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Life history aspects of the gray tilefish, Caulolatilus microps (Goode and Bean, 1878)

Jeffrey L. Ross
College of William and Mary - Virginia Institute of Marine Science

LIFE HISTORY ASPECTS OF THE GRAY TILEFISH, *CAULOLATILUS MICROPS* (Goode and Bean, 1878)

A Thesis

Presented to

The Faculty of the School of Marine Science

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In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

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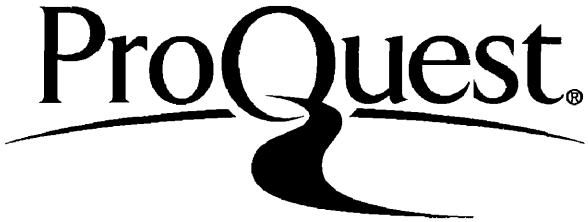
by

Jeffrey L. Ross

1978



APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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Jeffrey L. Ross

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John V. Merriner, Ph.D.
Co-chairman

Gene R. Huntsman, Ph.D.
Co-chairman

John A. Musick, Ph.D.

Joseph G. Loesch, Ph.D.

Craig L. Smith, Ph.D.

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This thesis is dedicated to Craig Smith; his strength and patience is much more than an inspiration.

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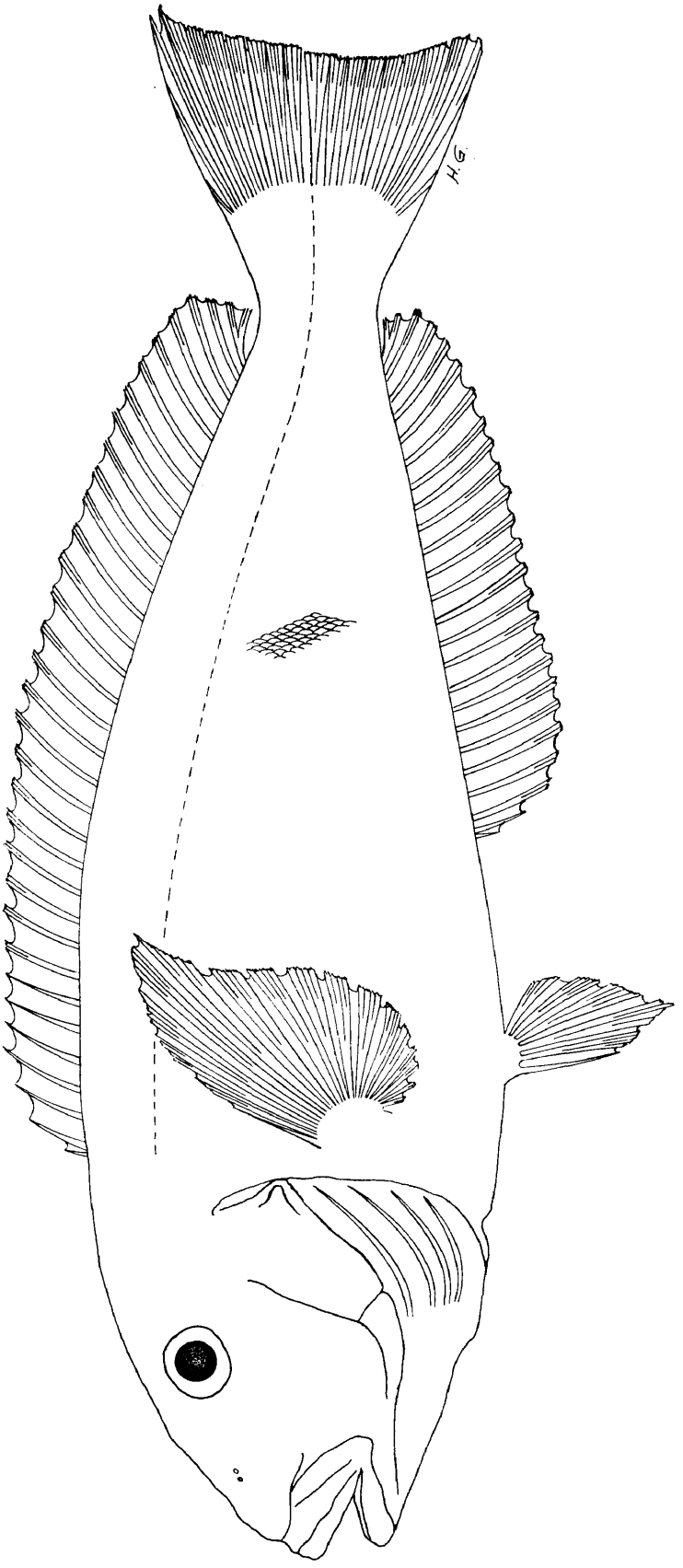
ABSTRACT

The gray tilefish, Caulolatilus microps, is the most common branchiostegid captured in the Carolinas' headboat fishery. Specimens were obtained by exploratory research fishing trips and port sampling operations. Ovarian and testicular morphology and development are described macroscopically and histologically. The transformation of ovaries to testes in three juvenile specimens (156-202 mm TL) was evidenced by the proliferation of testicular mesothelium containing primary spermatogonia (and the onset of spermatogenesis) within the ovigerous lamellae. Residual and atretic oocytes were present in more advanced stages of reversal. Residual previtellogenic oocytes observed in eight of 42 mature males (436-700 mm TL) further corroborate protogynous hermaphroditism in gray tilefish. Whether C. microps are strictly juvenile (non-functional) or functional hermaphrodites cannot yet be determined. Females maintain a slight numerical dominance from 300 to 500 mm; between 500 to 600 mm, the sex ratio is 1:1, while males predominate in size classes greater than 600 mm. Females generally mature between ages 4 and 5 (~435 mm TL). Males show pronounced testicular development after age 5 (TL>500 mm). Mature gray tilefish off South Carolina produce a greater relative gonad complement than those off North Carolina. The onset of gonadogenesis in March is correlated with photoperiod; spawning occurs from May through October off North Carolina and begins earlier off South Carolina. Females produce several batches of mature ova during this period; ripe (stage V) oocytes have been observed in April, May, June, July and September. Fecundity is best predicted by fish weight: ln Fecundity = 0.016 + 1.832 (ln fish weight). Fecundity estimates ranged from 207,008 eggs for a 412 mm (0.82 kg) gray tilefish to 4,107,035 eggs from a 736 mm (4.85 kg) individual.

Age and growth of C. microps off North and South Carolina was determined using otoliths. Annulus formation between January and April was correlated with gonadal development and photoperiod. Back-calculated lengths from otolith measurements correspond with empirical lengths. Von Bertalanffy growth models were derived from males, females, and sexes combined. Weight-length and standard length-total length relationships are provided. Males ($\bar{x}$ = 593.5 mm TL) are generally larger and live longer than females ($\bar{x}$ = 527.0 mm TL). Gray tilefish captured off South Carolina ($\bar{x}$ = 609.3 mm TL) were larger than those from North Carolina ($\bar{x}$ = 554.4 mm TL). Maximum longevity is at least 15 years. Gray tilefish are first susceptible to the hook and line fishery at age 4 (approximately 400 mm), mean age of recruitment is 4.53 years, and fish are fully recruited by age 5 (approximately 500-525 mm). Total annual mortality (A) is 0.27 based on a carch curve derived from recreational and exploratory fishing.

Gray tilefish are opporutnistic predators consuming fish and macroinvertebrates closely associated with the substrate. The principal components of their diets, in decreasing order of importance, are: crabs, shrimp, fish, echinoderms (holothurians, echinoids, stelleroids), polychaetes, ascideans, molluscs (gastropods and bivalves) stomatopods, and sipunculids. As tilefish grow, the consume larger prey. Their generalized feeding is similar to other branchiostegids. This strategy is advantageous for the utilization of the shelf-edge habitats' faunal assemblages, where the species diversity is generally high, but the number of individuals/species is generally low.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LIFE HISTORY ASPECTS OF THE GRAY TILEFISH, *CAULOLATILUS MICROPS* (Goode and Bean, 1878)

GENERAL INTRODUCTION

The gray tilefish, Caulolatilus microps (Goode and Bean, 1878) is a semi-tropical demersal species inhabiting the outer continental shelf, shelf break and upper slope from off Cape Charles, Virginia, south to Florida, and in the Gulf of Mexico, from Pensacola, Florida, to Campeche, Mexico (Dooley, 1974). Goode and Bean (1878) first described C. microps from a specimen captured on the Snapper Banks off Pensacola, in 35 fathoms. Goode and Bean (1884) established it as a valid species, providing distinguishing morphometric data from blackline tilefish, C. cyanops, and Atlantic golden-eyed tilefish, C. chrysops. Goode (1884) questioned its potential as a commercial species since only five specimens had been captured by hook and line. Bean (1885) documented the first capture of C. microps off the southeast coast and included a description of its fresh coloration. Jordan and Evermann (1898) included C. microps and C. cyanops from Atlantic collections; ocean whitefish, C. princeps, from southern California to the Galapagos; together with northern tilefish, Lopholatilus chameleonticeps, and sand tilefish, Malacanthus plumeri, in the family Malacanthidae. They suggested that the familial relationships were obscure. Further mention of C. microps through the 1960's was in the form of ichthyological notes: Firth (1937) extended its range to off Cape Henry, Virginia, and Burton (1940) reported its co-occurrence off Charleston, South Carolina with Warsaw grouper, Epinephelus nigritus;

speckled hind, E. drummond-hayi; red grouper, E. morio; vermilion snapper, Rhomboplites aurorubens; and whitebone porgy, Calamus leucosteus.

