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SOUTH FLORIDA RESEARCH CENTER

Report SFRC-83/02
Population Structure, Food Habits, and Spawning Activity of Gray Snapper, Lutjanus griseus, in EVER

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Population Structure, Food Habits, and Spawning Activity of Gray Snapper, *Lutjanus griseus*, in Everglades National Park

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April 1983

Rutherford, Edward S., Edith B. Thue, and David G. Buker. 1983. Population Structure, Food Habits, and Spawning Activity of Gray Snapper, *Lutjanus griseus*, in Everglades National Park. South Florida Research Center Report SFRC-83/02. 41 p.

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ABSTRACT

Population structure, food habits, and spawning activity of 1026 gray snapper, Lutjanus griseus, were studied in Everglades National Park from November 1978 through January 1980. Fish were sampled from sportfishermen catches and ranged in length from 111-451 mm F.L. ($\bar{x}$ = 257 ± 3.2 mm) and in weight from 0.05-1.6 kg ($\bar{x}$ = 0.33 ± .02 kg). There was no difference in mean length between sexes.

Fish aged from scale annuli ranged from one to seven years. Two- and three-year old fish dominated the catch. Recruitment was complete by age three.

The mean age of all fish was 3.0 ± 0.1 yrs. There was no difference in mean age between the sexes. Fish taken from the Cape Sable area were significantly older than fish taken from other areas.

Calculated growth of gray snapper was greatest in the first year and relatively linear before increasing in the fifth year. Calculated growth varied between sexes and among areas of capture. Females were significantly larger than males at ages one and two. Fish taken from hypersaline areas near the Gulf of Mexico were larger at ages one through four than fish taken from seasonally brackish waters. Males in the Shark River area did not show as great an increase in weight with length as did all fish in other areas. Females in the Coot Bay and Whitewater Bay area were heavier at a given length than all fish in other areas.

Annual survival rate of all fully recruited fish was s = 0.28 ± .03. Survival of males was higher than females. Gray snapper survival was higher in the hypersaline waters near the Gulf than in other areas.

Spawning activity probably occurs outside of park waters. Only four of 668 fish examined inside park waters were ripe.

Park gray snapper diet consisted mainly of fish, shrimp, and crabs. Species composition of the diet varied with age and among seasons and areas of capture.

Comparison of this study with an earlier study of park gray snapper (Croker 1960) showed increases in survival and longevity since 1960. No changes in diet, spawning activity, or growth rate were noted.

INTRODUCTION

Fishery harvest in Everglades National Park has been monitored nearly continuously since 1958 (Higman 1966; Davis 1980). The monitoring program has revealed that harvest of all fish and shellfish in the park declined from 1972-1978 (NPS Fishery Assessment 1979). Public concern over the decline in harvest prompted the South Florida Research Center to initiate an investigation of the age and growth, mortality, food habits, and spawning activity of the four park gamefish species most preferred by sportfishermen: gray snapper (*Lutjanus griseus*), spotted seatrout (*Cynoscion nebulosus*), red drum (*Sciaenops ocellatus*), and snook (*Centropomus undecimalis*). This paper, one of a series of papers reporting the results of these studies, describes the age, growth, mortality, spawning activity, and food of gray snapper in Everglades National Park from November 1978 through January 1980.

The gray snapper is a tropical and subtropical marine fish primarily found in the western Atlantic in the inshore waters of Florida, West Indies, Bermuda, and the Bahama Islands. Stragglers have been found as far north as Massachusetts and as far south as Brazil (Starck and Schroeder 1970). Tabb and Manning (1961) listed the gray snapper as the most common snapper species in northern Florida Bay and adjacent estuaries. Juvenile gray snapper inhabit shallow inshore grass beds or mangrove areas where salinities vary widely (Reid 1954; Starck 1964). Adults are apparently less tolerant of low salinity occurring in deeper saline waters in channels and on reefs. Tagging studies indicate that gray snapper are relatively non-migratory; adults make short coastwise movements and move offshore in summer to spawn (Beaumariage 1969; Starck 1964).

Previous studies have described gray snapper age and growth, food habits, and spawning activity in Everglades National Park (Croker 1960; Odum 1970) and in the Florida Keys (Starck 1964). Gray snapper may grow up to eight pounds (3.6 kg) and live to at least nine years (Starck 1964), although in Everglades National Park, fish older than three years are seldom caught (Croker 1960). Spawning occurs offshore from June through August (Starck 1964). Gray snapper are carnivorous, eating mainly crustaceans and fish. Their diet changes with size and habitat. Juveniles from grass beds eat mainly amphipods, palaemonid and penaeid shrimp, and few crabs. Adults from channels and around reefs consume mainly fish and crabs (Longley, Schmidt, and Taylor 1925; Croker 1960; Starck 1964; Odum 1970).

Description of Study Area

The mainland shoreline of Everglades National Park extends from the Florida Keys to Everglades City on Florida's west coast. It contains numerous bays, inlets, and rivers which lie at the terminus of the historically immense Everglades and Big Cypress swamp drainages. Tabb, Dubrow, and Manning (1962) have described the animal and plant communities of park waters and identified distinct ecological zones. Their work provided the basis for delineating the six fishing areas used in Everglades National Park fishery investigations since 1960 (Higman 1966; Fig. 1). These areas differ in their topographical, hydrological and biological characteristics (Tabb, Dubrow, and Manning 1962).

METHODS

Gray snapper were sampled from sportfishermen catches at Flamingo, Everglades National Park, from November 1978 through January 1980. Samples taken from Flamingo were representative of all park waters except south Florida Bay (Area 2) and the upper west coast (Area 6, Ten Thousand Islands; Fig. 1). Fork lengths (mm) were recorded for 1026 fish. For 689 of these fish, the following information was also obtained: weight (.01 kg), sex, gonad condition, stomach content, area of capture, time caught, time sampled, and gear used. Sex and reproductive condition were determined by inspection of the gonads. Reproductive condition was classified according to Lagler (1956). Scales for age analyses were collected from behind the left pectoral fin. Stomachs for food analyses were removed from the fish and immediately preserved in 10% buffered formalin. Detailed methods used in collection and processing of data are further described by Rutherford, Thue, and Buker (1982).

Gray snapper have previously been aged using scale annuli in Everglades National Park (Croker 1960) and in the Florida Keys (Starck 1964). We used the following criteria (Bagenal 1978) to verify age determinations from scale annular marks:

1. Fish body growth is proportional to scale growth.

2. Scale annular formation is seasonal and occurs only once each year.

3. Back-calculated lengths of fish at age N are between observed lengths at capture of fish aged N-1 and N.

4. Lengths at capture of fish aged by scales agree with modal lengths of age groups determined by the Petersen length-frequency method.

Fish body length was regressed on total scale radius for fish from each area of capture and for each sex to determine the proportionality of fish body growth to scale growth. The y intercept of this regression was used as the correction factor (a) in the Dahl-Lea formula (Bagenal 1978) to back calculate fish length at each annulus.

Seasonality of scale annulus formation was determined by plotting scale radius marginal increment against month of capture. Differences in back-calculated lengths and lengths at capture of fish among sexes and areas of capture were compared by a two-factor (area, sex) analysis of variance. Differences in calculated annual length increments among year classes were compared by a three-factor (area, sex, year class) analysis of variance. A Student Newman Keuls (SNK) test was used to indicate which specific differences were significant (Zar 1974).

Mean back-calculated lengths at time of annulus formation were fitted to the von Bertalanffy growth equation (Bayley 1977) to describe gray snapper growth. Length-weight relationships were calculated (Bagenal 1978) for each sex and area of capture and compared using analysis of covariance (Zar 1974).

Annual survival rates (S) and mortality rates (A) were calculated for fully recruited fish from the age distribution of the catch (Robson and Chapman 1961). Natural mortality coefficients (M) were estimated utilizing Pauly's (1980) equation. Fishing mortality coefficients were obtained by subtracting natural mortality coefficients from the $-\log_e$ transformation of (S). These coefficients were then used to calculate exploitation ratios (E) and rates of conditional fishing and conditional natural mortality (Ricker 1975).

Food items of stomach samples were identified to the species level when possible. For analysis of percent frequency and percent volume, prey species were grouped into six categories: shrimp, fish, crabs, molluscs, algae + plants, and other. The percent volume of each food item was taken by blotting dry the item, measuring its volume (ml) by water displacement and expressing this as a percentage of the total volume of food in a designated series (individuals of a species by area, sex and month). The percent frequency of a food item was calculated as the number of stomachs in which it occurred divided by the total number of stomachs in the series. Unless stated otherwise, statistical significance levels are at the $a = .05$ level. Mean values include 95 percent confidence intervals.

RESULTS

Length Frequency

Gray snapper ranged in length from 111-451 mm ($\bar{x} = 257 \pm 3.2$ mm; Fig. 2) and in weight from 0.05-1.6 kg ($\bar{x} = 0.33 \pm 0.02$ kg). The mean length of 241 females ($\bar{x} = 260 \pm 6.4$ mm) was not significantly different ($p < .50$) from the mean length of 237 males ($\bar{x} = 263 \pm 7.4$ mm; Fig. 3).

Length distributions of all gray snapper (combined sexes) varied significantly ($.005 < p < .01$) among seasons. Mean fish length was smallest in winter, when proportionately fewer large (≥ 300 mm) fish were caught. Mean fish length of each sex considered separately did not vary among seasons but did vary among areas of capture. Mean length of fish taken from the Cape Sable area was greater ($p < .001$) than mean lengths from other areas. In addition, the greatest proportion of large fish (≥ 340 mm) was taken from the Cape Sable area.

Verification of Aging Methods

The validity of using scale annuli to determine age of gray snapper was verified by meeting all criteria listed in the methods section except modal analysis by the Petersen length-frequency method. Fish body length was regressed on total scale radius to determine if a relationship existed between fish growth and scale growth. Fish body length was significantly ($p < .001$) correlated with scale growth for each sex in each area. Two significantly ($p < .001$) different fish length-scale radius regressions were determined by analysis of covariance (Fig. 4): one for Cape Sable (Area 3) females (y intercept = 135.52) and one for Cape Sable males and fish from all other areas (y intercept = 25.44). The y intercepts were used as the correction factor "a" in the Dahl-Lea formula (Bagenal 1978) to back calculate lengths at age for each particular group.

Time of annulus formation was determined by plotting scale margin increments by season for age two and three fish (Fig. 5). The mean margin increment was lowest in spring and increased steadily throughout the year until winter. Most minimal scale margin increments (0-4 mm) occurred in spring (March-May) indicating that gray snapper form annuli just prior to this time.

Back-calculated lengths at age were compared with lengths at capture for 664 aged fish. Mean observed lengths at annulus were larger than back-calculated lengths because of growth since annulus formation (Fig. 6; Appen. 1-3). Except for age one, lengths at capture closely parallel back-calculated lengths and lie between the calculated length for a given year and the following year.

Lengths at age of gray snapper determined by the Petersen length-frequency method were not similar to lengths at capture of scale-aged fish (Table 1). At ages one through four, median lengths at capture were lower than modal lengths. Failure of age analysis by length frequency to agree more closely with age analysis by scale annuli was assumed to be due to the great variability in modal lengths produced by the gray snapper's protracted spawning and growing seasons (Starck and Schroeder 1970).

Age Distribution and Sex Ratio

The dominant age classes in the sportfish catch were two-, three-, and four-year-old fish (Fig. 7). The mean age of the catch was $3.0 \pm .1$ yrs. The mean age of males ($\bar{x} = 3.1 \pm .1$ yrs) was not significantly different than the mean age of females ($\bar{x} = 3.0 \pm .1$ yrs). Gray snapper began to enter the fishery at age one and were fully recruited by age three. Catches of fish declined sharply after age four. Only one seven-year old (sex unknown) was caught and no young of the year fish were observed.

There was no difference in age distribution among areas for females. However, the mean age and the age distribution of males and combined sexes differed significantly ($p < .005$) among areas, with proportionately more older fish being taken from the Cape Sable area than from other areas.

The sex ratio of the catch was at unity and did not vary significantly with age or among areas of capture.

Growth

Back-calculated lengths at age indicate gray snapper growth was greatest in the first year ($\bar{x} = 126 \pm 2$ mm). Growth was fairly constant from age one through four (48-62 mm/year; Fig. 8), increased in the fifth year, and declined in the sixth year. Only one seven-year-old fish was available to back calculate growth past age six; therefore, growth rate was considered accurate only to age six.

Growth of gray snapper varied between sexes. Calculated lengths of females were significantly ($p < .001$) greater than males at ages one and two. Females grew significantly faster ($p < .001$) than males in the first year but grew slower thereafter (Fig. 9).

Significant differences were found among areas of capture for both calculated and observed lengths for given ages. Lengths at capture of fish of both sexes from the Cape Sable area were significantly ($.001 < p < .0025$) greater than fish from north Florida Bay, Shark River, and Whitewater Bay only at age four. Calculated lengths of fish taken from the Cape Sable area were significantly ($p < .001$) larger at ages one through three than fish taken from all other areas; at age four, they were significantly ($p < .001$) larger than fish from all other areas except the Shark River area (Fig. 10). Fish from the Cape Sable area grew significantly ($p < .001$) more at age one and significantly ($.025 < p < .05$) less at ages two and three than fish from all other areas. At age five, significant ($.01 < p < .025$) differences were found in growth rate among areas by an analysis of variance, but were not identified by the SNK test.

Significant ($.025 < p < .05$) differences in calculated growth rate of year classes were found only for the first growth year. Mean back-calculated length of the 1975 year class was greatest, followed by the 1976 and 1977 year classes, although these differences in growth were undetected by a SNK range test.

The regression of the instantaneous growth coefficient (G) (change in mean weight per unit time) on the reciprocal of mean length was significant ($p < .001$) for all fish (Fig. 11). The parameters (K, L_∞, t_o) derived from this regression using Bayley's (1977) method were inserted into the von Bertalanffy equation to predict gray snapper lengths at age (Fig. 12). The von Bertalanffy equations for gray snapper in the park are:

males $L_t = 831\,(1-e^{-.09\,(t\,+\,0.69)})$,

females $L_t = 1208\,(1-e^{-.05\,(t\,+\,1.28)})$,

combined sexes $L_t = 1178\,(1-e^{-.06\,(t\,+\,0.92)})$

The calculated maximum-length values (L_∞) using the von Bertalanffy growth equations were much higher than the largest fish (451 mm) examined in this study or elsewhere in south Florida (650 mm) (Starck and Schroeder 1970) because of the increase in calculated growth of park gray snapper in the fifth year (Fig. 8). Therefore, we believe that the von Bertalanffy equation did not accurately describe growth of park gray snapper.

