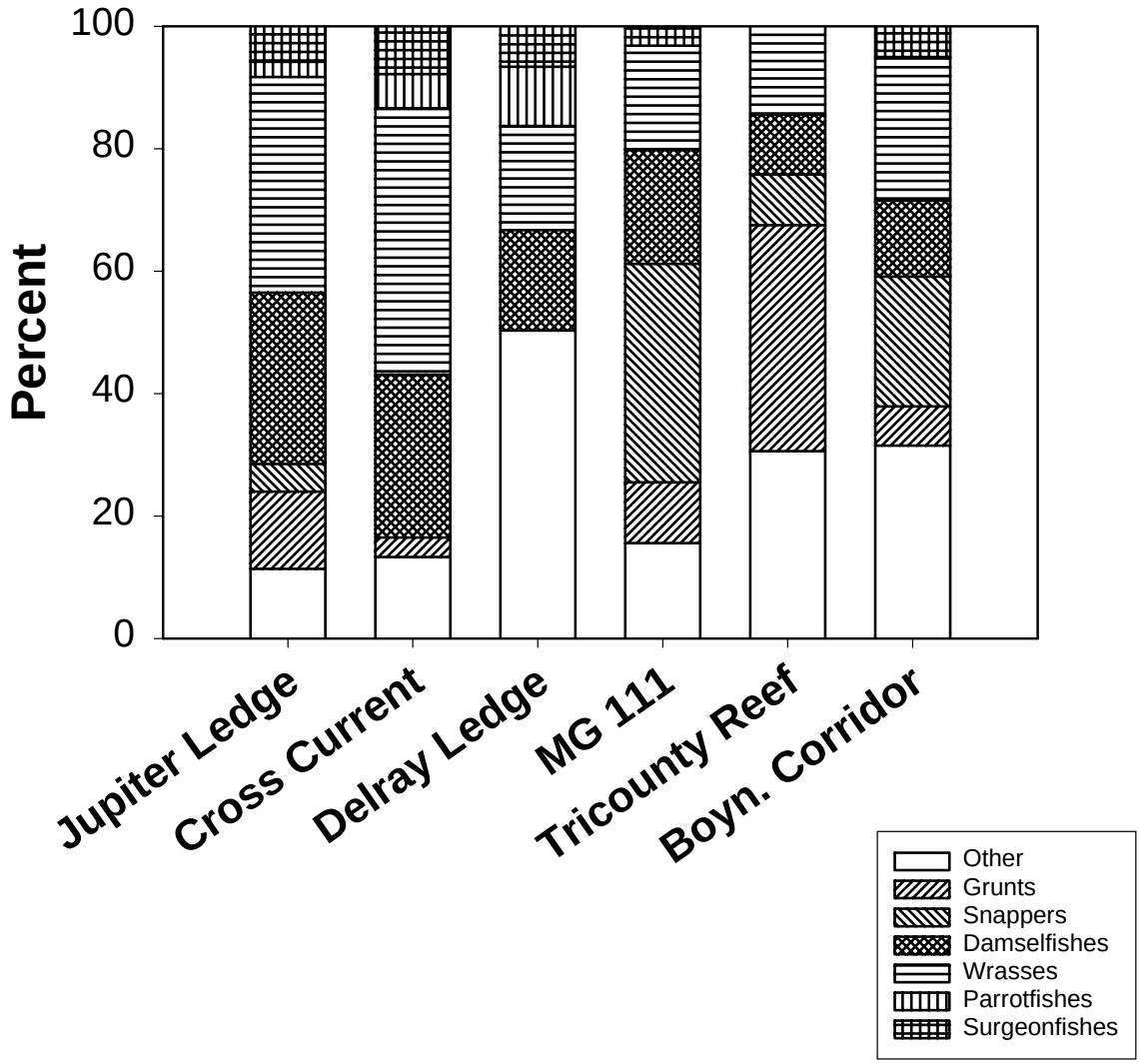

Figure 7. Ordination of life-stage coded stationary count data for artificial and natural reefs surveyed between March 2000 and March 2001 (see text).