Dooley's (1974) review of Branchiostegidae and Malacanthidae systematics furnished the first comprehensive discussion of tilefishes including synonomys, diagnoses, meristics, morphometrics and coloration, as well as brief notes on stomach contents, gonad condition, depth distributions and geographical ranges.

There are currently six known species of Caulolatilus in the western Atlantic and at least two co-occur with C. microps (Dooley, 1978). C. microps is sympatric with C. chrysops, and is nearly twenty times more abundant in catches off North and South Carolina from 40 to 80 fathoms. The distribution of C. microps continues into the Gulf of Mexico, but C. chrysops is recorded from Cuba, Venezuela, and Brazil, at depths of 45 to 65 fathoms (Dooley, 1974). Four C. cyanops have been captured by recreational fishermen off North Carolina. Their infrequent occurrence may represent stray individuals from southern populations or occurrence of populations at greater depths than are commonly fished (Dooley, 1974). In the Gulf of Mexico, C. cyanops occur at 75 to 125 fathoms over coral sand and shell hash bottoms (Springer and Bullis, 1956). Malacanthus plumeri is a frequent inhabitant of shallower (15-25 fathoms) waters around live bottom areas in Onslow and Long Bay. L. chameleonticeps has also been captured with C. microps off South Carolina in depths of 80 to 130 fathoms. In New England waters it is abundant from 40 to 130 fathoms along the heads and walls of submarine canyons and over gentler sloping mud bottoms of the outer shelf (Freeman and Turner,

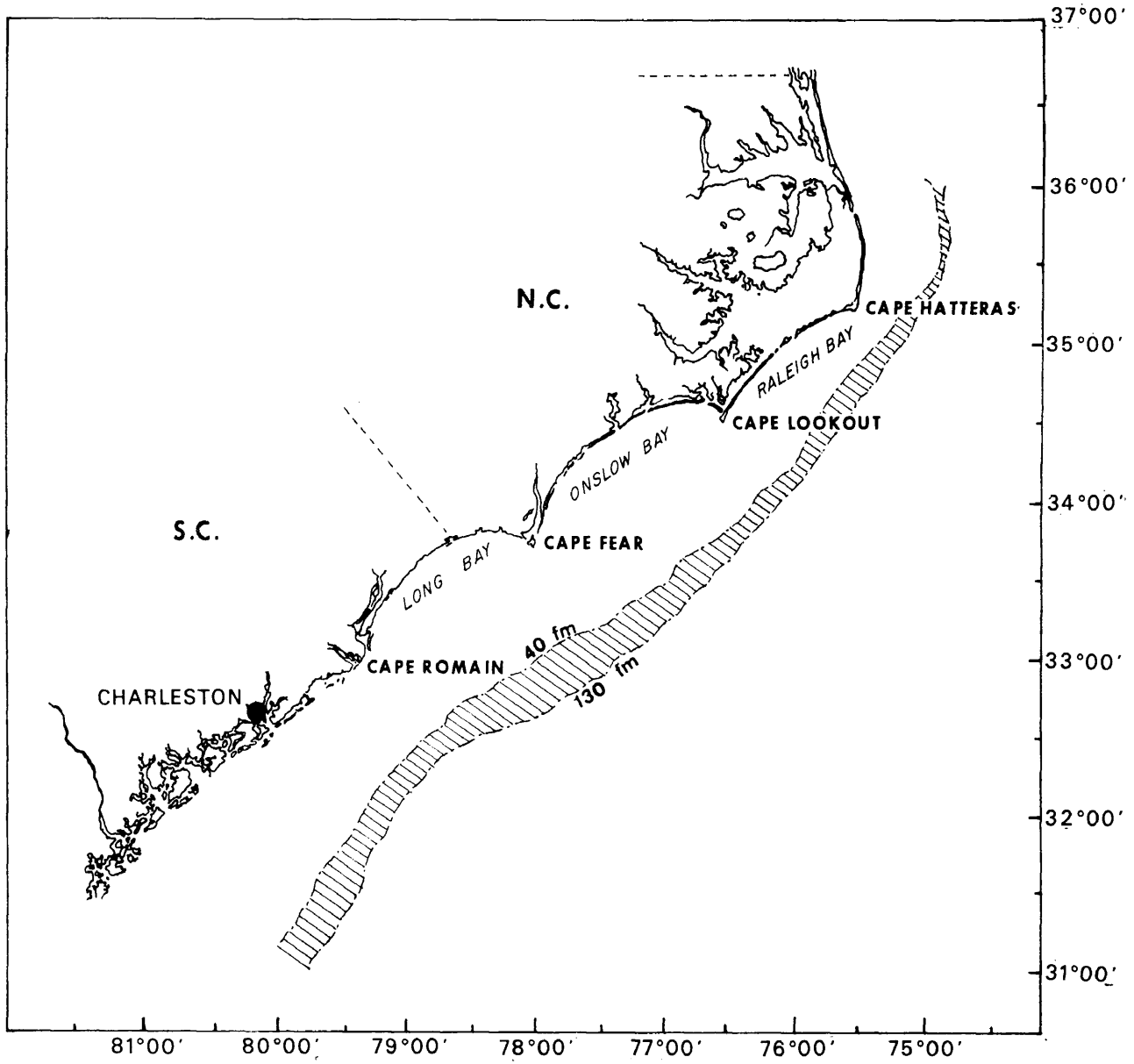
1977). In the Gulf of Mexico it occurs in depths of 128 to 188 fathoms over mud and shell bottoms (Bullis and Springer, 1956). As with L. chameleonticeps, the most important factor limiting distribution of C. microps is probably constant temperature; the bottom structures, substrate, and depths they inhabit are generally more diverse (Freeman and Turner, 1977).

Off the Carolinas, the gray tilefish is a component of a community of fishes and other marine organisms whose center of distribution is the coral reefs and banks of the Bahamas, Caribbean and Gulf of Mexico (Cereme-Vivas and Gray, 1966; Huntsman, 1976; Huntsman and Manooch, 1978). The existence of this faunal assemblage north to Cape Hatteras is attributable to the warming and moderating influence of the Florida Current. The adjacent continental shelf waters of Raleigh Bay and Onslow Bay experience annual temperature variations of 15 to 18°C annually. Winter cooling is often augmented by intrusions of the Virginian current. The outer continental shelf, shelf break and adjacent upper slope are subjected to less severe fluctuations, bottom temperatures usually stay between 15 and 23 C (Stefansson and Atkinson, 1967). Bottom temperature fluctuations over the shelf-edge habitat are related not only to seasonal variations but also to Gulf Stream meanders and cold water intrusions (Stefansson and Atkinson, 1967). The cold water intrusions impart a natural fragility to the existing community, as evidenced by massive fish mortalities (i.e. red snapper, Lutjanus campechanus, and vermilion snapper off North Carolina (Huntsman, 1976); L. chameleonticeps off New England (Collins, 1884).

Gray tilefish are captured in depths of 40 to 80 fathoms off North and South Carolina but they occur to at least 129 fathoms (Figure 1). From Cape Hatteras to Cape Fear, the shelf-edge zone is characterized by a series of ridges, troughs and terraces paralleling the axis of the shelf break. South of Cape Lookout, N.C., the more precipitous areas of the shelf break become increasingly interspersed by regions of gentler, more undulating profile (MacIntyre and Millman, 1970). The substrate is generally composed of sand, shell hash and coral rubble between eroded and encrusted rocky outcroppings. Gray tilefish are associated with the precipitous regions of the shelf break and are often concentrated along the steep slopes. They also occur over less rugged terrain seaward of the shelf break, occasionally concentrated where no distinct dropoffs are detectable. Springer and Bullis (1956) report their capture in the northern Gulf of Mexico in 37 to 78 fathoms over mud and sand bottoms.

The perennially warm waters overlying a rugged topography have provided a substrate which is encrusted and inhabited by a diverse tropical invertebrate fauna (Cereme Vivas and Gray, 1966; Cain, 1972). This, in turn, has created an environment similar in physical structure and biological diversity to that associated with coral reefs. Strusaker (1969), Manooch (1975), Grimes (1976) and Huntsman (1976) provide comprehensive lists of fishes known from the shelf-edge habitat. Those most fequently caught with the gray tilefish off North and South Carolina include: red porgy (Pagrus pagrus), vermilion snapper, snowy grouper (Epinephelus niveatus), Warsaw grouper, speckled hind, yellowedge grouper (E. flavolimbatus), amberjack (Seriola dumerili), almaco jack (S. rivoliana), silky snapper (L. vivanus) and

Figure 1. Distribution of Caulolatilus microps off North and South Carolina.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N.C.
S.C.
CAPE HATTERAS
RALEIGH BAY
CAPE LOOKOUT
ONSLOW BAY
CAPE FEAR
LONG BAY
CAPE ROMAIN
CHARLESTON
40 fm
130 fm

the golden-eyed tilefish.