Length-Weight Relationship

The length-weight relationship of 689 gray snapper was $W = 8.0223 \times 10^{-6} L^{2.7187}$ (Fig. 13). A regression of logarithmically (base 10) transformed data was significant ($p \leq .001$) and provided the best fit ($r = 0.94$). Significant ($.005 \leq p \leq .01$) differences in slope and intercept were found in length-weight regressions among sexes and areas. The regression slope for males in the Shark River area was smaller than the slope calculated for females in the same area and for all other fish in other areas, indicating that males in the Shark River area increased in weight per unit length more slowly than females in Shark River or all fish in other areas. The regression intercept for females in the Coot Bay-Whitewater Bay area was larger than that calculated for males in the same area and all fish in other areas, indicating that females in Coot Bay-Whitewater Bay are heavier per unit length than all other fish.

Survival

Survival rates were calculated for fully recruited gray snapper from the age distribution of the catch. Both males and females were fully recruited by age three; therefore survival estimates apply only to fish aged four and older.

Annual survival rate of male gray snapper was higher ($s = 0.33 \pm .06$) than for females ($s = 0.27 \pm .06$) or sexes combined ($s = 0.28 \pm .03$; Table 2). Survival rates calculated for individual areas in the park show that survival was greater for all fish in the Cape Sable area than in other park areas (Table 3). Since the von Bertalanffy equation did not adequately describe gray snapper growth, we were unable to use the parameters (L_∞, K) to calculate natural mortality rates using Pauly's (1980) equation.

Food Habits

The results of stomach analysis of 689 gray snapper are shown in Figure 14, and a list of prey items is given in Appendix IV. Forty-two percent (N = 287) of the stomachs analyzed contained food items. Shrimp, primarily Penaeus duorarum, was the predominant food item, occurring in 76.7 percent of the stomachs and comprising 48.3 percent of the total volume. Other identifiable shrimp species in the diet were Alpheus heterochaelis, A. armillatus, and Periclemenes longicaudatus.

Fish species were the second-most important item in the diet, occurring in 33.5 percent of the stomachs and totalling 40.4 percent of the volume. Commonly consumed families were: Cyprinodontidae (Floridicthys carpio), Batrachoididae (Opsanus beta), Sparidae (Lagodon rhomboides), Clupeidae (Anchoa mitchilli, Harengula pensacolae), Ophichthidae (Myrophes punctatus, Ahlia spp.), and Gobiidae (Microgobius gulosus).

Crab species ranked third in frequency (24.0%) and volume (9.1%). The most common crabs were: Portunidae (Callinectes sapidus), Majidae (Libinia spp.), Xanthidae (Hexapanopeus spp., Panopeus spp., Neopanope spp., Eurypanopeus spp.), Grapsidae (Sesarsma spp.), and Ocypodidae (Uca pugilitor, U. minax).

Algae and marine plants (14.5% frequency, 1.3% volume) were the fourth-most important food item in gray snapper stomachs but may have been consumed accidentally. Commonly consumed species included Dictyota spp, Cymodacea manatorum, Thalassia testudinum, Ruppia maritima, Halodule wrightii, and Udotea flabellum.

Molluscs and amphipods comprised a very small portion of the diet, occurring in 7.3 percent and 6.3 percent of the stomachs and totalling 0.3 percent and 0.2 percent by volume, respectively. Bulla striata, Marginella apicina, Ceritheum eburneum, and Brachidontes exustus were the most commonly consumed molluscan species. Common amphipods were in the family Corophoididae.

The last category, "other," included polychaetes (Pectinaridae), isopods (Flabelliferidae, Sphaeromidae, Anthuridae), and holothurians (Dendrochirote spp.). Together, these prey organisms occurred in 7.3 percent of the stomachs and accounted for 0.5 percent of the volume.

There was no significant ($x^2 = 6.755$; $0.1 < p < 0.5$), difference in gray snapper food consumption by sex. Food consumption did vary significantly by area of capture, size of fish and season (Fig. 15, 16 and 17). The frequency of prey items in the diet varied significantly by area ($x^2 = 66.677$; $p < .001$). Fish taken from Whitewater and Coot Bays consumed proportionately more amphipods than fish from other areas while fish taken from the Shark River area consumed proportionately more crabs than fish from other areas (Fig. 15). When gray snapper from all park areas were pooled and divided among season of capture, they ate crabs proportionately more often in spring than in other seasons and ate amphipods and "other" organisms more often in winter than in other seasons ($x^2 = 35.474$; $p < .001$) (Fig. 16).

Gray snapper from all park areas were pooled and divided into three size groups. Comparisons of diet among these size groups were made using shrimp, fish, crabs, and a pooled group of algae, molluscs, amphipods, and "other" prey items. Food consumption varied significantly ($x^2 = 13.780$; $.025 < p < .05$) by predator size. Large gray snapper (≥ 309 mm) consumed fish more frequently than shrimp, while medium (230-309 mm) and small-sized gray snapper consumed shrimp more often than fish (Fig. 17). When all food groups were considered separately, significant ($x^2 = 23.281$; $p < .001$) differences in food consumption between small- and medium-sized fish were found. Small gray snapper consumed amphipods proportionately more often than medium-sized gray snapper. However, when diet of all fish within any particular area was analyzed for differences among season or predator size, no significant differences were found.

Nearly all gray snapper (99%) were caught with a baited hook or lure, making it impossible to determine if the type of gear used influenced prey frequencies in stomachs.

Spawning Activity

Gray snapper apparently spawn outside of park waters. Only four out of 668 fish examined during the study were in spawning condition. Three ripe males ranging in size from 240-400 mm were taken in July, August, and October from North Florida Bay, South Florida Bay, and Coot Bay, while one ripe female (361 mm) was taken from the Cape Sable area in June.

DISCUSSION

Age and Growth

Mean size of park gray snapper caught during our study ($\bar{x} = 257$ mm) was larger than that reported by Croker in 1960 ($\bar{x} = 243$ mm). This size increase was due to increased harvest of older fish and not to increased growth rates. Calculated growth of fish was similar in both studies (Fig. 18), while proportionately more older fish were harvested in 1979 than in 1960 (Fig. 19).

Park gray snapper caught during winter months were smaller in mean size than fish caught during the rest of the year in both 1959 and 1979. Croker attributed this to an influx of small fish into the fishery. We found that catches of small ($\leq$240 mm) gray snapper remained constant throughout the year, while catches of large fish decreased in winter, probably because of offshore movement. However, in the reef habitat of Matecumbe Key, Florida, Starck (Starck and Schroeder 1970) found that large gray snapper moved offshore in summer and inshore in winter.

Both Croker's (1960) study and our study indicate that park gray snapper grow faster in the first two years than gray snapper from Matecumbe Key, Florida, (Starck 1964; Fig. 18). Starck (Starck and Schroeder 1970) attributed the slower growth of gray snapper from Matecumbe Key to its reef environment. He postulated that gray snapper living on reefs might have a poorer food supply and more competition from other species than gray snapper inhabiting the mangrove and grass-bed areas of Florida Bay.

Area differences in calculated growth of park gray snapper may be artifacts of differences in age distribution; although more large (old) fish were taken from the Cape Sable area, growth rates are probably similar in all areas of the park. The faster calculated growth determined for fish within the Cape Sable area is most likely accounted for by Lee's phenomenon: when more older fish are used in back calculating growth rates, size selective mortality may operate on the smaller members of an age class, leaving a greater proportion of faster-growing individuals. We found only small differences (although statistically significant) in back-calculated lengths of fish among areas and differences in lengths at capture only of age-four fish.

The large mean size of fish taken from the Cape Sable area was due to a larger number of older male fish in that area than in other areas. Proportionately fewer small males were also caught there making the sex ratio the same (1/1) as in other areas. Croker (1960) did not report size differences among gray snapper taken from various park areas.

Large gray snapper are more likely to be caught in the Cape Sable area because of its proximity to offshore gulf waters and its stable high salinities. Starck (1964) stated that while juvenile gray snapper are euryhaline and common in inshore waters, adults are less tolerant of salinity fluctuations and generally inhabit offshore waters.

Sexual differences in calculated growth found for gray snapper in this study were not statistically tested by previous investigators (Croker 1960, Starck 1964).

Growth differences among the three year classes for which adequate samples were available occurred only in the first growth year. The 1975 year class grew faster than the 1976 or 1977 year class. Air temperature data for Everglades National Park were examined to determine if cold weather had occurred which caused poor growth in 1976 and 1977 relative to 1975. Unusually cold weather occurred in January 1976 and 1977 which could have affected gray snapper growth. Tempertures dropped below 4.4°C for three days in January 1976 and for five days in January 1977, which represented drops of 1.6°C and 3.3°C respectively from the long-term average temperature for that month (NOAA Climatological Data 1976, 1977). Year class differences in calculated growth may have also been influenced by Lee's phenomenon; the largest estimated fish lengths (highest growth rate) at age one were from the oldest age class.

The von Bertalanffy equation did not accurately describe park gray snapper growth. The von Bertalanffy equation assumes that fish growth in either weight or length declines with age. Because gray snapper growth is linear after the first year and increases in the fifth year (Fig. 8), an equation fit to these data predicted a maximum theoretical length (L) much larger than would be expected for the size range of fish (111-451 mm) in the study or for the maximum size (650 mm) of gray snapper reported for south Florida (Starck and Schroeder 1970).

We are presently unable to explain why the length-weight relationship of gray snapper males from the Shark River area and females from the Coot Bay-Whitewater Bay area were different from fish in those and other park areas. The sample sizes, frequency of prey items consumed, length and age range of each sex were similar within those given areas. If the differences in length-weight relationship were related to sex, one would have expected to see differences among all park areas. The lack of spawning activity in all park areas eliminates the possibility of reproductive condition affecting length-weight regressions.

Mortality

Total mortality rates reflected the sex ratio of park gray snapper. Male and female fish died at roughly equivalent rates, making the sex ratio 1/1. Other investigations of gray snapper (Croker 1960; Starck 1964) also reported sex ratios of 1/1.

Snapper annual survival rates in the Cape Sable area were almost twice that of fish from other areas; survival rates were lowest in the Coot Bay-Whitewater Bay area. These differences in survival were due to the greater proportion of large fish ($\geq$300 mm) taken from Cape Sable than from other areas.

Comparison of annual mortality estimates for 1979 park snapper with estimates that we calculated using Croker's data (1960) indicates that gray snapper survival and longevity were greater in 1979 than in 1960 (Table 4). No fish older than five years were sampled by Croker, while we observed fish up to seven years old. The dominant age class in the park fishery shifted from age two in 1960 to age three in 1979, although age at full recruitment stayed the same (3 years; Fig. 19). The increase in gray snapper survival was probably due to a decrease in natural mortality. Although estimated numbers of fishing boats in the park declined in 1979 from peaks in the late 1960's and early 1970's, they still were nearly twice the number of boats estimated in 1960 (NPS unpublished data). Gray snapper catch rates have also increased since 1960, indicating that fishing mortality probably has increased. Natural mortality rates would have had to decline for total mortality rates to decrease.

We were unable to estimate gray snapper natural mortality using von Bertalanffy growth parameters since the von Bertalanffy equation did not describe park gray snapper growth accurately.

The only reported estimate of natural mortality for south Florida gray snapper is $M = 0.30$ (Manooch 1982). Estimates reported for other lutjanid species are higher, ranging from $M = 0.54$ for Lutjanus apodus to $M = 2.24$ for Lutjanus buccarrella (Munro 1974). These estimates were calculated for exploited stocks of Jamaican reef snappers and may be higher due to the great abundance of predatory species occurring there (Munro 1974).

Food

The results of the food analyses corroborate results of other food studies reported for gray snapper in Everglades National Park (Croker 1960; Roessler 1967; Odum 1970), the Florida Keys (Starck 1964), and the Dry Tortugas (Longley et al. 1925). Gray snapper diet changes with predator size and habitat. Juvenile gray snapper are generally found in inshore grass-bed areas and eat mainly shrimp, crabs, and amphipods. Adults are generally found in deeper waters and consume mainly fish and shrimp.

Differences in diet attributed to season and predator size were probably artifacts of area differences in food consumption. Gray snapper taken during summer and fall consumed mainly fish and shrimp and generally came from the Cape Sable area. Mean size of these fish was greater than in other areas or seasons. Gray snapper caught during the winter and spring consumed mainly shrimp, small fish, crabs, and amphipods. Most of the fish taken during this time were small ($\leq$ 230 mm) and came from inshore areas of the park. Within any given area, there were no significant differences in diet among seasons or predator sizes.

Spawning Activity

The lack of spawning activity observed in this study indicates spawning probably occurs outside of park waters. Croker (1960) also found no ripe individuals in an earlier study of 790 park gray snapper, even though size ranges (80-500 mm) of fish in both studies included adults. Starck (1964) reported that gray snapper reach maturity in the Florida Keys at 190 mm (2+ years) and migrate to offshore reefs to spawn during June, July, and August (Starck and Schroeder 1970). Recruitment to the park gray snapper population is therefore provided by fish outside of park waters.

CONCLUSIONS

1. Most gray snapper harvested by sportfishermen in Everglades National Park are two and three years old. Gray snapper are recruited to the fishery at age one and are fully recruited by age three. Once fully recruited, annual mortality rate is 72 percent.

2. Gray snapper occurring within the Cape Sable area of the park are on the average larger, older, and experience less mortality than gray snapper from other park areas. However, since growth rates of fish are generally similar in all park areas, the park gray snapper population may be considered a single unit stock.

3. Park gray snapper taken by sportfishermen eat mainly pink shrimp, fish, and crabs.

4. Gray snapper do not spawn in park waters. Recruitment of juveniles to the fishery is dependent upon spawning elsewhere. Additional studies are needed to identify park gray snapper spawning areas.

5. Comparison of our study with an earlier (1960) study of park gray snapper indicated that gray snapper lived longer and experienced less mortality in 1979 than in 1960, despite an increase in fishing effort. Growth rates of fish in both studies were similar. The decrease in mortality in 1979 was probably due to a decrease in natural mortality.

ACKNOWLEDGEMENTS

We are indebted to the following people for their help: Gary Davis proposed the project; Dr. Edward Houde helped with statistical analyses; Julio Garcia Gomez and Robert Work helped to identify food items; Dr. Enid Sisskin drew the figures; Dee Childs, Betty Curl, and Jessie Brundige typed the manuscript. We especially thank the fishermen at Flamingo for their patience and Jim Tilmant for his critical review.