The shelf-edge community which includes C. microps is exploited primarily by a recreational headboat fishery off North and South Carolina (Huntsman, 1976). Although they are not a dominant component of the headboat catch, increased effort over the offshore fishing grounds could yield a greater proportion of gray tilefish. Gray tilefish comprised only 1.4% by number and 2.7% by weight of the total estimated catch from the offshore fishing grounds (>25 fathoms). Approximately 4,718 gray tilefish weighting a total of 12,429 kg were captured in 1975-1976 by recreational fishing boats from North and South Carolina. Considering only research fishing trips concentrating in waters 45 fathoms and deeper, gray tilefish ranked second to red porgies in abundance, and third to red porgies and snowy groupers in total weight (Manooch, 1975).

This study was undertaken to provide a bioprofile of the gray tilefish for use in the management of continental shelf fisheries. My results are presented in the topical segments: reproductive biology, age, growth, and mortality, and food habits.

SECTION I: REPRODUCTIVE BIOLOGY

INTRODUCTION

The reproductive biology of the gray tilefish, Caulolatilus microps, (and other species of Caulolatilus) is essentially undescribed in the literature. From collections off North Carolina Dooley (1974) reported the capture of ripe female gray tilefish in January and May through September and ripe Atlantic golden-eyed tilefish, C. crysops, in September (collected only in May, July and September). The seasonal occurrence of gravid females is reported for Pacific golden-eyed tilefish, C. affinis (Dooley, 1974) and ocean whitefish, C. princeps (Fitch and Lavenberg, 1971; Dooley, 1974) from the eastern Pacific.

Freeman and Turner (1977) reviewed aspects of the reproductive biology of northern tilefish, Lopholatilus chameleonticeps, including ova analysis, sex ratio, fecundity and seasonality. Hayashi (1977) discussed the protracted spawning season and age of maturity for red tilefish, Branchiostegus japonicus japonicus from the China Sea. Dooley and Paxton (1975) related the broad size distribution of ova in maturing B. wardi and B. serratus to multiple spawnings and found anomolous sex ratios within size classes for both species.

Pelagic eggs and larvae are probably characteristic of the family Branchiostegidae. They have been collected in the North Atlantic for Caulolatilus sp. (J. Olney, pers. comm.) and L. chameleonticeps (Freeman and Turner, 1977), and in the Pacific for C. princeps (Fitch and Lavenberg, 1971).

Herein, gray tilefish reproduction off North and South Carolina is described through analysis of gonadal development, sex ratios, seasonality and duration of spawning season, age and size of sexual maturity, and fecundity. Notes on golden-eyed tilefish are included for comparative purposes.

METHODS AND MATERIALS

Collection of Specimens

The primary source of biological specimens was fishing trips of one day duration aboard the R/V Onslow Bay, NMFS, from 1972 to 1977. Most specimens were captured in the northern and central portions of Onslow Bay. Bimonthly collection trips were scheduled, but weather often precluded sampling.

Tilefishing was accomplished from a drifting boat. Preferred drifts were up or down sharp dropoffs above the more precipitous bottoms or along productive depth contours over flatter terrain. Fishing tackle included Penn Senator 9/0 electric reels filled with 80 pound test line mounted on fiberglass rods. Terminal gear included two 4/0 to 9/0 hooks attached by triple swivels and 50 ounce lead weights. Preferred baits included frozen squid, fresh caught red porgy, almaco and amberjack fillets. Fishing for tilefish was most successful when baits were maintained as close to the bottom as possible. Due to the prevailing strong currents, rugged bottom and limitations of the vessel, trawling, traps and longlines were precluded as alternate sampling gear.

Catches were processed upon return to the laboratory. Total length and weight were recorded for each fish, otoliths removed and stored in glycerine, and stomachs and gonads excised and preserved in 10% formalin.

Specimens were also obtained from a headboat sampling program which encompassed Hatteras, Morehead City, Atlantic Beach, Carolina Beach and Wrightsville Beach in North Carolina, and Little River, Murrell's Inlet and Charleston in South Carolina (Huntsman, 1976). Port sampling provided length and weight data representative of the daily catch as well as some onboard collections of gonads, stomachs and otoliths.

Gonad Index

Gonads were removed from formalin, blotted dry and weighed to the nearest 0.1 g on an analytical beam balance (Mettler P1000).

Gonad index was calculated as the percent contribution of preserved gonads to total body weight. This index removes the effect of fish size relative to gonad development (Gonor, 1972). Index values of mature tilefish compiled by month define the time and duration of the spawning season (Merriner, 1976; Manooch, 1975; Grimes, 1976). Index values were plotted by 25 mm TL classes for North and South Carolina fish to evaluate the effects of environmental differences in the regulation of reproductive potential (Gonor, 1972).

Ova Diameter Analysis

Sections were removed from the anterior, central, and posterior portions of three developing ovaries to assess uniformity of ova development. These sections were placed in separate bowls, washed and ova were teased free of the ovigerous lamellae. A subsample was removed from each section with a wide mouthed pipette and placed in a gridded petri dish. Ova diameters were measured under a dissecting microscope using incident light over a dark background at a magnification

of 70X. One hundred ova from each subsample were measured. Analysis of variance showed no significant differences ($P<0.01$) between subsamples ($F = 0.987, 0.924, 0.995$), thus any section of the ovary could be removed for the subsequent ova diameter analysis (Grimes, 1976).

Frequency distributions of ova diameters documented the seasonality and the duration of spawning (Clarke, 1934; deSylva, 1973; Grimes, 1976). Two representative females were selected for each available month and designated ovarian development stage. Five distinct stages were evident based on size, nucleus, optical density and yolk deposition of the ova. Excluding the undifferentiated oocytes (Stage I), 50 ova diameters for each stage were measured for each sample. Ova stage frequencies were determined by reducing the magnification to 20X and two or more entire grids were counted (generally over 500 ova). The ratios obtained were proportionally reduced to a base of 200; the relative frequency of each stage was then multiplied by the number of ova/two ocular unit divisions within that stage.

Fecundity

Well developed ovaries from fish captured in April through September were selected for fecundity estimations. Both ovaries were blotted dry and weighed on an analytical beam balance to the nearest 0.1 gram. One ovary from each pair was then placed in a glass wash bowl with water and the egg mass was freed from the ovarian tunic and connective tissue. Two subsamples of greater than 1,000 ova were removed by pipette and stored. The remaining ova were washed onto filter paper, oven dried at 40 C for approximately two days and weighed

on an analytical beam balance to the nearest 0.001 gram. The subsamples were placed in gridded dishes and the remaining clumps of ova and ovigerous lamellae were separated. All vitellogenic ova were counted under a binocular microscope at a magnification of 20X. The subsample was then washed onto filter paper, oven dried and weighed to the nearest 0.001 gram. With total ovarian dry weight = original ova sample dry weight + subsamples dry weight:

$$\text{Fecundity} = \frac{\text{No. ova from combined subsamples}}{\text{dry weight of subsamples}} \times \frac{\text{total ovarian dry weight}}{\text{wet weight of single ovary}} \times \text{Total combined ovarian wet weight}$$

Functional regressions were calculated for relationships with length and weight since all factors are subject to natural variability and sampling error (Ricker, 1975).

Histological Preparations

Gonads used for histological preparations had been preserved in 10% formalin, 40% ethanol or Davidson's fixative. Those in formalin or ethanol were placed in 90% ethanol prior to dehydration in Technicon reagents (S-29 dehydrant VC-670 solvent). The gonads were embedded in Paraplast tissue embedding medium, sectioned at 5-7 μ, stained using Mayer's Haematoxylin and counterstained with Eosin Y. Photomicrographs were obtained using a Zeiss Photomicroscope II, bright field and Kodak Panatomic X film.

RESULTS AND DISCUSSION

Ovarian Development

The paired cystovarian ovaries of gray tilefish are suspended below the swim bladder by mesovarium in the most posterior portion of the body cavity. The mesovarium extends the entire length of the ovary and contains the ovarian arteries. Oogenesis and vitellogenesis occur within the ovigerous lamellae which are distributed evenly and project laterally and medially from the tunica albuginea. The absence of lamellae from a narrow band in the ventral portion of the ovary forms an ovocoel. This facilitates the ovarian expansion and collection of ripe ova released from the lamellae prior to extrusion through the common oviduct (Moe, 1969). The following macroscopic designation of ovarian stages of development is based on a modified scheme from deSilva (1973) and Manooch (1975).

Immature ovaries (stage 1) (Fish over 200 mm TL) are maroon, sausage-shaped organs. The ovigerous lamellae consist of dense aggregations of undifferentiated oogonia (Figure 2A). Ensuing early development imparts a teardrop, saclike shape.

Ovaries undergo initial seasonal development in February and vitellogenesis continues through October. Early developing ovaries (stage 3) are inflamed, light-reddish, triangular sacs with a granular interior mass discernable through the tunic. Subsequent development imparts a rotundity to the basic triangular shape and the

ovary appears yellowish-orange; the tunic becomes increasingly transparent and developing ova are clearly visible.

Nearly ripe (stage 3+) and ripe ovaries (stage 4) containing mature (stage V) ova in the ovocoel were observed from May through October. Ripe ovaries observed from May to July were usually greatly distended, bulbous sacs occupying greater than a third of the peritoneal cavity, and comprised 2 to 4% of the body weight. The ova were clearly visible through a delicate, nearly transparent tunica albuginea. The entire organ appeared whitish-orange, with densely packed light yellow eggs. In September and early October, well developed and ripe ovaries were smaller and more triangular in shape and represented only 1 to 2.4% of the body weight.

Recently spent and redeveloping (stages 5-3) females were captured in June, July and August. These ovaries resembled deflated early developing ovaries (stage 3) and were distinguished by their inflamed ventral-posterior portions and the presence of residual and atretic mature ova.

Recently spent females (stage 5) showing no signs of continuing vitellogenesis were captured from July through October. The ovaries were flaccid, reduced in size and the muscular tunic was contracted. They were typically inflamed due to increased internal vascularization and atresia of residual vitellogenic oocytes.

Ova Development

Ova development proceeds through five distinguishable morphological stages from primary oogonia and is similar to that of red grouper, Epinephelus morio (Moe, 1969). The gross morphological

characteristics of oocytes (after preservation in formalin) and intracellular structure based on histological examination are as follows:

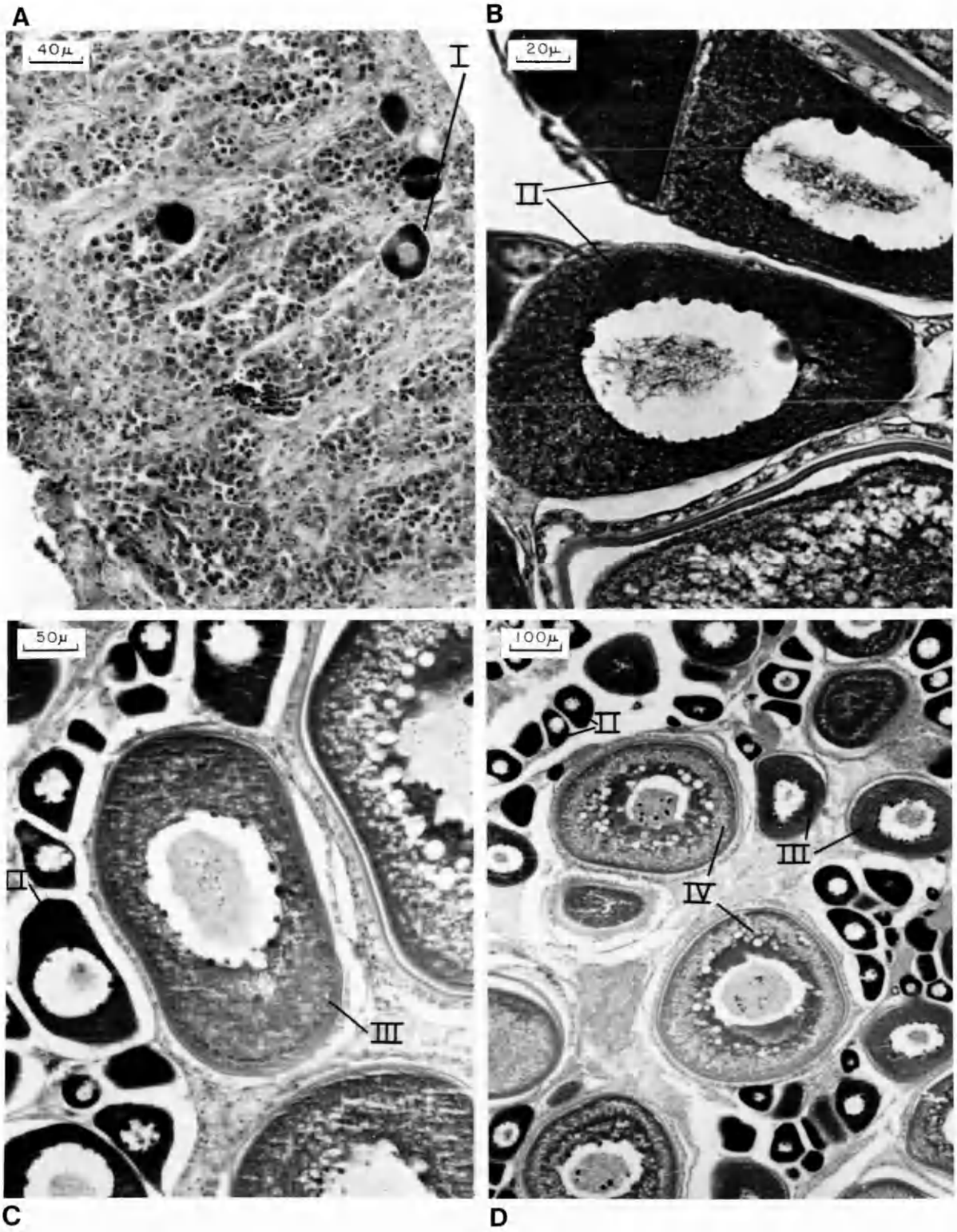
Oogonia: (2-8 microns: avg. 4-6μ) were only discernable at higher magnifications facilitated by histological preparation. They are densely packed within the acidophilic fibroblast cells of the ovigerous lamellae. Under low magnification (100X) they appear as granular, deeply basophilic cells (Figure 2A). At higher magnifications, a faintly acidophilic cytoplasm and a distinct (thin) dark, irregular cell membrane are apparent. The nuclear membrane is masked by unevenly distributed, basophilic nuclear material (probably meiotic structures) located peripherally on opposing sides and comprising a variable portion of the nucleus.

Stage I: Early oocytes (20-50 μ) are most apparent in resting and early developing ovaries as transparent irregular cells with a barely discernable nucleus. Histologically, they are characterized by their deeply stained basophilic cytoplasm, a nucleus approximately 50% the oocytes diameter, a single nucleolus and unorganized chromatin strands (Figure 2A).

Stage II: Resting or previtellogenic oocytes (40 to 170 μ) are present in all maturing ovaries; they are transparent, irregularly shaped cells with rounded and/or sharply angular sides (due to densely packed nature of ovigerous lamellae). The nucleus is a sharply defined, nearly perfect circle, transparent, but more granular than the cytoplasm. Histologically, the distinct nuclear membrane encompasses multiple darkly stained (basophilic) nucleoli around its periphery and the centrally located acidophilic chromatin (Figure 2B). Basophilic lampbrush chromosomes are first observed during this stage. The cytoplasm remains deeply basophilic.

Stage III: Early vitellogenic oocytes (110 to 260 μ) become increasing rotund. Both cytoplasm and nucleus appear translucent, silvery white. The nucleus is more granular and clearly discernable; the nuclear membrane is a broad whitish band. Histologically, the nuclear margin is less distinct and contains multiple small nucleoli scattered peripherally (Figure 2C). The chromatin mass and density has increased, encompassing nearly the entire nucleus; the basophilic lampbrush chromosomes are more apparent. Tiny clear oil vesicles of primary yolk begin developing in a decreasingly basophilic cytoplasm. A vitelline membrane (thin acidophilic band) and follicular layer (theca granulosa;

Figure 2. Histological sections of ovarian tissue from Caulolatilus microps. A. Immature ovary with oogonia and stage I oocytes. B. Stage II, previtellogenic oocytes. C. Stage III, early developing oocytes. D. Stage IV, active vitellogenic oocytes.


A
40μ
I
B
20μ
II
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50μ
I
III
D
100μ
II
III
IV

basophilic) are closely adherent to the cell membrane, channeling in a raw materials for yolk production (Brackevelt and McMillan, 1967).

Stage IV: Active vitellogenic oocytes (215 to 640 μ) present in developing ovaries are opaque, evenly yellow spheres. Their surface appears granular but smooth; the nucleus (enclosed within) not apparent. Histologically, the nucleus, chromatin mass and nucleoli become less prominent as yolk vesicles surround and coalesce towards it (Figure 2D). The yolk vesicles increase in size with development. Their production of acidophilic yolk globules gradually replaces and dominates the basophilic cytoplasm. The vitelline membrane is prominent as a bright acidophilic band, increasing in width through the duration of this stage, with ensuing appearance of radial bands. The follicular layer (theca granulosa) is also prominent as a granular basophilic band encompassing the oocyte.

Stage V: Mature ova (785-910 μ, avg. 843 μ) present in ripe and spent ovaries, contain a single oil globule peripherally located and 140-196 μ in diameter. These eggs are spherical, translucent and evenly white due to the coalescing yolk. The vitelline membrane is distinct and appears separated from the yolk by a clear margin. The mature eggs were not observed in histological preparation.

Description of Testes

The paired testes of gray tilefish are solid structures and are much smaller, thinner, more elongate, and smoother in texture than ovaries from equal sized fish. The testes are suspended from the swim bladder by the mesorchium, which maintains a wide base of attachment along the medial surface. The gonadal artery branches and passes along nearly the entire length of the testes within the mesorchium. The lateral surface is partially bisected by a horizontal groove which bisects the testes into lobules; this groove becomes indistinguishable in larger, well developed testes. Each testis enters the urinary papilla by a separate sperm duct.