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Table 1. Median lengths of scale-aged fish and length-frequency modes as determined by Cassie's (1954) method for gray snapper combined sexes, September-November 1979.

	Age			
	1	2	3	4
Median (mm F.L.) of length-frequency modes	190	235	268	322
Median (mm F.L.) lengths at capture of scale-aged fish	168	223	255	295
Numbers of fish for each age class	9	56	140	35

Table 2. Annual survival (S) and mortality (A) rates with 95% confidence intervals for gray snapper in Everglades National Park. All fish were fully recruited by age three.

1979	S	A
Males	$0.33 \pm .06$	$0.67 \pm .06$
Females	$0.27 \pm .06$	$0.73 \pm .06$
Sexes combined	$0.28 \pm .03$	$0.72 \pm .03$

Table 3. Annual survival (S), mortality (A) rates and age of recruitment (t_R) of all gray snapper collected from sportfishermen fishing in various park areas. Survival and mortality rates have 95% confidence limits.

	North Florida Bay	Cape Sable	Coot and Whitewater Bays	Shark River
S	.23 ± .08	.41 ± .07	.18 ± .06	.23 ± .06
A	.77 ± .08	.59 ± .07	.82 ± .06	.77 ± .06
t_R	3	3	3	3
Number of fish	105	122	187	207

Table 4. Annual survival (S) and mortality (A) rates with 95 percent confidence intervals for gray snapper in Everglades National Park, 1960 and 1979. All fish were fully recruited by age three.

	S	A
Males		
1960	0.12 ± .06	0.88 ± .06
1979	0.33 ± .06	0.67 ± .06
Females		
1960	0.06 ± .04	0.94 ± .04
1979	0.27 ± .06	0.73 ± .06
Sexes combined		
1960	0.09 ± .03	0.91 ± .03
1979	0.28 ± .03	0.72 ± .03

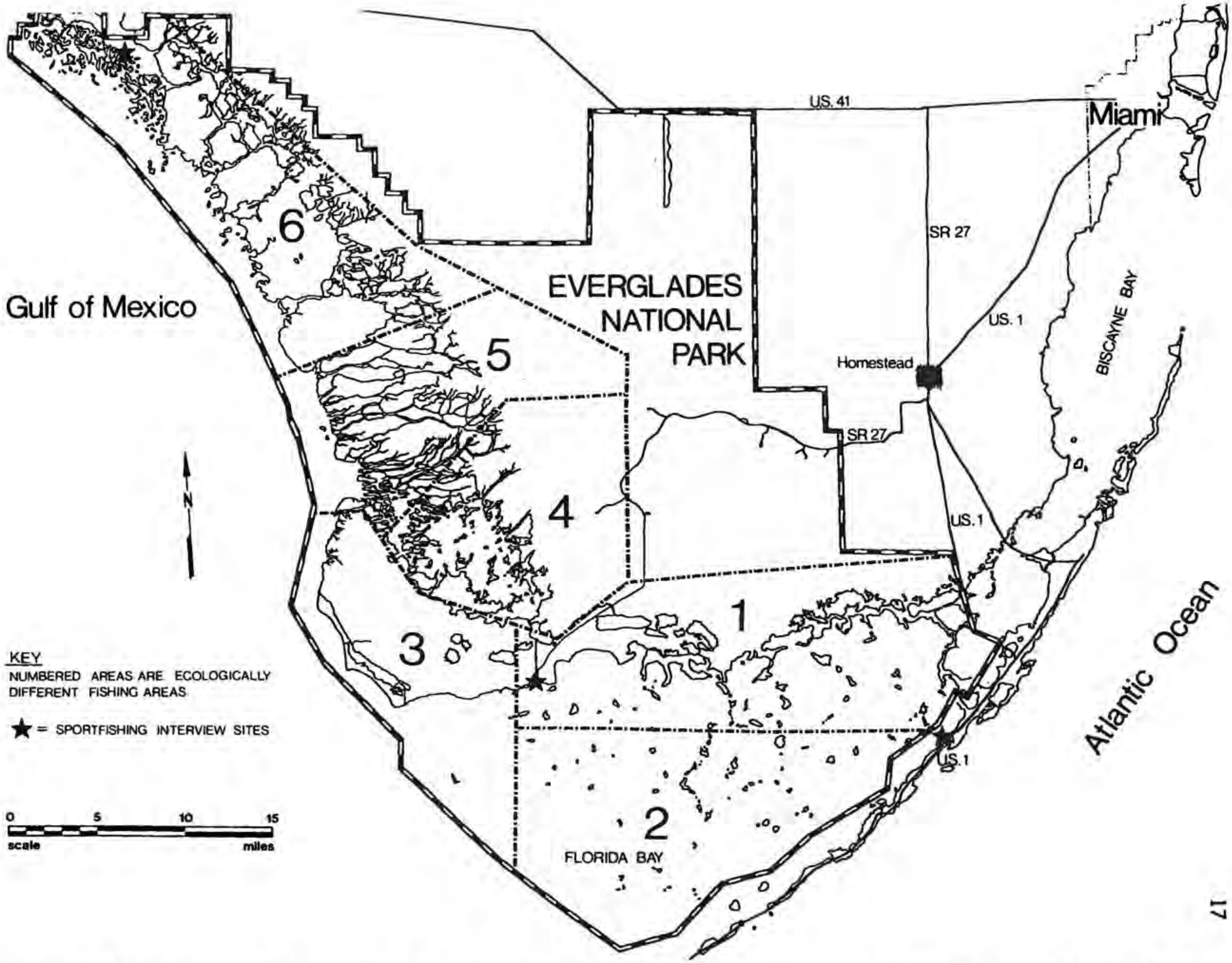


Figure 1. Fishing areas in Everglades National Park, Florida. Numbered areas are: (1) North Florida Bay (2) South Florida Bay (3) Cape Sable (4) Coot-Whitewater Bays (5) Shark River area (6) Ten Thousand Islands.

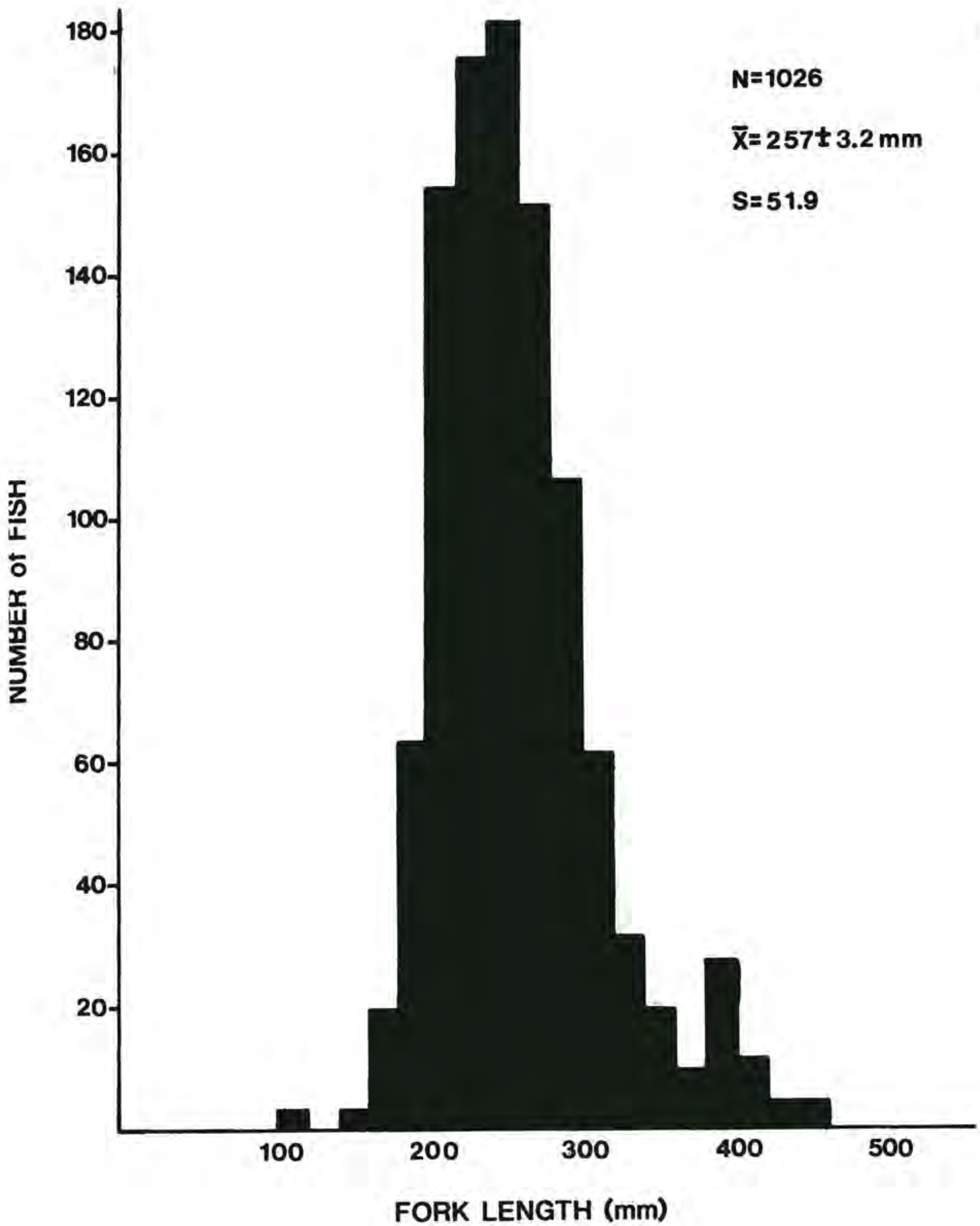
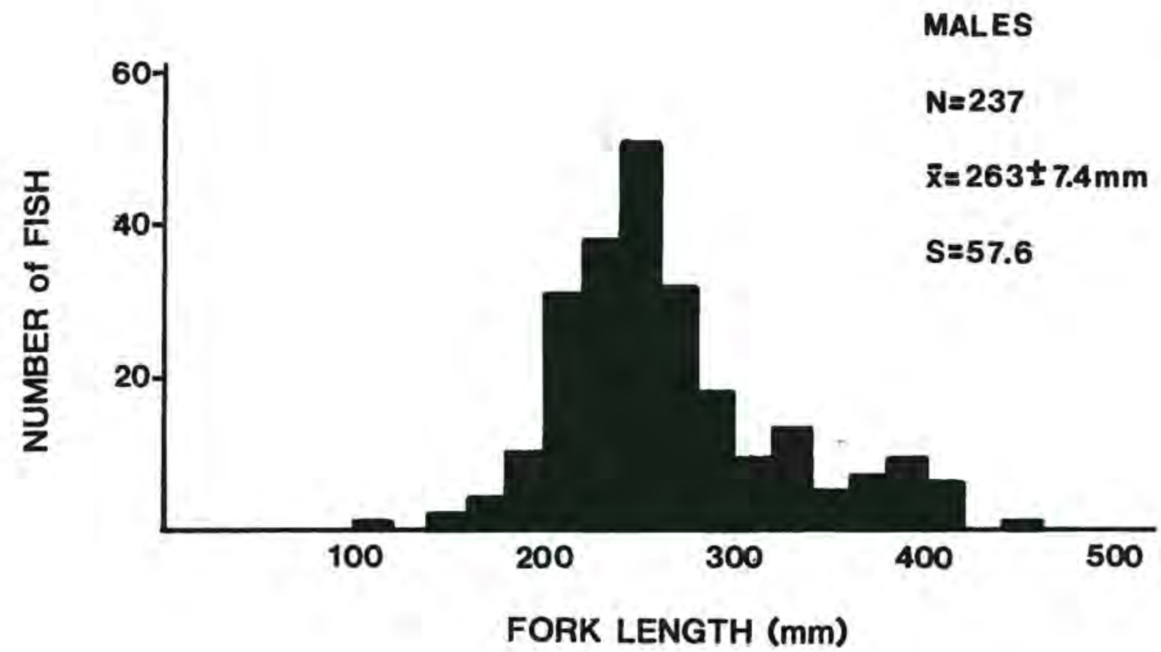


Figure 2. Length-frequency distribution for all gray snapper collected from sportfishermen catches in Everglades National Park, Florida, 1978-1980. Mean fish length has 95% confidence intervals.



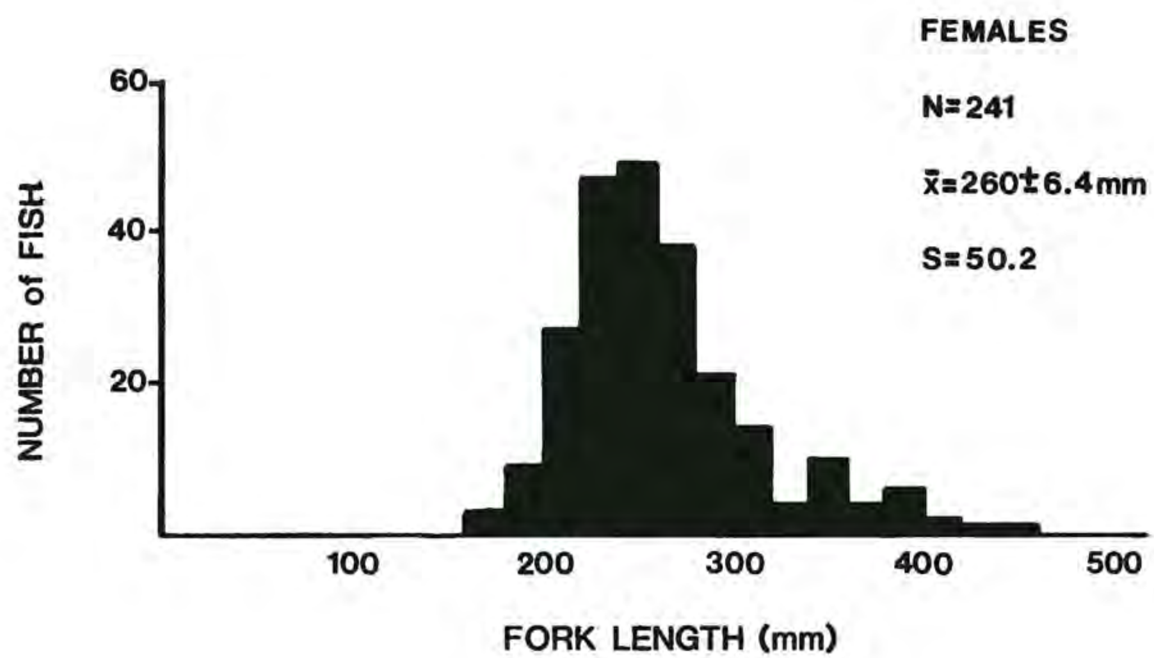


Figure 3. Length-frequency distribution for male and female gray snapper collected from sportfishermen catches in Everglades National Park, Florida, 1978-1980. Mean fish lengths have 95% confidence intervals.

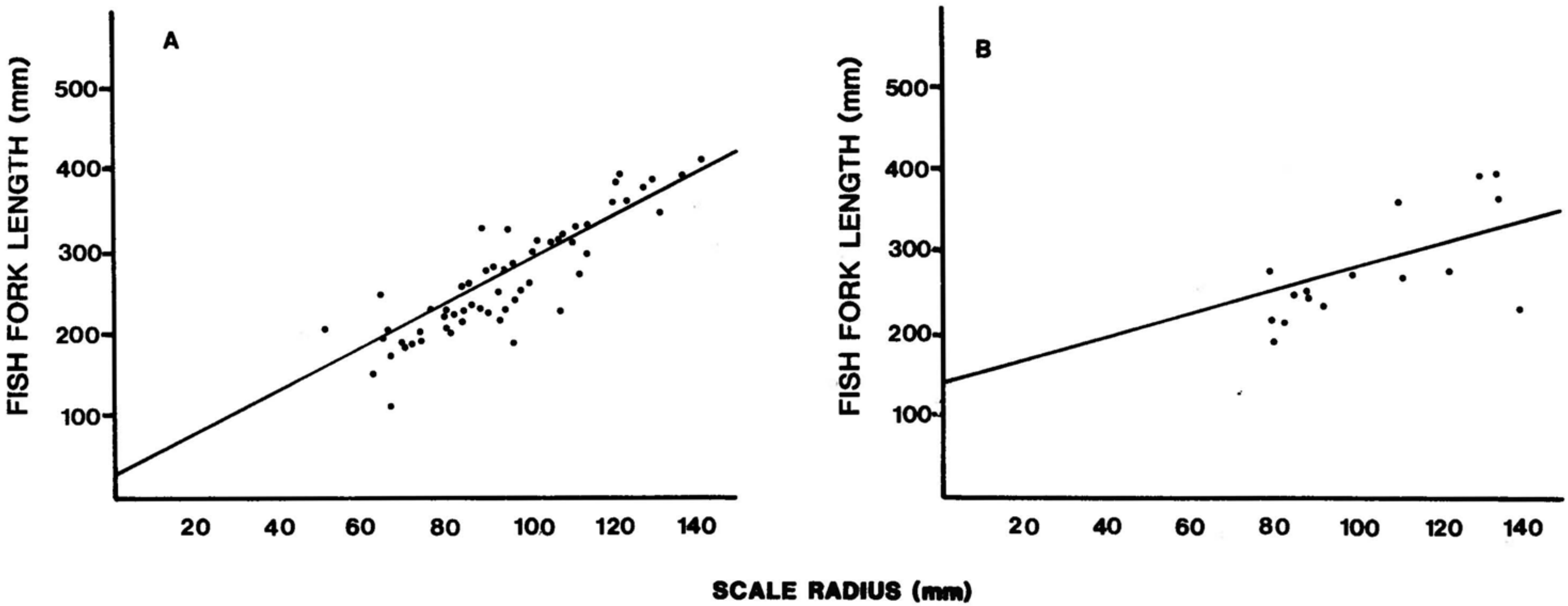


Figure 4. Fish length-scale radius regressions for gray snapper in Everglades National Park, Florida, 1978-1980.

A. Males from Cape Sable area plus males and females from north North Florida Bay, Coot Bay, Whitewater Bay, and Shark River areas. N = 587, r = 0.85. Length = 25.44 + 2.53 (scale radius).

B. Females from Cape Sable area. N = 63, r = 0.49. Length = 135.52 + 1.42 (scale radius).

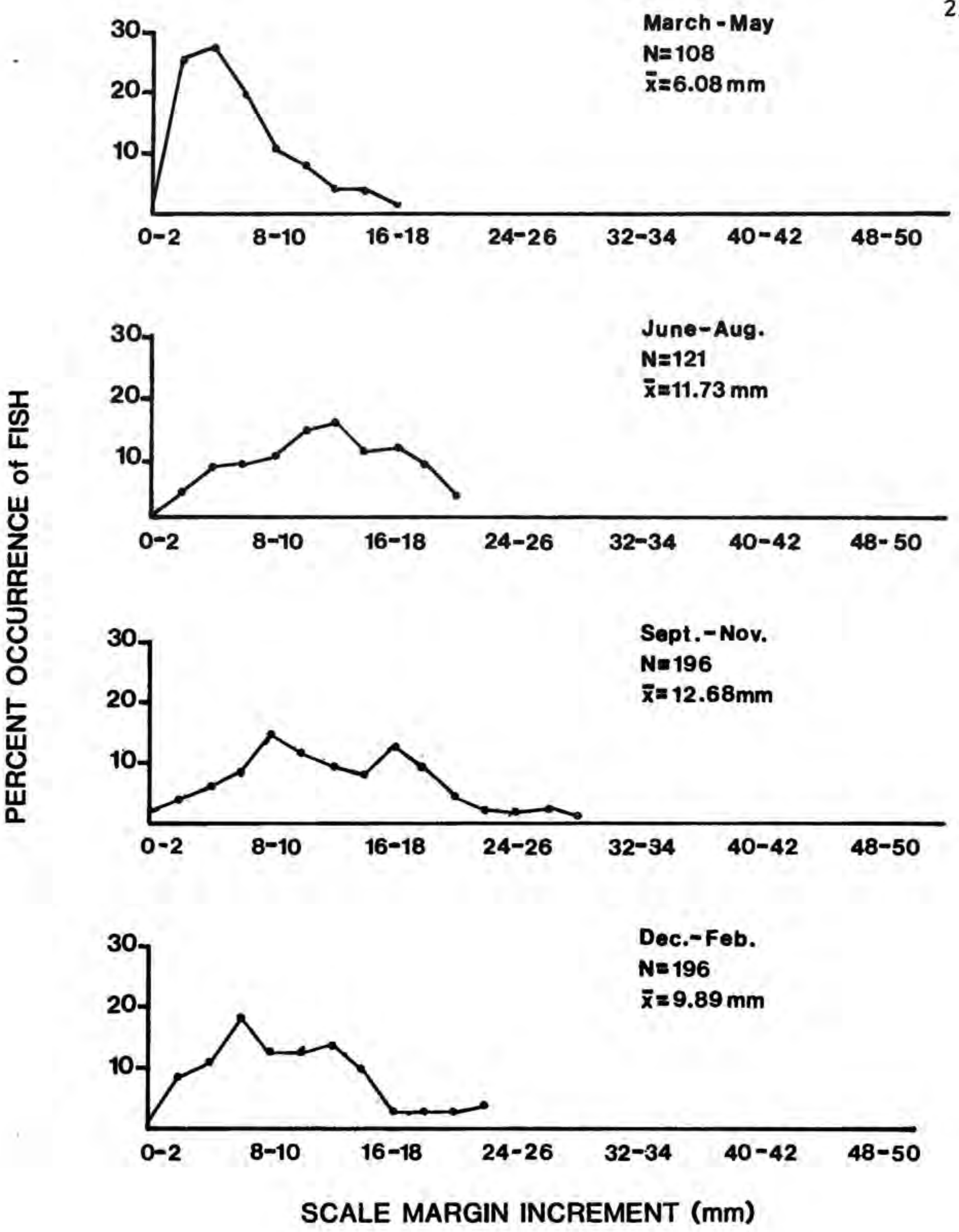


Figure 5. Scale margin increments for two- and three-year old gray snapper in Everglades National Park, Florida, 1978-1980.

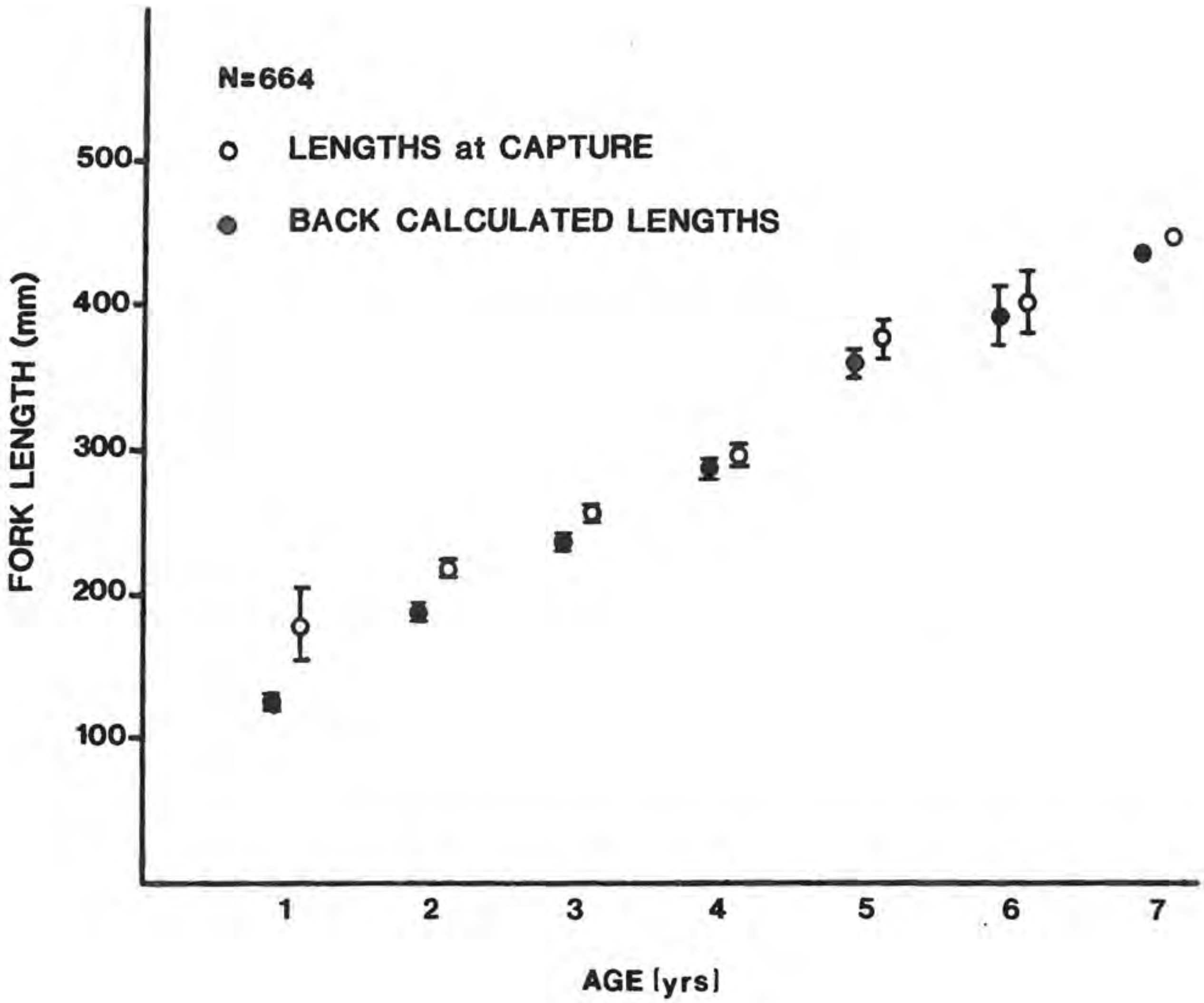


Figure 6. Mean back-calculated lengths and lengths at capture of all gray snapper in Everglades National Park, Florida, 1978-1980. Bars indicate 95% confidence intervals around mean.

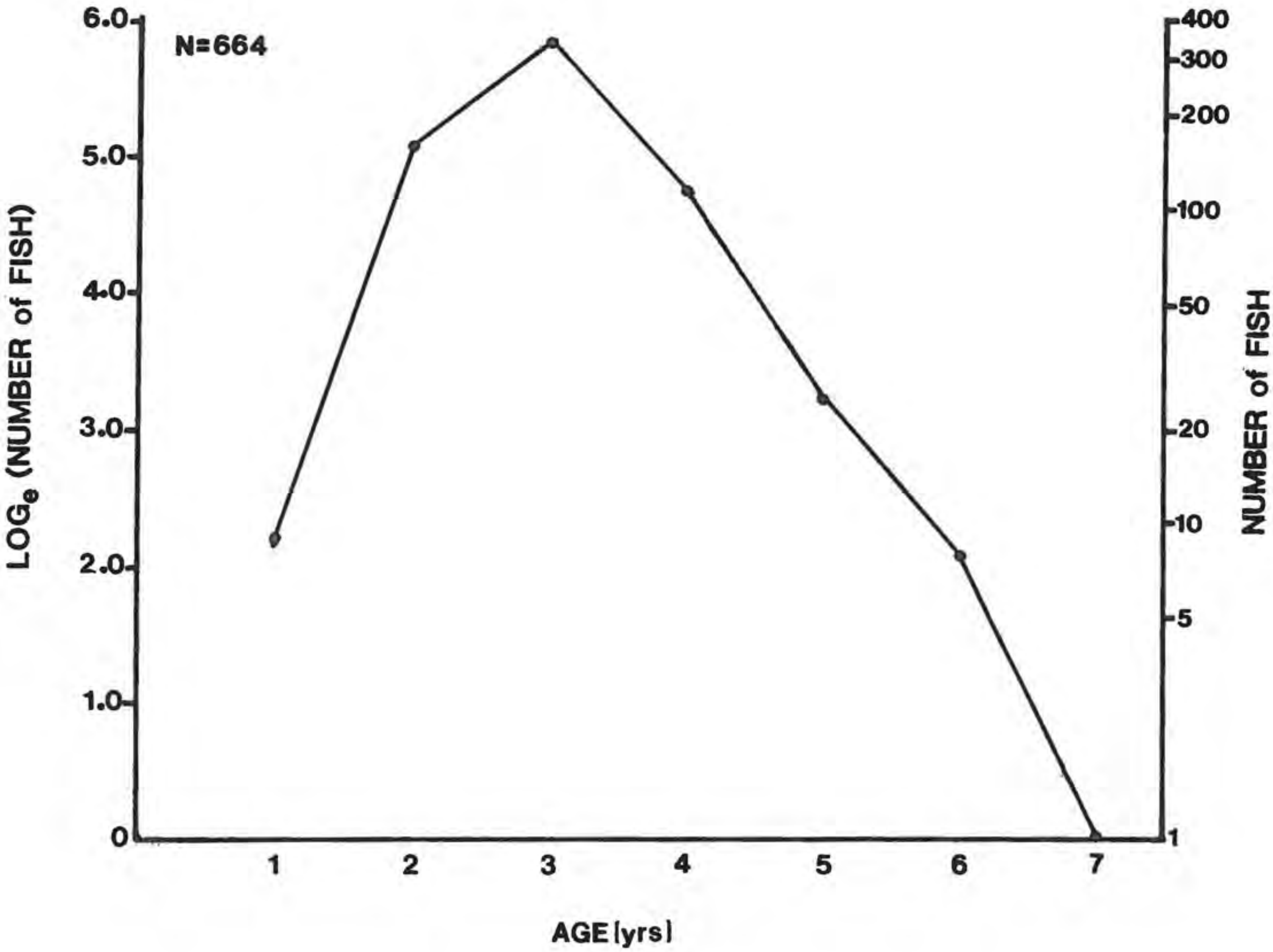


Figure 7. Age distribution of all gray snapper collected from sportfishermen catches in Everglades National Park, Florida, 1978-1980.