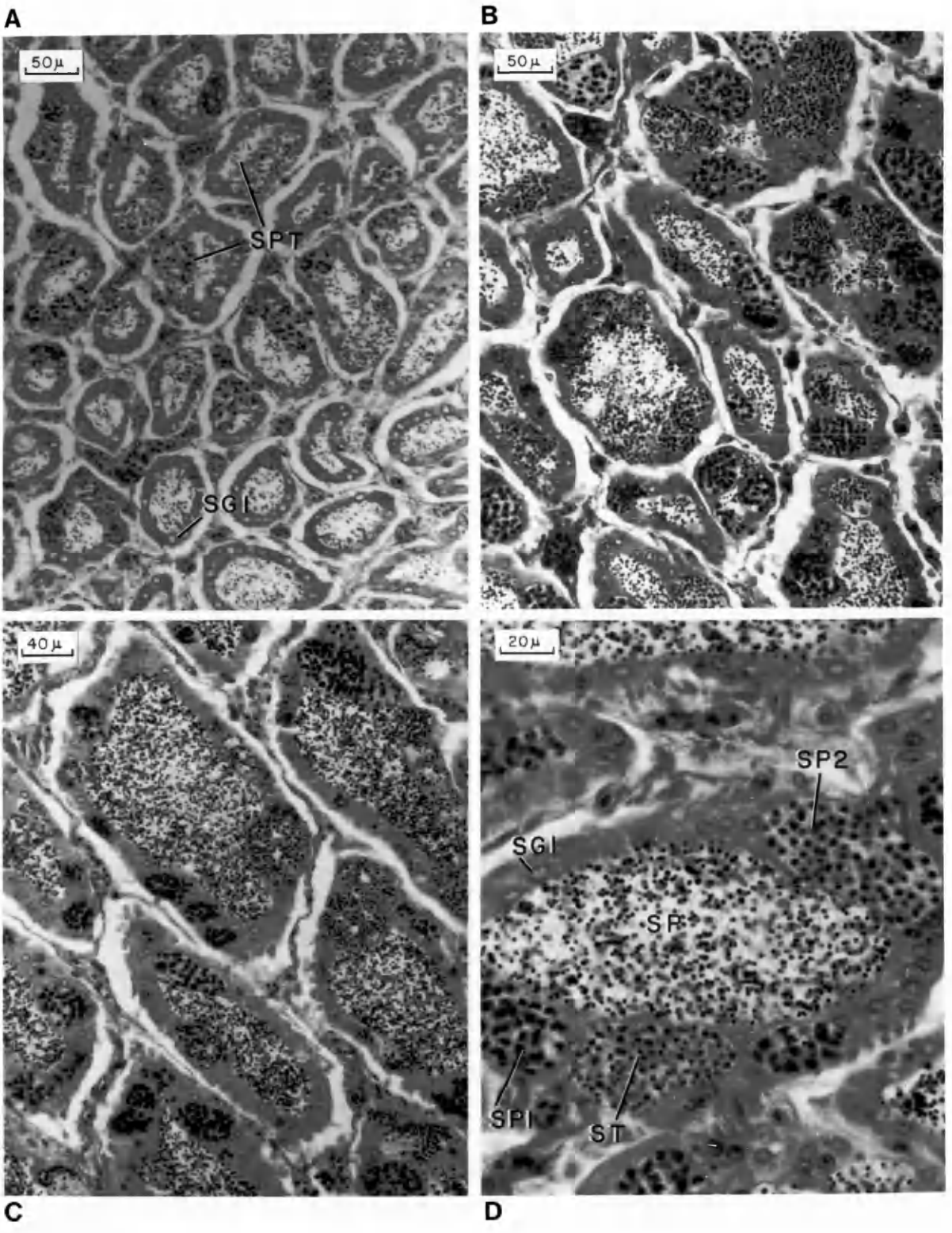
Testes from males 350 to 500 mm TL were often classified immature or resting on the basis of their small size (0.3-0.8% body weight) and dark red color. These organs are solid, compressed and elongate. Testes taper from a maximum depth above the sperm duct to a filamentous projection nearly the length of the swim bladder. Histological analysis revealed collections of spermatozoa in greater than 90% of the fish examined within this size range.

Testes in the larger males (>550 mm TL) become more robust, triangular to nearly cornucopia shaped and a creamy, off-white color. The largest testes observed weighed 12.7 grams and none had free-running sperm.

Internal Testicular Structure

The primary spermatogenic units within the testes of gray tilefish are seminiferous tubules and cysts. A cross section of an undeveloped seminiferous tubule reveals a ring of primary spermatogonia one cell thick within a connective tissue matrix (Figure 3A). These tubules expand and diverge from the basic spherical structure with ensuing development of cysts and collection of spermatozoa in the lumen (Figure 3B, C, D). An elastic connective tissue (Sertoli cells) encapsulates and maintains the integrity of the individual developing cysts and presumably serves as site of steroidogenesis (Lofts, 1968; Hoar, 1969). Interstitial tissue composed of fibroblast cells and vascularized Leydig cells encompasses and separates individual spermatogenic tubules. Along with their function as nutritive sources Leydig cells are sites of steroidogenic activity (Lofts, 1968; Hoar, 1969; Chan et al., 1975).

Figure 3. Histological sections of testicular tissue from Caulolatilus microps. A. Undeveloped seminiferous tubules. B. Developing seminiferous tubules. C. Developing seminiferous tubules. D. Developing seminiferous tubule. Abbreviations: SG1, primary spermatogonium; SG2, secondary spermatogonia; SP1, primary spermatocytes; SP2, secondary spermatocytes; ST, spermatids; SP, spermatozoa; SPT, spermatogenic tubules.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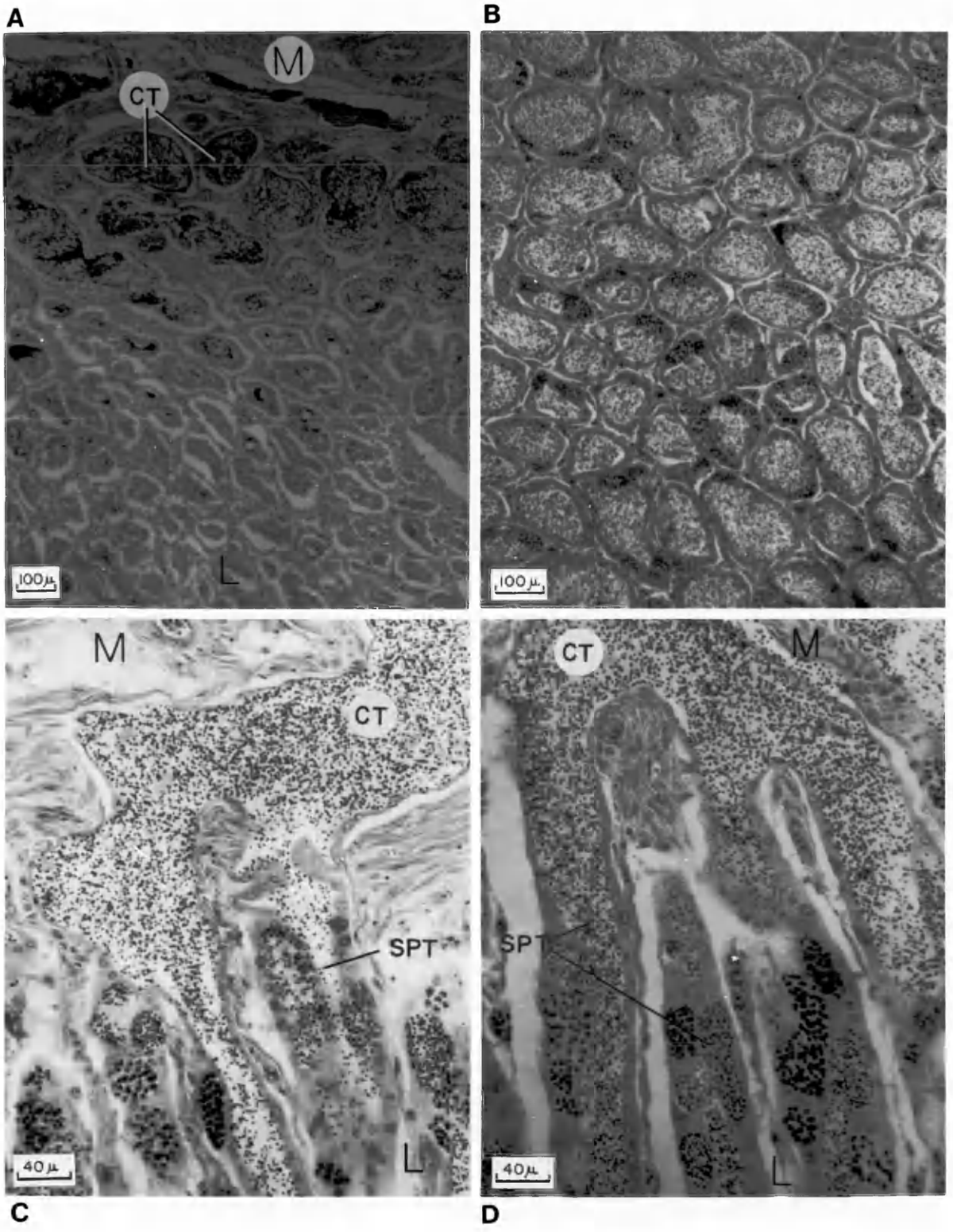
50μ
SPT
SGI
B
50μ
C
40μ
D
20μ
SP2
SGI
SP
SPI
ST

Development within individual spermatogenic tubules and the testes as a whole proceeds as a continual succession of maturing cysts (analogous to ovarian development). Within a single tubule cysts of all stages of development can co-occur (interconnected) with primary spermatogonia (Figure 3B, C, D). The one cell-one cyst thick structure is maintained during tubule development while the lumen is gradually filled by spermatozoa evacuating ripened cysts.