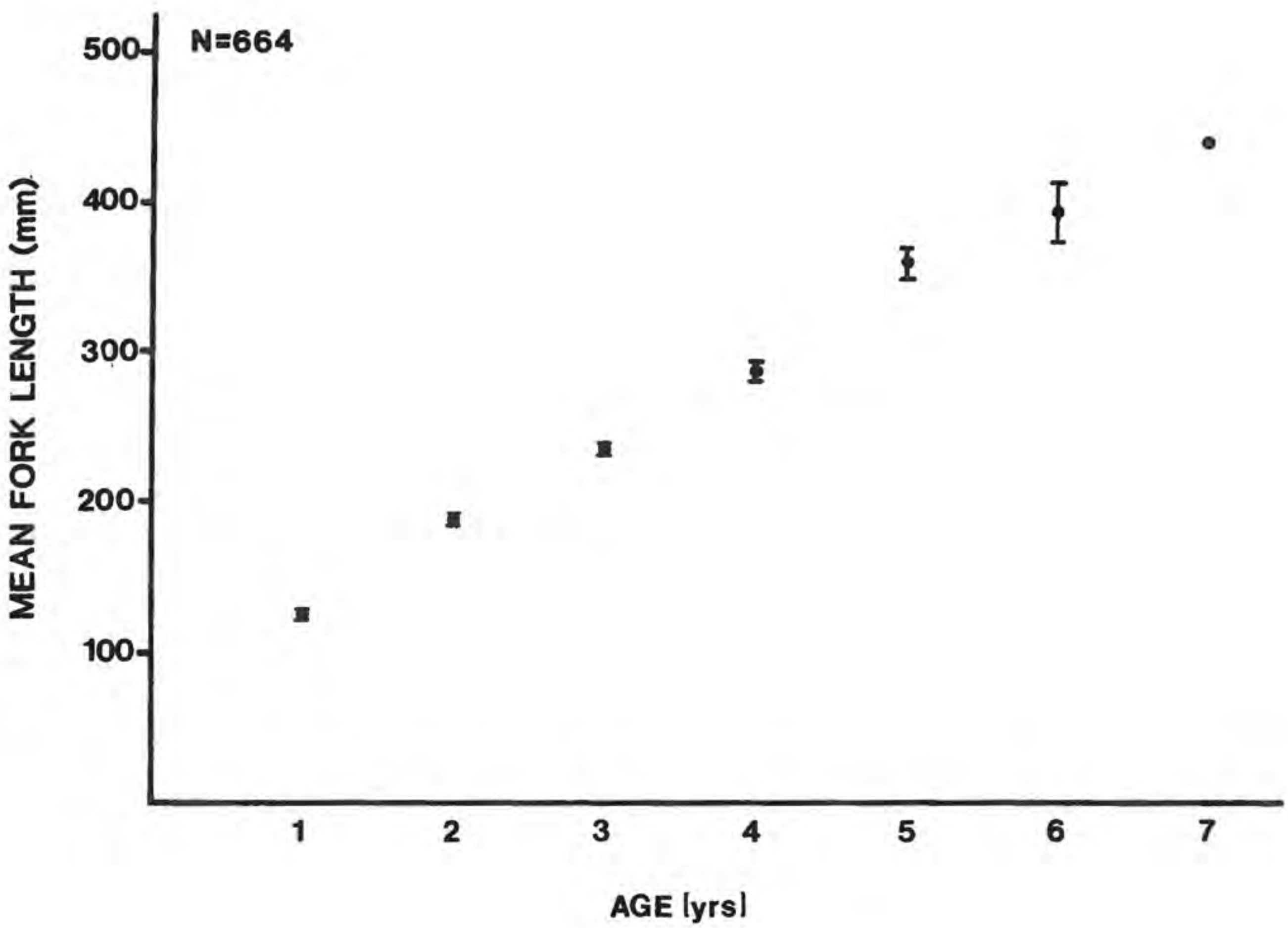


Figure 8. Back-calculated mean lengths at age for all gray snapper in Everglades National Park, Florida, 1978-1980. Bars indicate 95% confidence intervals around mean.

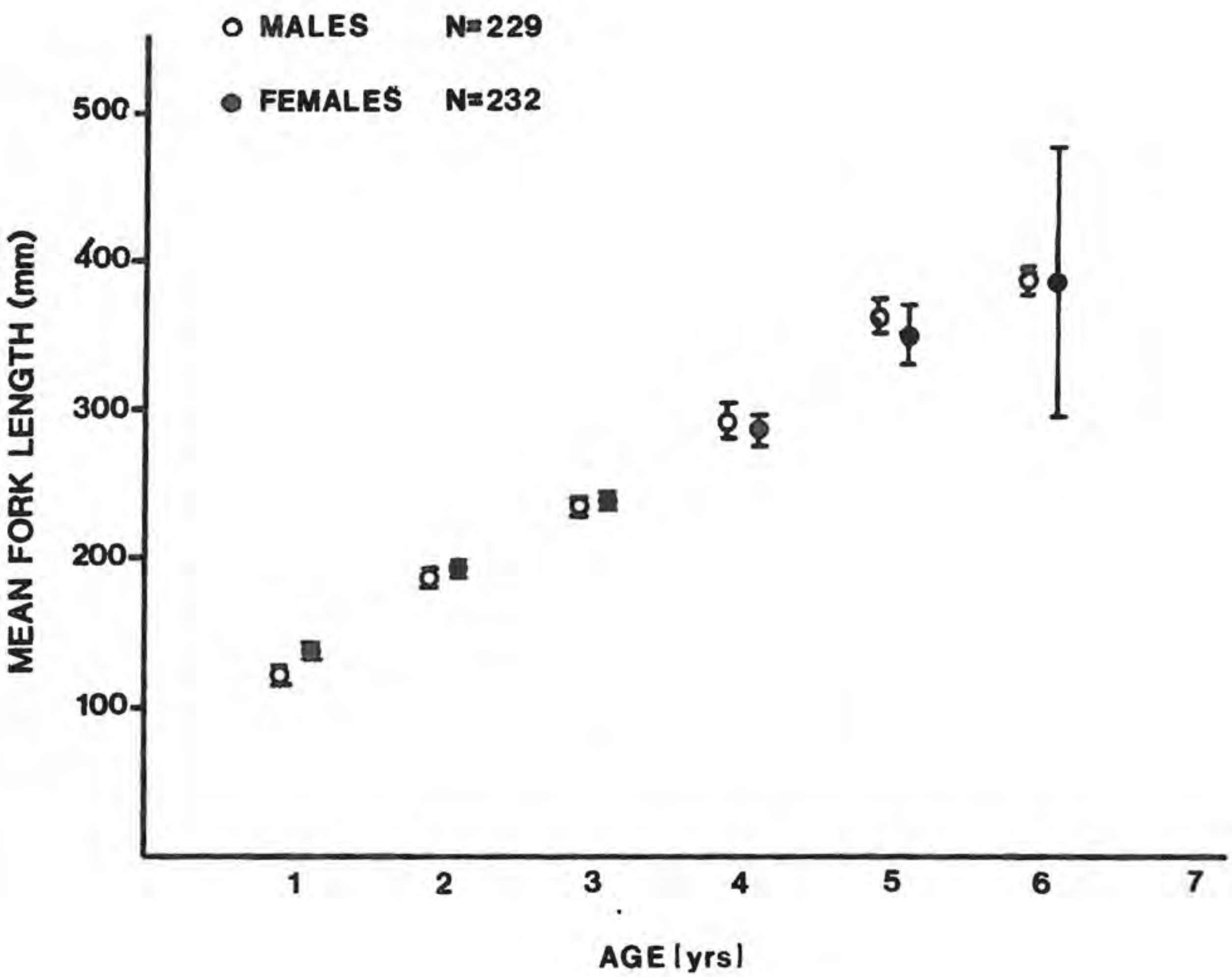


Figure 9. Back-calculated mean lengths at age for male and female gray snapper in Everglades National Park, Florida, 1978-1980. Bars indicate 95% confidence intervals around means.

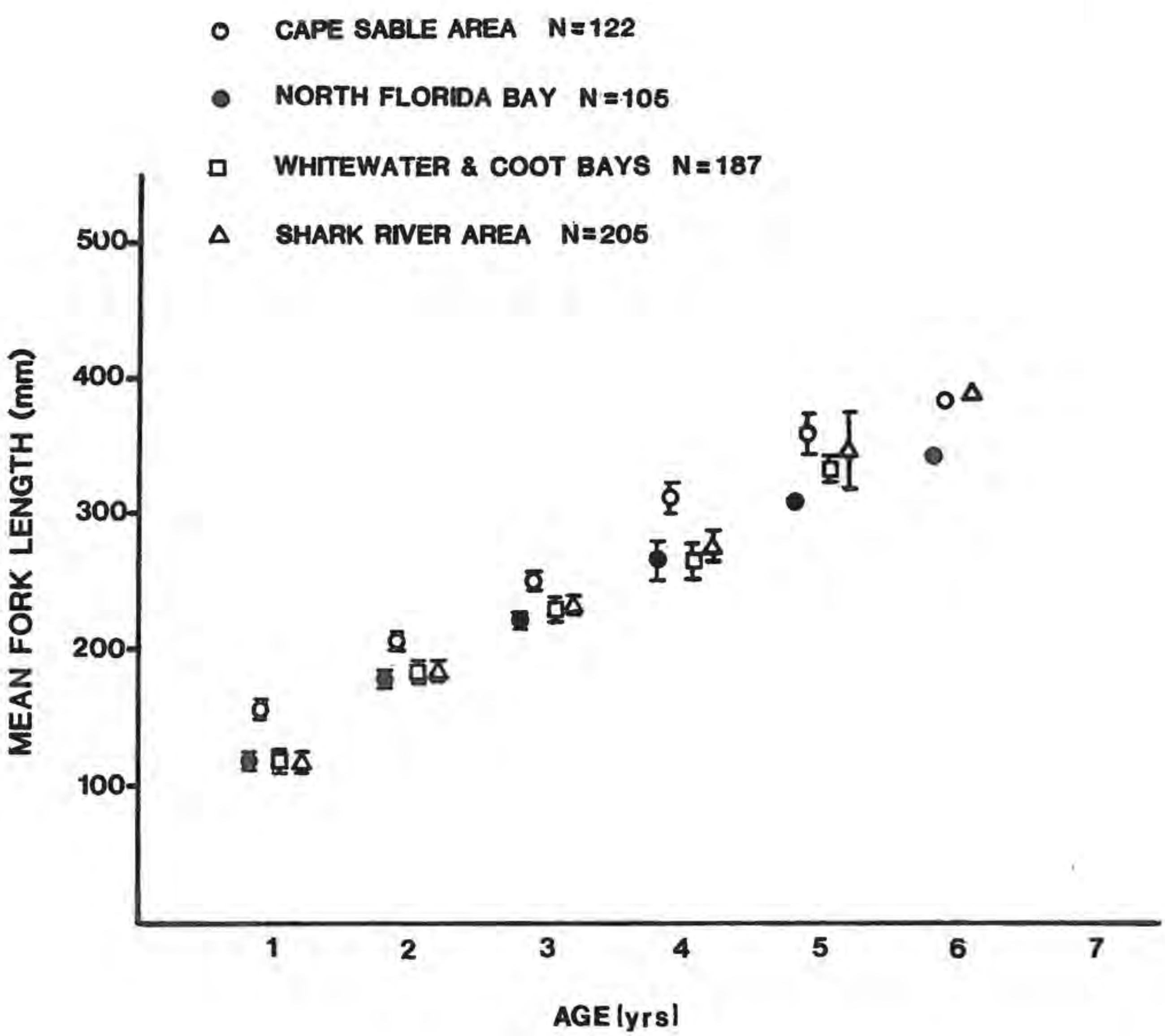


Figure 10. Mean back-calculated lengths at age for all gray snapper collected from areas in Everglades National Park, Florida, 1978-1980. Bars indicate 95% confidence intervals around means.

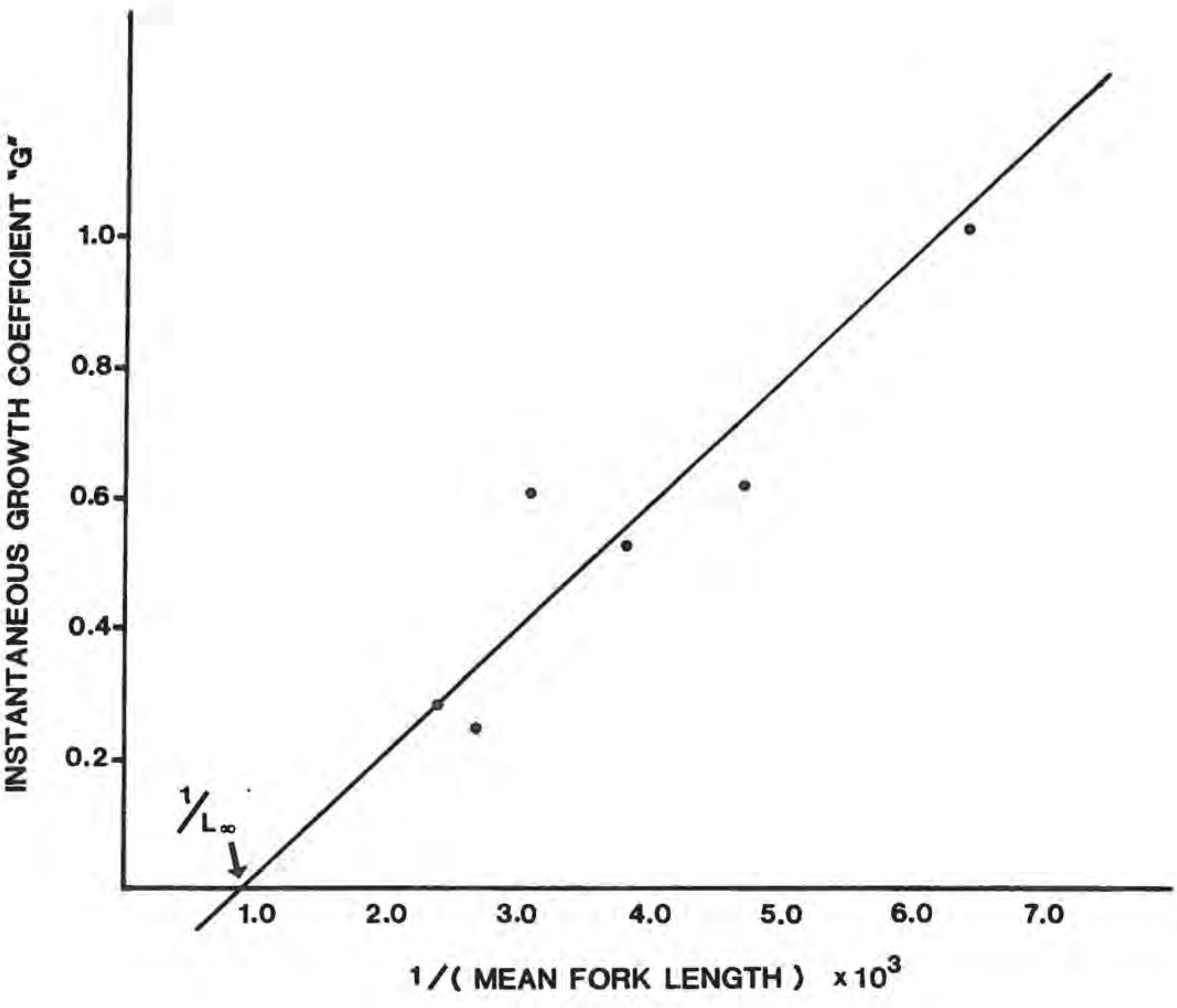


Figure 11. Regression of G, the instantaneous growth coefficient, on the reciprocal of mean back-calculated length of all gray snapper, Everglades National Park, Florida, 1978-1980.

$G = -0.1599 + 0.1883\ (^1/_{L_t} \times 10^3)$,

$N = 6$, $r = .93$, $P < .05$; $L_\infty = 1178$ (mm F.L.),

$K = 0.06 \pm .22$, $t_o = -0.92 \pm .34$.

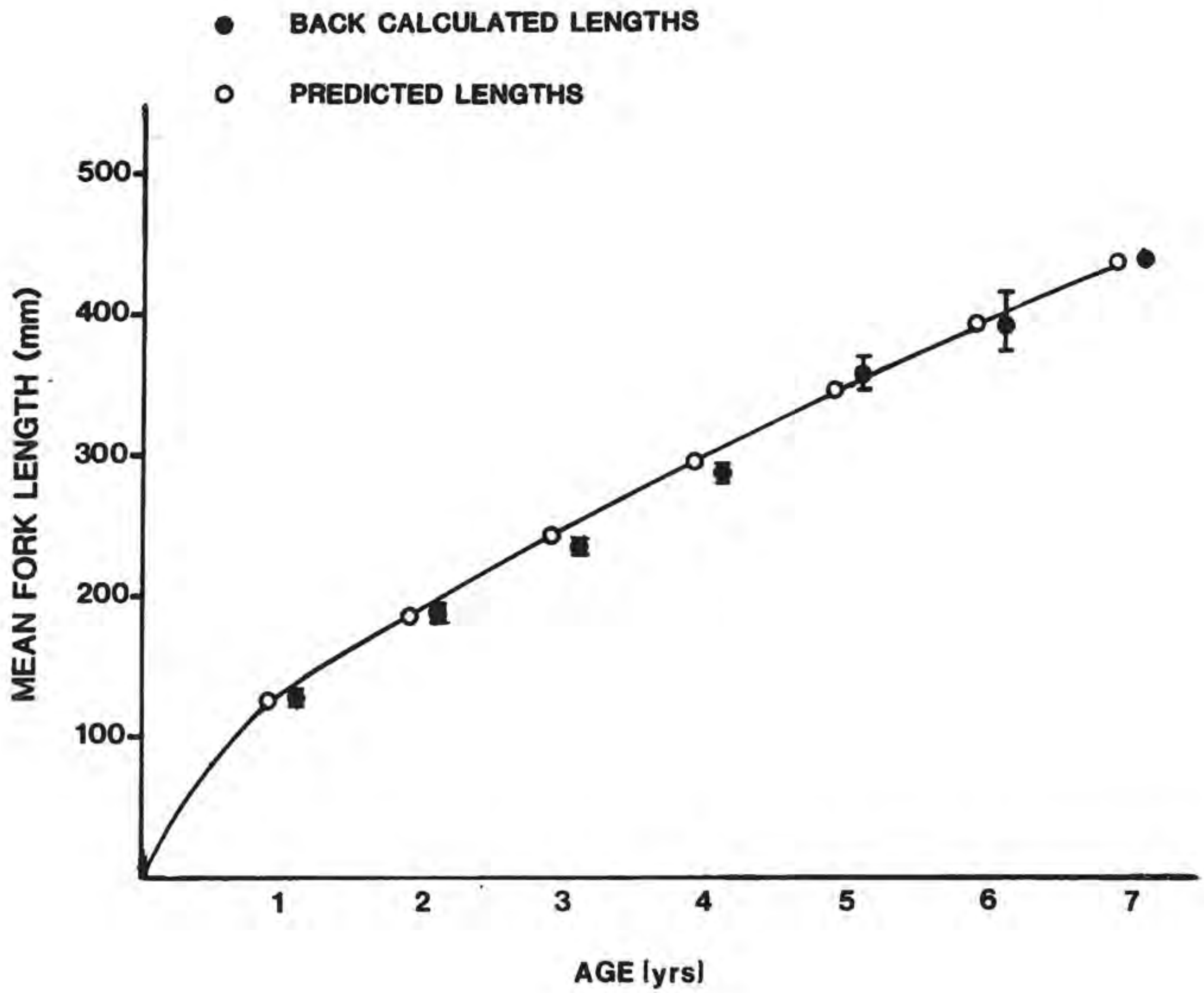


Figure 12. Back-calculated mean lengths at age and lengths predicted by the von Bertalanffy equation for all gray snapper in Everglades National Park, Florida, 1978-1980. Bars indicate 95% confidence intervals around means.

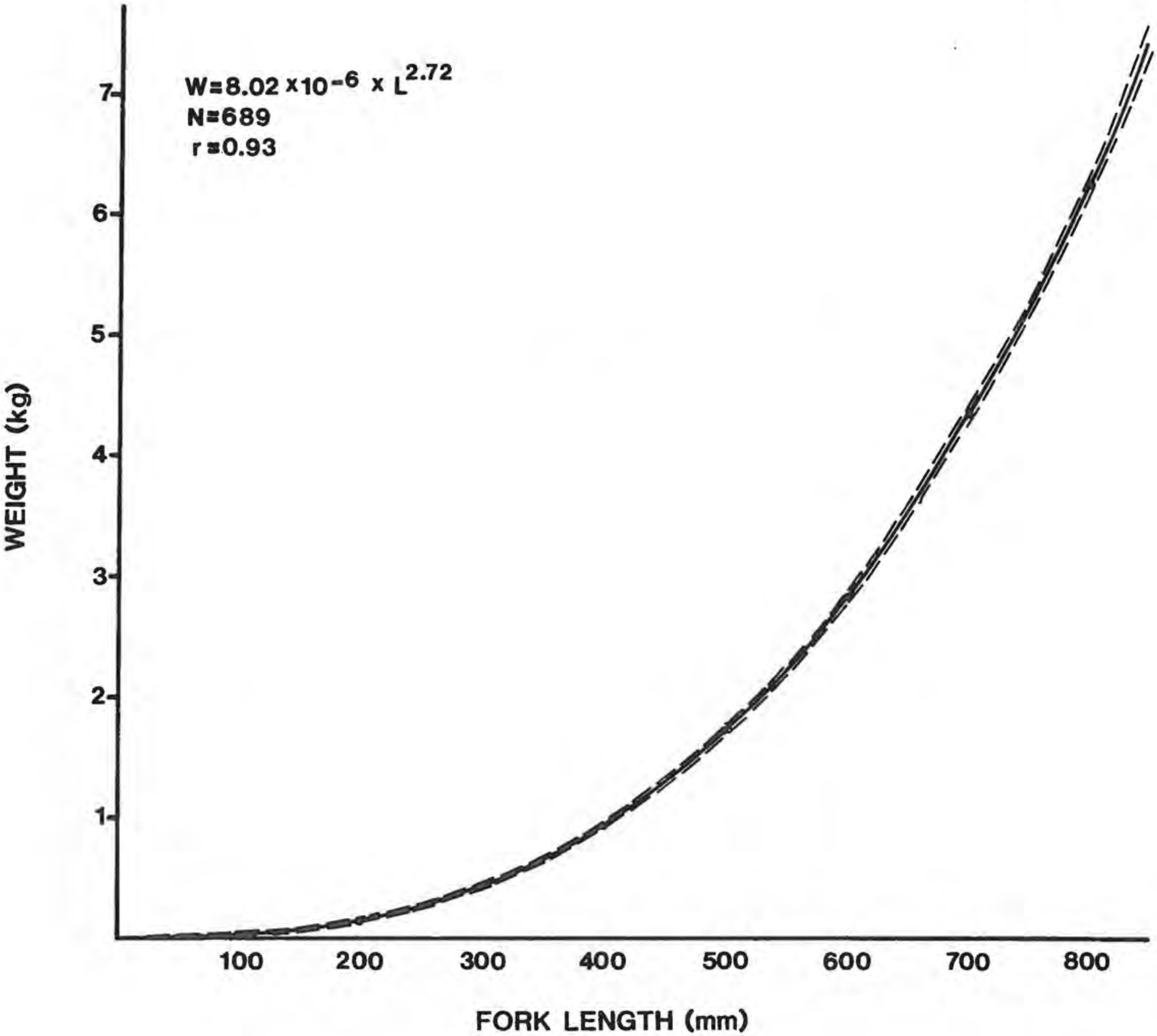
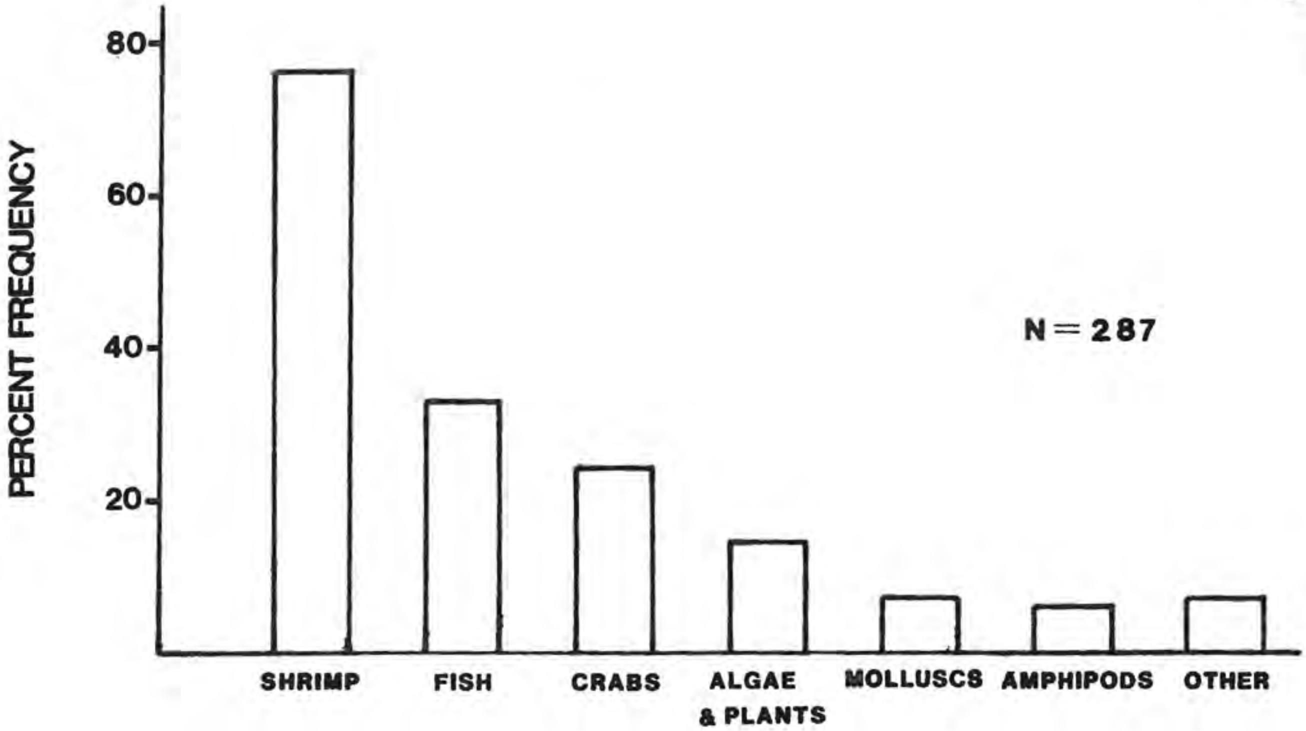


Figure 13. Length-weight relationships for all gray snapper in Everglades National Park, Florida, 1978-1980. Dashed lines indicate 95% confidence intervals.