The seminiferous tubules seem to be dynamic structures which migrate from the distal epithelium of the tunica albuginea medially in the course of their development. This migration is the principal means of testicular drainage. Several observations support this hypothesis. First, the generation of spermatogonia probably occurs in the distal epithelium (Lofts, 1968) where the least developed tubules and those comprised solely of primary spermatogonia occur in well developed testes (Figure 4A). Second, the longevity of a spermatogenic tubule extends through several seasons. In March, tubules containing spermatozoa in the lumen are dormant or undergoing initial phases of spermatogenesis (Figure 3A & 4A). Third, the medial spermatogenic tubules adjacent to the secondary collecting tubules are the most developed in the testes (contain the largest quantities of spermatozoa) (Figure 4A). These merge with other medial spermatogenic tubules to channel spermatozoa into the secondary collecting tubules (Figure 4C & D). Primary and secondary collecting tubules are composed primarily of fibroblast cells which contain no spermatogenic cysts. Fourth, there is no distinct network of collecting tubules for peripherally generated spermatozoa (Figure 3A-C, 4A, B) as in typical acanthopterygian tubular testes (Hann, 1927; Hyder, 1969).

Figure 4. Histological sections of testicular tissue from Caulolatilus microps. A. Overview of a resting testes with spermatozoa in collecting tubules. B. Overview of a developing testes, with no apparent system for channeling spermatozoa. C. Spermatogenic tubules merging with collecting tubules. D. Spermatogenic tubules merging with collecting tubules. Abbreviations: M, medial portion of testes; L, lateral portion of testes; CT, collecting tubules; SPT, spermatogenic tubules.


A
M
CT
L
100μ
B
100μ
M
CT
SPT
L
40μ
C
CT
M
SPT
L
40μ
D

Interconnected spermatogenic tubules radiating peripherally appear to serve this function on a limited basis. Spermatozoa collected in the secondary tubules are directed into the primary tubules. A network of primary tubules adjacent to the medial epithelium extends the length of the testes and channels the spermatozoa posteriorly and ventrally, merging in route to the sperm duct.

Testicular Development

The ontogeny of the testes seems to proceed through a juvenile ovarian stage. The possibility of sex reversal at a later stage or of a primary (gonochorist) male stage cannot be precluded. Four specimens under 205 mm TL included one immature female and three fish with gonads at various stages of transformation from ovary to testes.

In the fish exhibiting the earliest observed stage of sex reversal (202 mm TL; Figure 5A, B) most of the gonad was ovarian (oogonia and Stage I oocytes prevalent). A proliferation of germinal testicular mesothelium proceeded through the ovigerous lamellae adjacent to the medial connective tissue. The proliferating mesothelium would be the site of steroidogenesis which would induce atresia, thus recycling the ovarian elements (Hoar and Randall, 1971). The formation of spermatogenic tubules and the onset of spermatogenesis would follow the appearance of spermatogonia. These tubules might be precursors of the primary collecting tubules considering their orientation and location adjacent to the medial connective tissue. Gonads of two specimens in advanced stages of sex reversal (Figure 5C, D; 6A, B, C) (TL = 175 and 184 mm) had differentiated into primary testicular constituents and were comparable in structure to "normal"

Figure 5. Histological sections of gonadal tissue from Caulolatilus microps. A. Gonad undergoing initial stages of sexual transtion; the lateral portion is ovarian, and the medial portion proliferating testicular mesothelium (202 mm TL). B. Closer view of gonad undergoing transition with influx of primary spermatogonium (202 mm TL). C. Overview of gonad undergoing advanced stages of sexual transition with residual oocytes (178 mm TL). D. Closeup of gonad undergoing later stages of transition, with residual oocytes within proliferating testicular mesothelium. Abbreviations: RO, residual oocyte; SPT, spermatogenic tubule; M, medial; L, lateral.

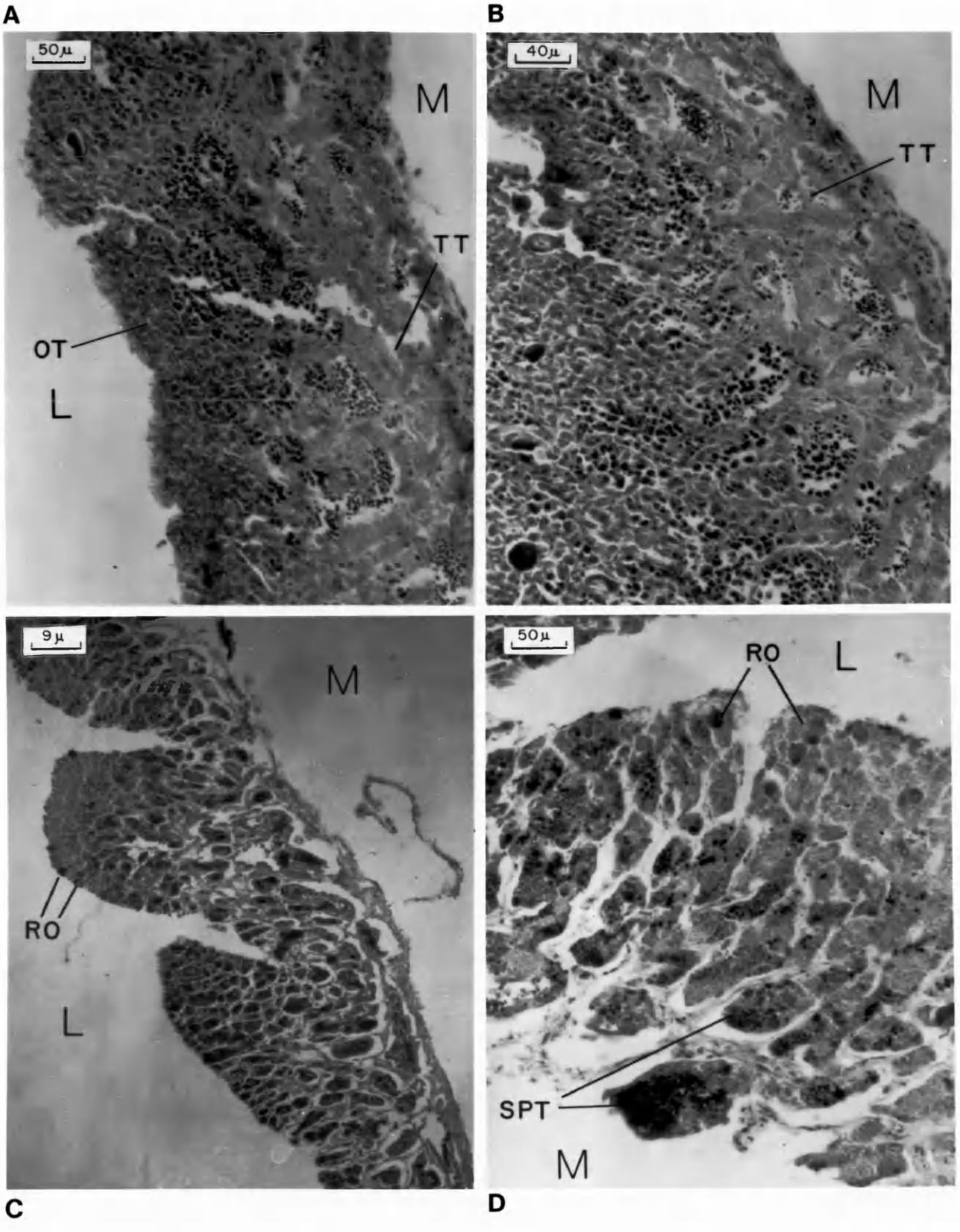
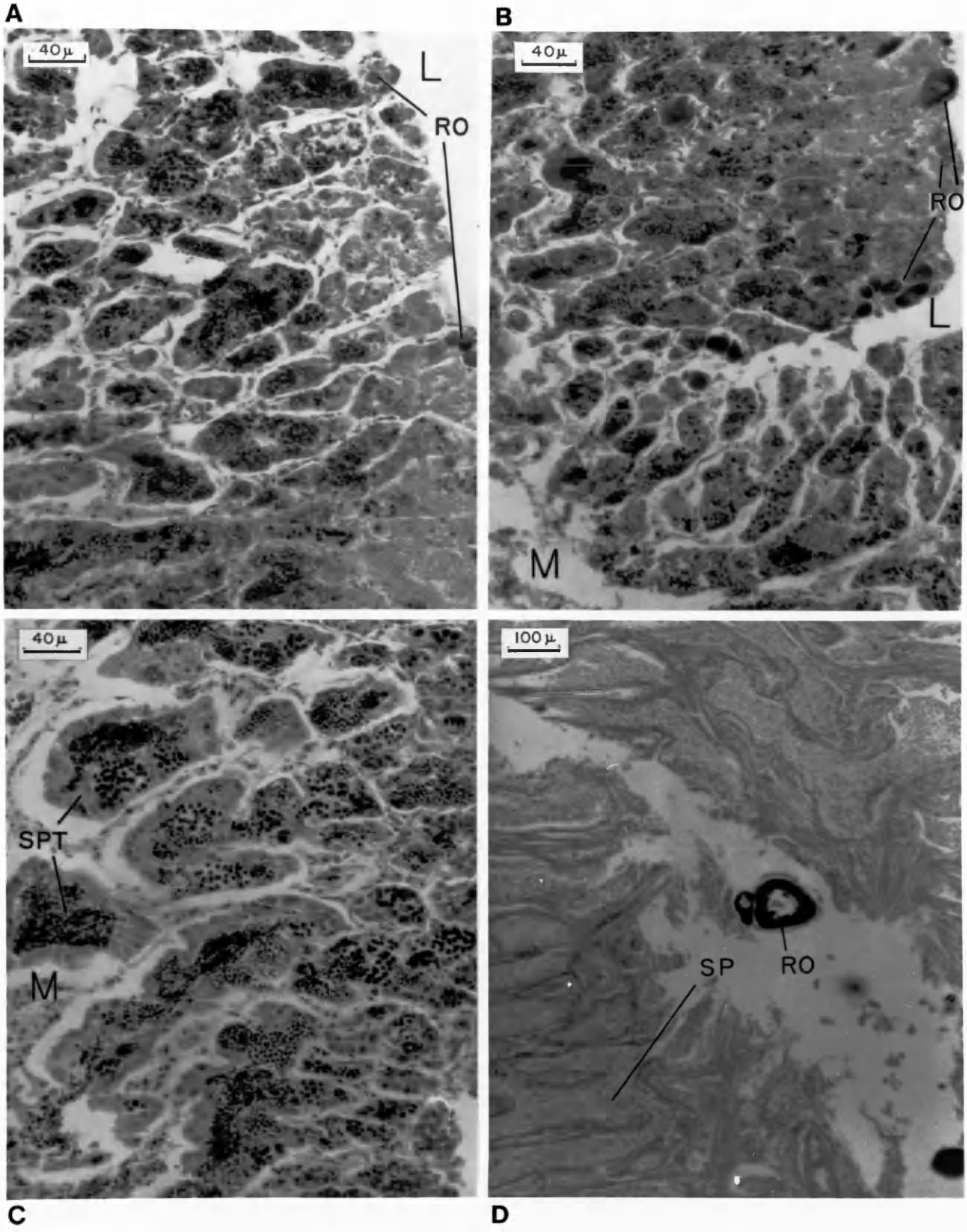