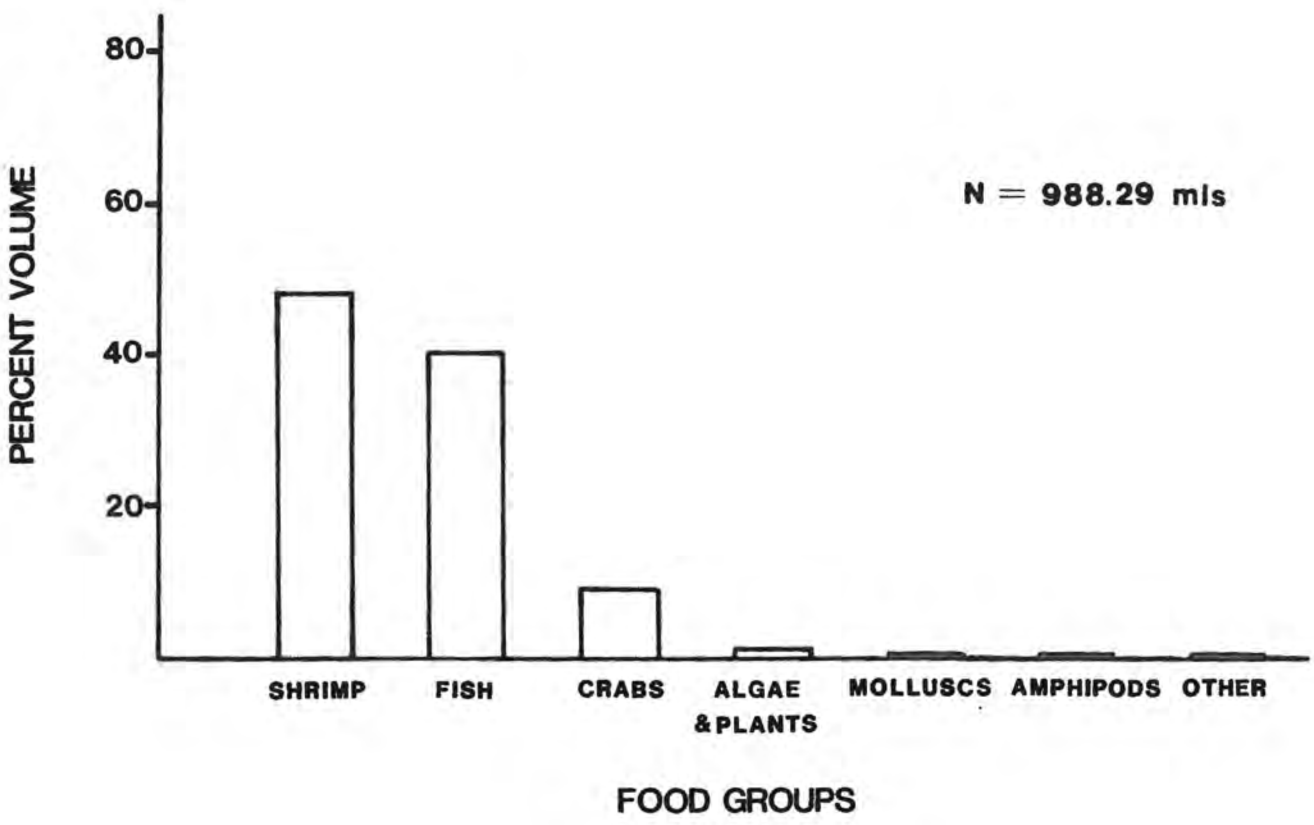


Figure 14. Percent frequency and volume of prey species consumed by gray snapper in Everglades National Park, Florida, 1978-1980.

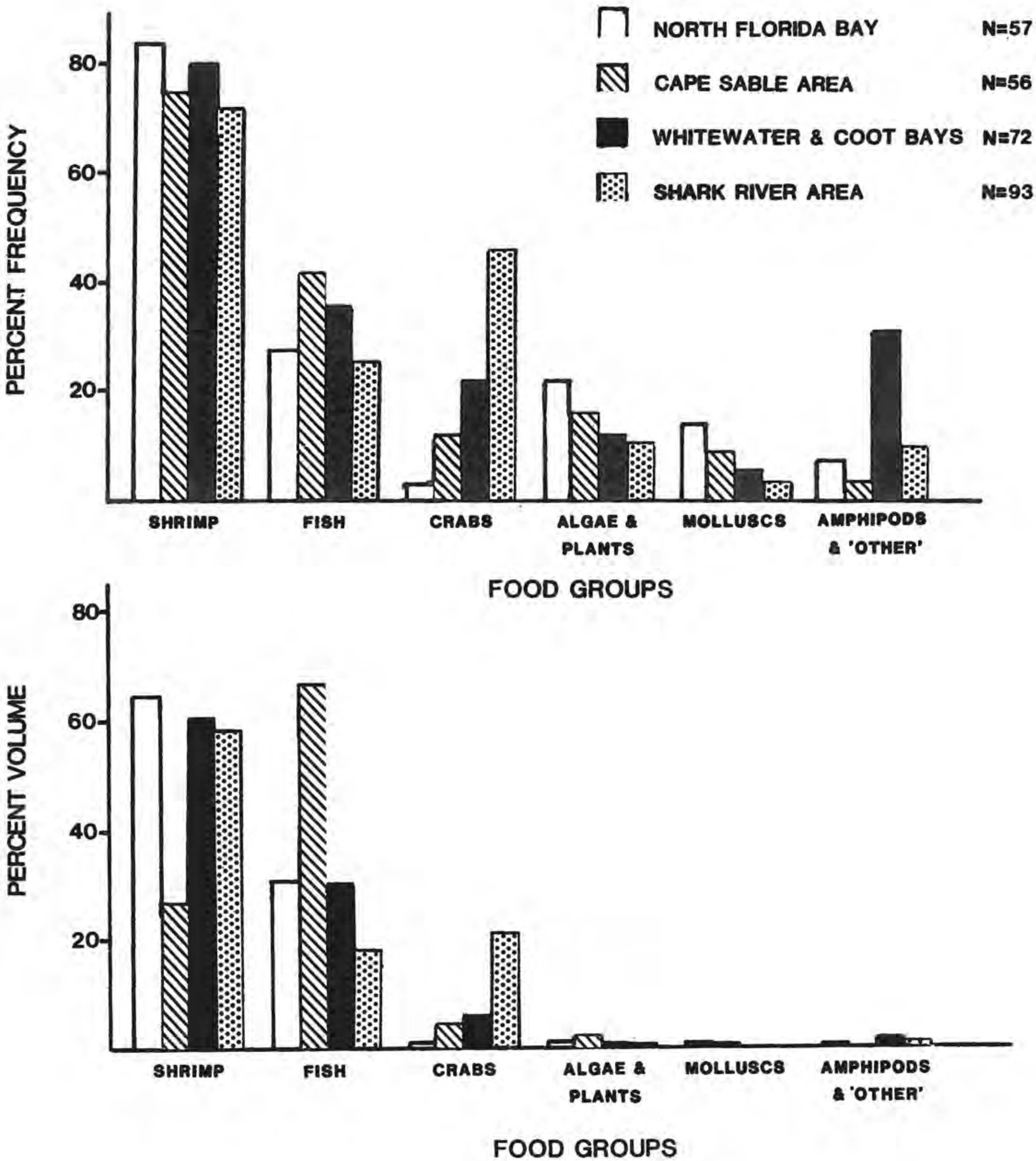


Figure 15. Percent frequency and volume of prey species consumed by gray snapper among areas of capture in Everglades National Park, Florida, 1978-1980.

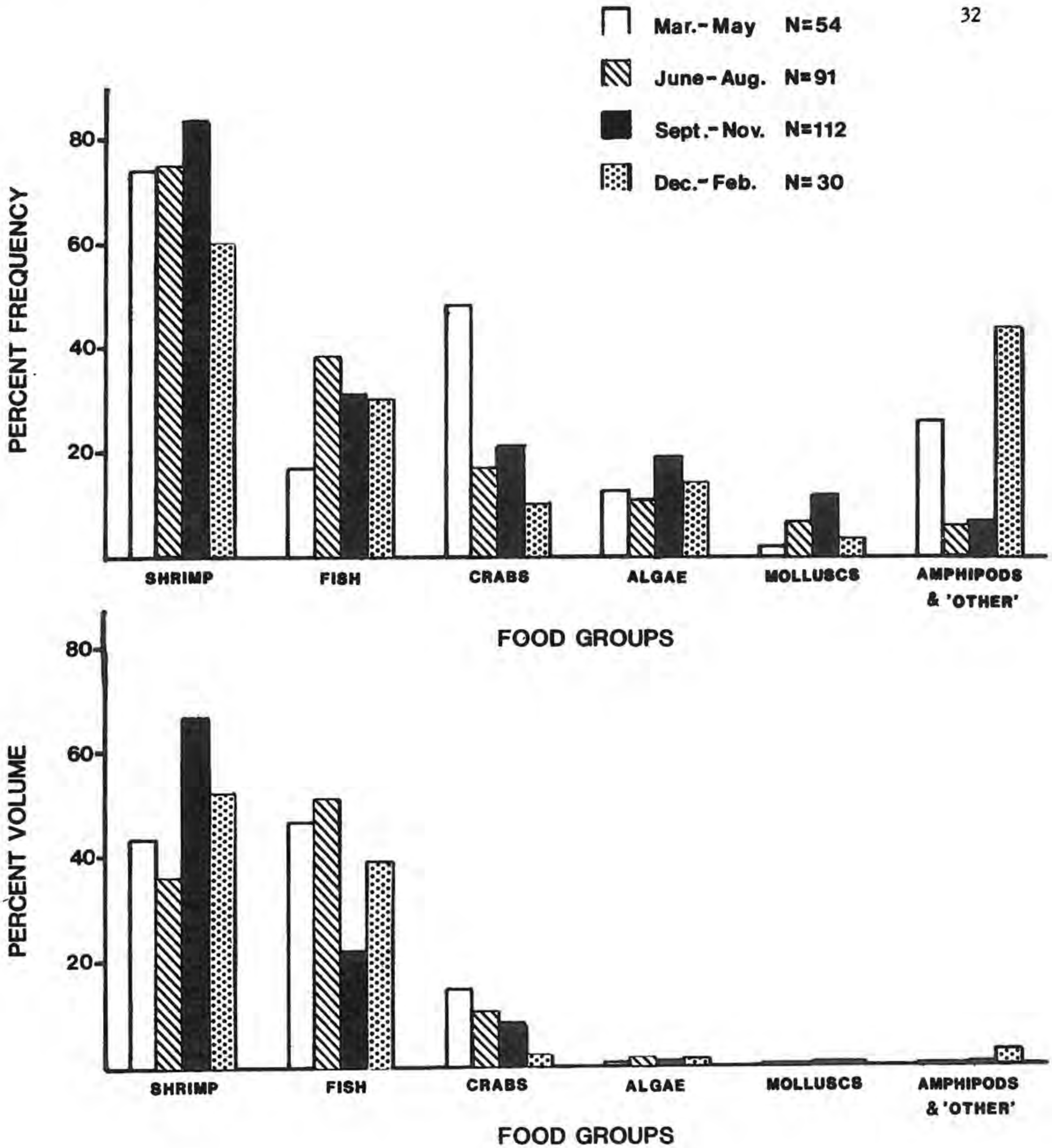


Figure 16. Percent frequency and volume of prey species consumed by gray snapper by seasons in Everglades National Park, Florida, 1978-1980.

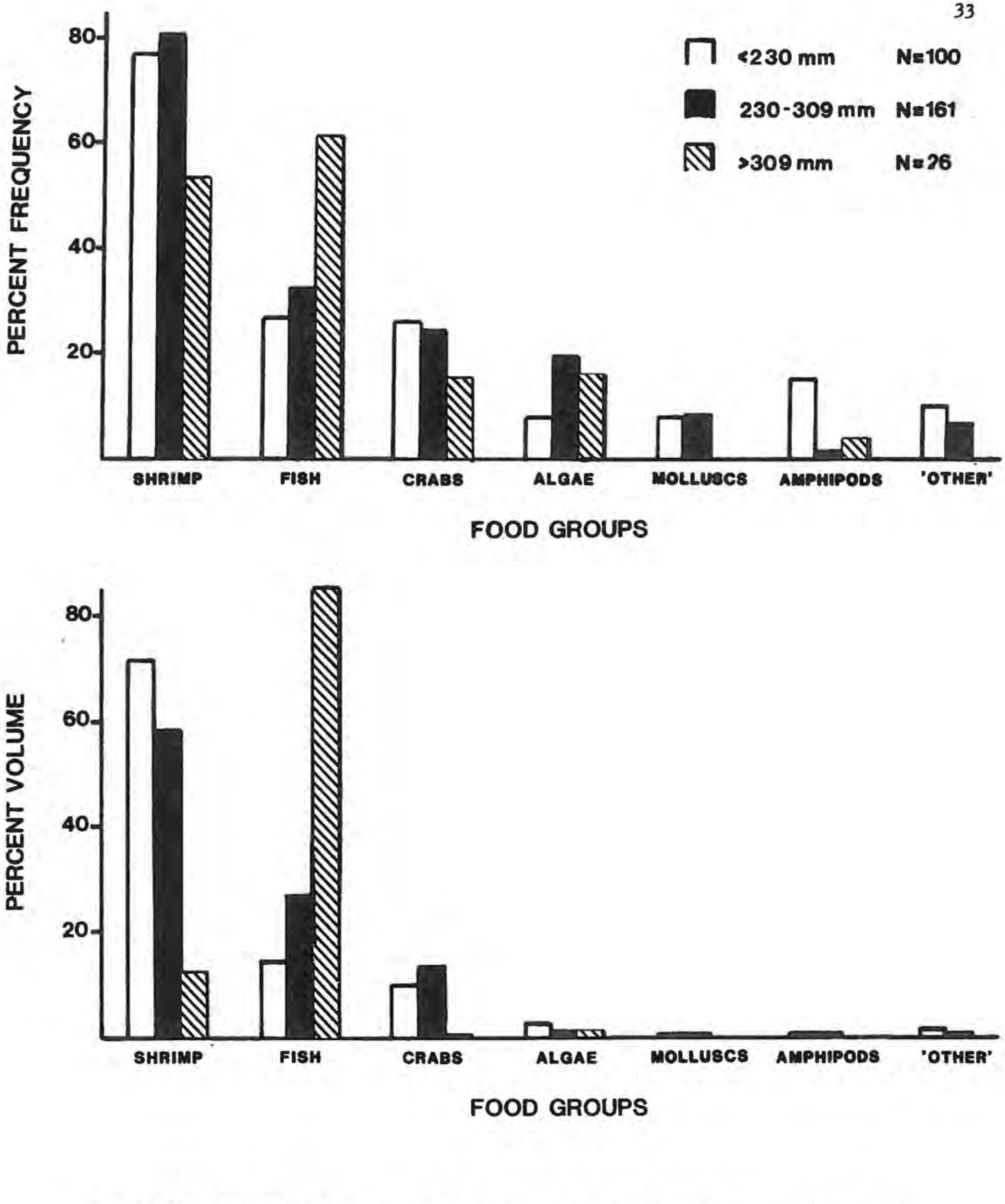


Figure 17. Percent frequency and volume of prey species consumed by gray snapper according to predator size in Everglades National Park, Florida, 1978-1980.