A
50μ
M
TT
OT
L
B
40μ
M
TT
C
9μ
M
RO
L
D
50μ
RO
L
SPT
M

Figure 6. Histological sections of gonadal tissue from Caulolatilus microps. A. Advanced stage of gonadal transition, with residual oocytes along lateral epithelium and active spermatogenic tubules (184 mm TL). B. Advanced stage of sexual transition (184 mm TL). C. Advanced stage of sexual transition with active spermatogenic tubules along medial portion of gonad (184 mm TL). D. Mature testes with residual oocytes and sperm in collecting tubules (507 mm TL). Abbreviations: RO, residual oocyte; SP, spermatozoa; SPT, spermatogenic tubules; M, medial; L, lateral.


A
40μ
L
RO
B
40μ
RO
L
M
C
40μ
SPT
M
D
100μ
SP
RO

maturing testes. Cysts of various spermatogenetic stages comprised the tubules which contained spermatozoa in the lumen. Both specimens contained evidence of an earlier ovarian state adjacent to the distal (peripheral) epithelium in the form of atretic structures, residual ovigerous lamellae or proliferating germinal testicular mesothelium.

Gray tilefish follow a pattern of gonadal transition similar to that described as juvenile hermaphroditism for the zebrafish, Brachydanio rerio (Takahashi, 1977). Degradation of oocytes was concurrent with proliferation of interstitial tissue and primary spermatogonia. These steps preceed the formation and development of the testicular lobules.

Spermatogenesis

Spermatogenesis proceeds through six distinct stages (Figure 3D) analogous to those described by Hyder (1969) for Tilapia and Moe (1969) for E. morio.

Primary spermatogonia are the precursors of spermatogenic cysts. They are the largest cells within the seminiferous tubule (7-12 μ), and are distinguished by their thin dark nuclear membrane encompassing an unstained nucleus (4-5 μ). One or two nucleoli, often located peripherally and opposing, and mitotic structures are observed within the nucleus. The cytoplasm is slightly acidophilic, its boundary usually undeterminable.

Secondary spermatogonia result from a succession of mitotic divisions from the primary spermatogonia. These are the smallest cysts and contain the fewest constituents within the developing tubule. The nucleus of secondary spermatogonia are similar though smaller (3.5-4.5 μ) than their predecessor, and are usually observed with basophilic mitotic apparatus.

Primary spermatocytes (4-5 μ) arise from the final synchronous mitotic divisions within the cysts. They are distinguished by their denser, unevenly distributed, basophilic nucleus (3 μ) and are usually observed undergoing early phases of meiotic division (prophase and metaphase).

Secondary spermatocytes, the result of the first meiotic division, are more often seen not dividing. They are distinguished by their compact, basophilic nucleus (1.5-2 μ). Secondary spermatocytes often appear as an interconnected maze of cells (3.4-4 μ) with slightly acidophilic cytoplasm.

Spermatids are the most numerous and smallest cells occurring within cysts. Their nucleus is a densely packed basophilic mass, 1-1.5 μ in diameter.

Spermatozoa are the result of a metamorphosis from spermatids, which occurs concurrent with their passage through the cysts connective tissue into the tubules central lumen. The appearance of their flagella, the slightly smaller size (1-1.3 μ), and their presence within the lumen distinguish spermatozoa from spermatids.

Sex Ratio

Sex determinations were made by gonad examination since gray tilefish exhibit no sexually dimorphic characteristics. Males outnumbered females in the combined North and South Carolina collections (195 to 176) but this is not significantly different from a 1:1 ratio ($\chi^2 = 0.97$).

Size frequency distributions by sex (Table 1, Figure 7) revealed several anomolous conditions. Only 5 (museum) specimens between 0 and 300 mm were obtained. Three were females undergoing transition to males (TL = 165, 178, 202 mm) and two were immature females. Abundance of females in some intervals from 300 to 500 mm TL was significantly greater than 1:1. Between 500 and 600 mm TL males and females were equally abundant. Male predominance increased significantly for intervals over 600 mm. The observed sex ratio suggests protogynous hermaphroditism beyond the juvenile stage.

Male gray tilefish containing ova ranged from 430 to 700 mm TL and were captured between March and May. One to five residual ova were found in 8 of 41 testicular samples examined histologically.

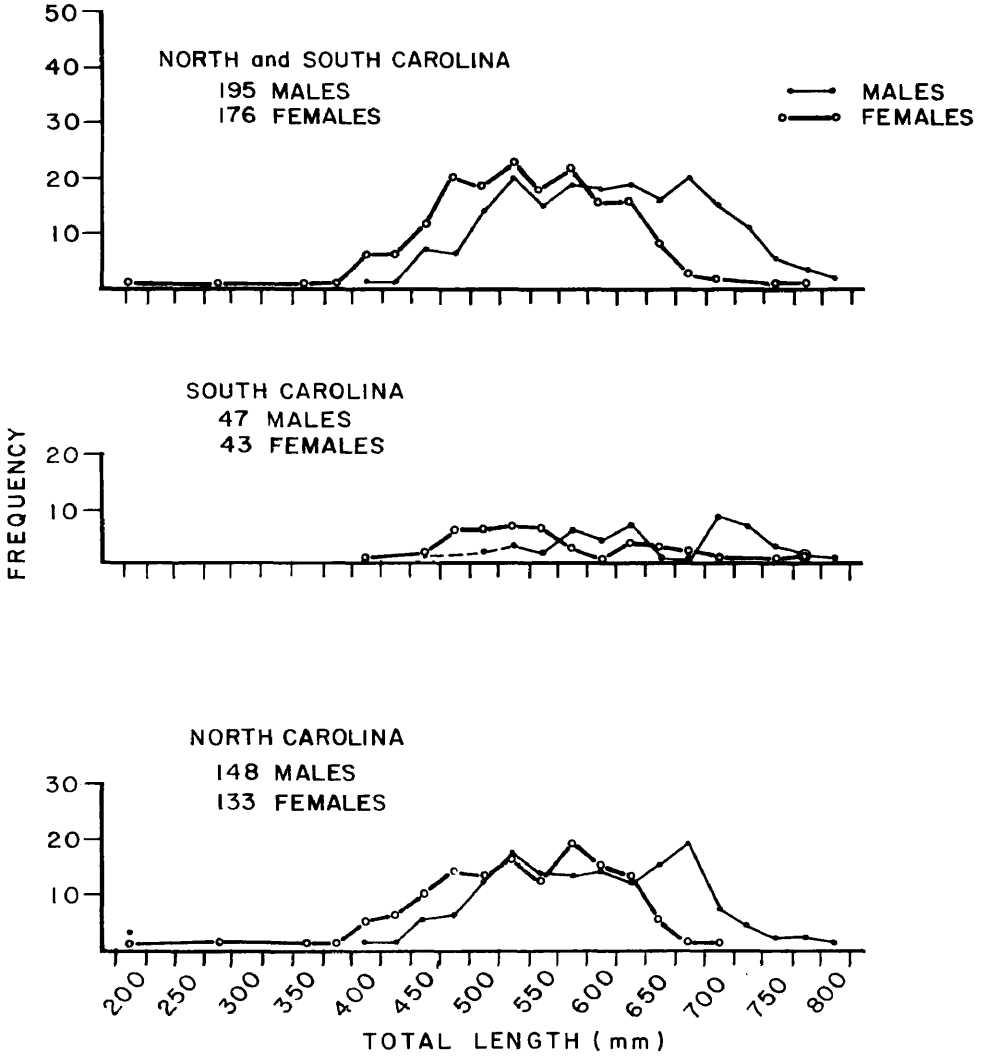
TABLE 1

FREQUENCY OF MALE AND FEMALE CAULOLATILUS MICROPS FROM NORTH AND SOUTH CAROLINA WITHIN 25 MM AND 100 MM TOTAL LENGTH INTERVALS, WITH CHI SQUARE VALUES ASSUMING A 1:1 SEX RATIO