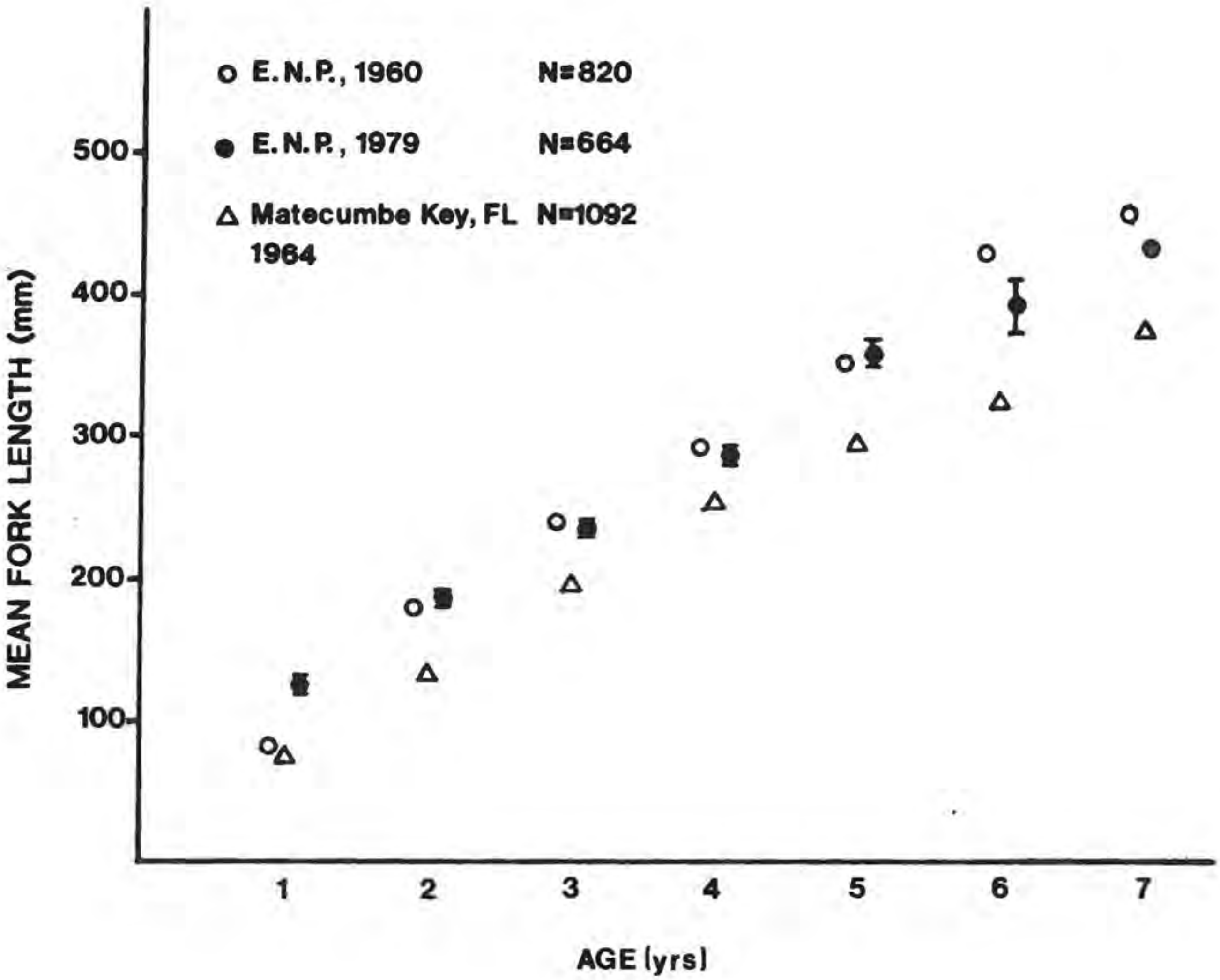


Figure 18. Back-calculated mean lengths at age for gray snapper in Everglades National Park, 1960 and 1979, and Matecumbe Key, Florida. Bars indicate 95% confidence intervals around means.

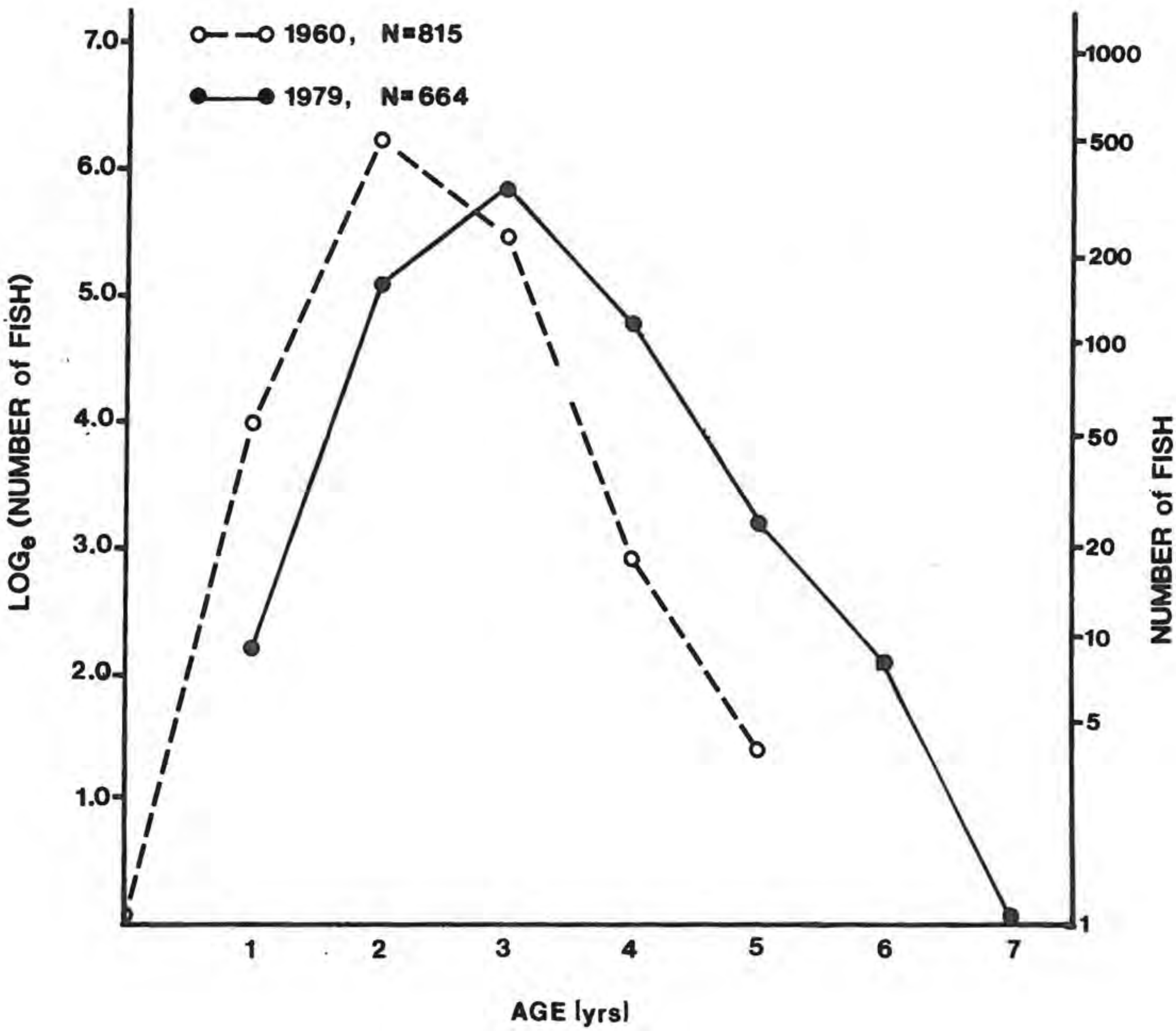


Figure 19. Age distribution of gray snapper sampled from sportfishermen catches in Everglades National Park, Florida, 1960 (Croker 1960) and 1979.

Appendix I. Distribution of gray snapper lengths (F.L.) calculated (c) and length at capture (o) for ages 1-7. All fish (combined sexes and unsexed fish).

Annulus	I		II		III		IV		V		VI		VII	
Length (mm)	c	o	c	o	c	o	c	o	c	o	c	o	c	o
60-79	3													
80-99	58		1											
100-119	260	1	2	2										
120-139	215		16											
140-159	52	1	70	2	1									
160-179	38	4	162	8	9	2								
180-199	25	1	194	29	42	3								
200-219	10		138	44	112	36	4	1						
220-239	1	2	50	49	130	67	12	2						
240-259	2		15	18	86	89	24	13						
260-279			3	8	72	73	27	29						
280-299			3	2	27	48	29	21						
300-319			1		9	11	21	23	4					
320-339					5	6	17	14	7	3				
340-359						4	11	5	8	5	1	1		
360-379						4	4	2	5	5	1			
380-399							1	7	6	6	4	1		
400-419									3	3	1	4		
420-439											2	2	1	
440-459										2				1
460-479														
n	664	9	655	162	493	343	150	117	33	24	9	8	1	1
$\bar{x}$	126	178	188	216	236	256	287	297	359	377	393	403	437	448
s	26.18	32.61	26.79	27.95	31.38	32.30	38.46	38.44	28.76	32.02	25.70	26.81	0	0

average age = 3.0 $\pm$ .1 yrs
average length = $\overline{259}$ $\pm$ 4 mm

Appendix II. Distribution of gray snapper lengths (F.L.) calculated (c) and length at capture (o) for ages 1-6. Males, all areas.

Annulus	I		II		III		IV		V		VI	
Length (mm)	c	o	c	o	c	o	c	o	c	o	c	o
60-79												
80-99	26											
100-119	101	1	1									
120-139	73		9									
140-159	23	1	30	1	1							
160-179	4	1	55	2	4	1						
180-199	1		66	9	19	1						
200-219	1		52	16	39	13	2	1				
220-239			10	19	39	18	6	1				
240-259			2	8	22	37	8	5				
260-279			1	3	30	16	6	11				
280-299				1	10	13	10	3				
300-319					2	1	10	7				
320-339					1	4	10	7	3	1		
340-359						1	7	4	7			
360-379						2	1	1	2	4	1	
380-399								4	3	4	3	1
400-419									1	2		3
420-439												
440-459										1		
460-479												
n	229	3	226	59	167	107	60	44	16	12	4	4
$\bar{x}$	120	148	185	219	234	254	292	302	362	387	385	402
s	18.06	26.91	24.92	25.18	32.69	34.42	41.69	46.13	20.28	27.81	6.02	7.41

age = 3.1 ± .1 yrs

Appendix III. Distribution of gray snapper lengths (F.L.) calculated (c) and length at capture (o) for ages 1-6. Females all areas.

Annulus	I		II		III		IV		V		VI	
Length (mm)	c	o	c	o	c	o	c	o	c	o	c	o
60-79												
80-99	19											
100-119	77											
120-139	59		7									
140-159	7		23									
160-179	34		51	2	4	1						
180-199	24	1	60	11	12	2						
200-219	9		44	12	41	13	1					
220-239	1	1	26	20	46	24	4					
240-259	2		13	8	27	33	11	6				
260-279			2	2	24	26	7	10				
280-299			3	1	9	15	7	4				
300-319			1		7	8	6	6	4			
320-339					4		5	3	3	1		
340-359						3	3	1	1	5	1	1
360-379						2	2	1	3	1		
380-399							1	3	1	2	1	
400-419									1		1	1
420-439												1
440-459										1		
460-479												
n	232	2	230	56	174	127	47	34	13	10	3	3
$\bar{x}$	137	201	194	221	238	257	286	296	349	367	384	392
s	35.02	29.70	31.22	24.82	34.95	34.04	42.13	42.14	32.86	34.40	36.45	41.04

$\bar{x}$ age = 3.0 $\pm$ .1 yrs
$\bar{x}$ length = 260 $\pm$ 6 mm

Appendix IV. Prey species of gray snapper. Occurrence of prey in greater than 5% of the stomachs is noted as common (C), less than 5% as rare (R)

MARINE PLANTS

Algae	
Chlorophyta	
Dictyota spp.	R
Caulerpa spp.	R
Udotea flabellum	R
Phaeophyta	
Sargassum spp.	R
Rhodophyta	
Acanthophora specifera	R
Phanerograms	
Thalassia testudinum,	C
Halodule wrightii	R
Ruppia maritima	R
Cymodacea manatorum	R

MARINE ANIMALS

Polychaeta	
Pectinaridae	R
Mollusca	
Gastropoda	
Olividae	R
Marginella apicina	R
Bulla striata	R
Ceritheum eburneum	R
Pelecypoda	
Brachidontes exustus	R
Chione cancellata	R
Anomalocardia cumeimeris	R

Arthropoda

Crustacea

Alpheus heterochaelis	R
Alpheus armillatus	R
Penaeus duorarum	C
Palaemonetes spp.	R
Periclemenes longicaudatus	R
Callinectes sapidus	R
Eurypanopeus spp.	R
Hexapanopeus spp.	R
Eurytium limosum	R
Neopanope spp.	R
Panopeus spp.	R
Planes minutus	R
Pilumnus lacteus	R
Libinia spp.	R
Petrolisthes galathinus	R
Sesarsma spp.	R
Uca pugilitor	R
Uca minax	R
Cymothoe spp.	R
Dynamene spp.	R
Cirolana spp.	R
Flabelliferidae	R
Anthuridae	R
Corophoididae	R
Aega spp.	R

Echinodermata

Dendrochirote spp.	R

Vertebrata (Chordata - Pisces)

Myrophes punctatus	R
Ahlia spp.	R
Syngnathus spp.	

Perciformes

Cyprinodontidae	R
Floridicthys carpio	R
Gambusia affinus	R
Hippocampus spp.	R
Opsanus beta	R
Lagodon rhomboides	R
Archosargus probatocephalus	R

Anchoa mitchilli	R
Harengula pensacolae	R
Balistidae	R
Gobiidae	R
Microgobius gulosus	R