Length	Male	Female	Percent Female/25 mm	χ^2	Percent Female/100 mm	χ^2
101-200	3	1			25	1.0
201-300		1			100	
301-325						
326-350		1	100		88	5.4*
351-375		1	100			
376-400	1	6	86	3.57		
401-425	1	6	86	3.57		
426-450	7	12	63	1.32	67	9.89**
451-475	6	20	77	7.54*		
476-500	14	19	58	0.75		
501-525	20	23	53	0.21		
526-550	15	18	55	0.27	52	0.32
551-575	19	22	54	0.22		
576-600	18	16	47	0.12		
601-625	19	16	46	0.26		
626-650	16	8	33	2.67	30	16.9**
651-675	20	3	13	12.57**		
676-700	15	2	12	9.94**		
701-725	11	0	0			
726-750	5	1	17		9	15.6**
751-775	3	1	25			
776-800	2	0	0			

*$p \leq 0.05$
**$p \leq 0.01$

Figure 7. Length frequency distribution of Caulolatilus microps males and females from North and South Carolina.


NORTH and SOUTH CAROLINA
195 MALES
176 FEMALES
MALES
FEMALES
SOUTH CAROLINA
47 MALES
43 FEMALES
NORTH CAROLINA
148 MALES
133 FEMALES
FREQUENCY
TOTAL LENGTH (mm)

The ova were previtellogenic oocytes (Stage II) located within the connective tissue or collecting tubules of well developed testes (Figure 6D). Oocyte occurrence could be attributed to several circumstances:

1. residual from a recent ovarian stage,
2. residual from a juvenile sex reversal since stage II oocytes are the most resistant oocytes to atresia (Bruslé and Bruslé, 1975), or
3. recent generation from gonocytes (primary female germ cells) residual from a previous (juvenile or later) female stage. An influx of estrogens (its presence implicit from previous female stage), coincident with the increased hormonal activity initiating spermatogenesis, could induce limited oogenesis (Bruslé, 1969; Bruslé and Bruslé, 1975).

Protogynous hermaphroditism beyond the juvenile stage (1, above) could account for anomalous sex ratios at each end of the size scale. However, the testes containing residual oocytes were fully developed externally and internally. No transitional gonads were observed (excluding juveniles) either with germinal testicular ridges or proliferating spermatogonial crypts outside or within an ovary (Moe, 1969; Warner, 1975; Mercer, 1978). Collections of gray tilefish from October through February are needed before the possibility of sex reversal of mature females can be refuted.

Dominance of females in the smaller size classes could be attributable to differential growth rates (Wenner, 1972) if all male gray tilefish go through a juvenile female stage (= rudimentary

hermaphrodism, Atz, 1964). Females partition more metabolic energy into gonad development at an earlier age than do males (considering relative gonad quantity) (Warner, 1975). The slower growth rate of females coincides with maturation. The dominance of males above 600 mm TL could be related to their faster growth rate, greater longevity or protogyny (Wenner, 1972). Fishing selectivity should not affect sex ratios within size classes (Manooch, 1975; Grimes, 1976), but it may account for the overall dominance of males by selecting for larger fish.

The C. chrysops collections from off North and South Carolina (n = 19) included eight females less than 510 mm TL (385-508 mm) and 11 males over 500 mm TL (503-620 mm). Histological analysis provided no further evidence but protogynous hermaphroditism is strongly suggested. Dooley (1974) reported similar anomalous sex ratios for L. chameleonticeps, Branchiostegus wardi and B. serratus.

Dooley (1974) suggested that tilefishes evolved primarily in the Caribbean area. C. microps (C. chrysops and other tilefish) could have developed there as normal protogynous hermaphrodites since coral reefs are the locale of the greatest proliferation of hermaphroditism in fishes i.e. serranids (Smith, 1965), labrids (Roede, 1962) and scarids (Choat and Robertson, 1975). Radiation of C. microps to deeper waters away from the coral reefs could have reduced the advantage of protogynous sex reversal. Assuming Ghiselin's (1969) size advantage model the most appropriate, increased availability of mating territories or spawning females could mitigate the implicit selective forces of the model; this could have favored transition to the male state at earlier ages, hence tending towards juvenile

(rudimentary) hermaphroditism. Prematurational sex changes have been reported in parrotfishes, Scaridae. Robertson and Warner (1978) suggest development of secondary gonochorism might be attributable to loss of the primary males in the evolutionary past.

Sexual Maturity

The onset of sexual maturity often relates to the attainment of a particular size or age at which an individual is capable of fulfilling its metabolic needs for growth, maintenance and reproduction (Nikolsky, 1963). Maturity of female gray tilefish was attained at 425 mm TL; more than 50% of the fish contained developing, ripe or spent ovaries at that size (Figure 8). One age 3 female (n = 3) had active vitellogenic ovaries. Forty-five percent of the age 4 and 73% of the age 5 females were mature. All females were mature by age 6. Female C. chrysops had a similar developmental timetable: one age 3 fish (385 mm TL) was immature; one of two age 5 females (448 and 455 mm TL) was sexually mature; and three females from 477 and 508 mm TL had developing ovaries. Fitch and Schultz (pers. comm.) report 100% maturity for five female C. princeps between 500 and 640 mm TL (ages 6-11).

Ovarian development (index) was closely related to total length (Figure 9). Initial increases in relative gonad quantity occurred at 400-500 mm TL; thereafter, ovarian development assumed a more rapid rate with increasing length.

Gonad index for female gray tilefish from South Carolina was greater than that for fish captured off North Carolina (May through August) through all sizes. Increased reproductive potential coincided with faster growth rates off South Carolina (see age and

Figure 8. Percent of sexually mature fish within 25 mm total length intervals for male and female Caulolatilus microps.

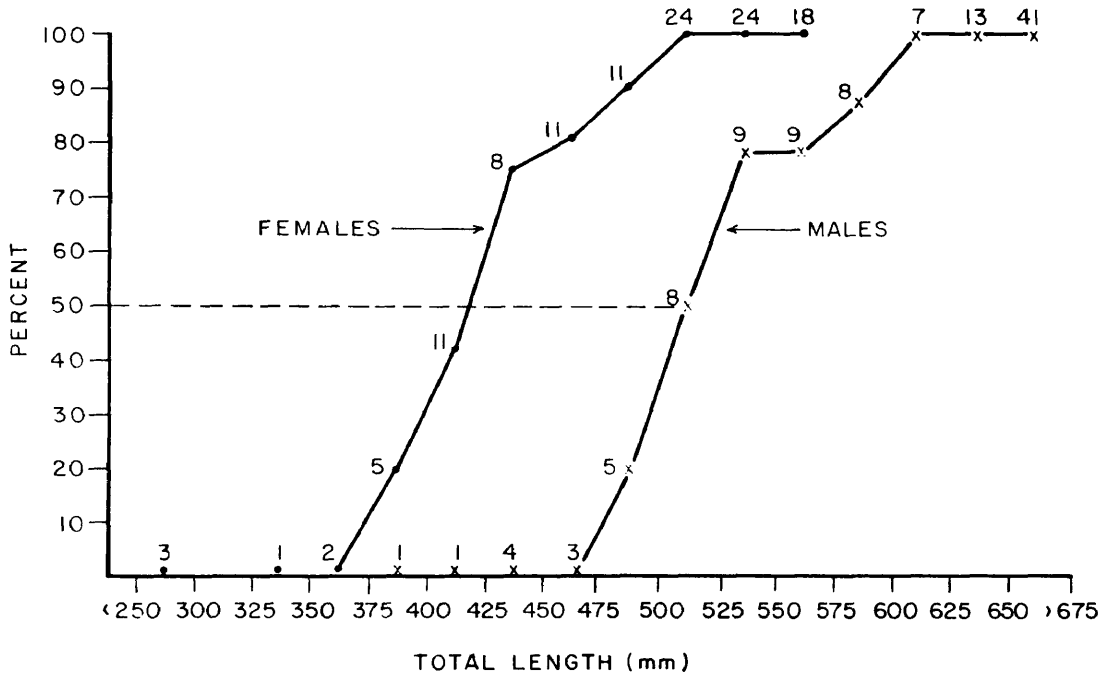
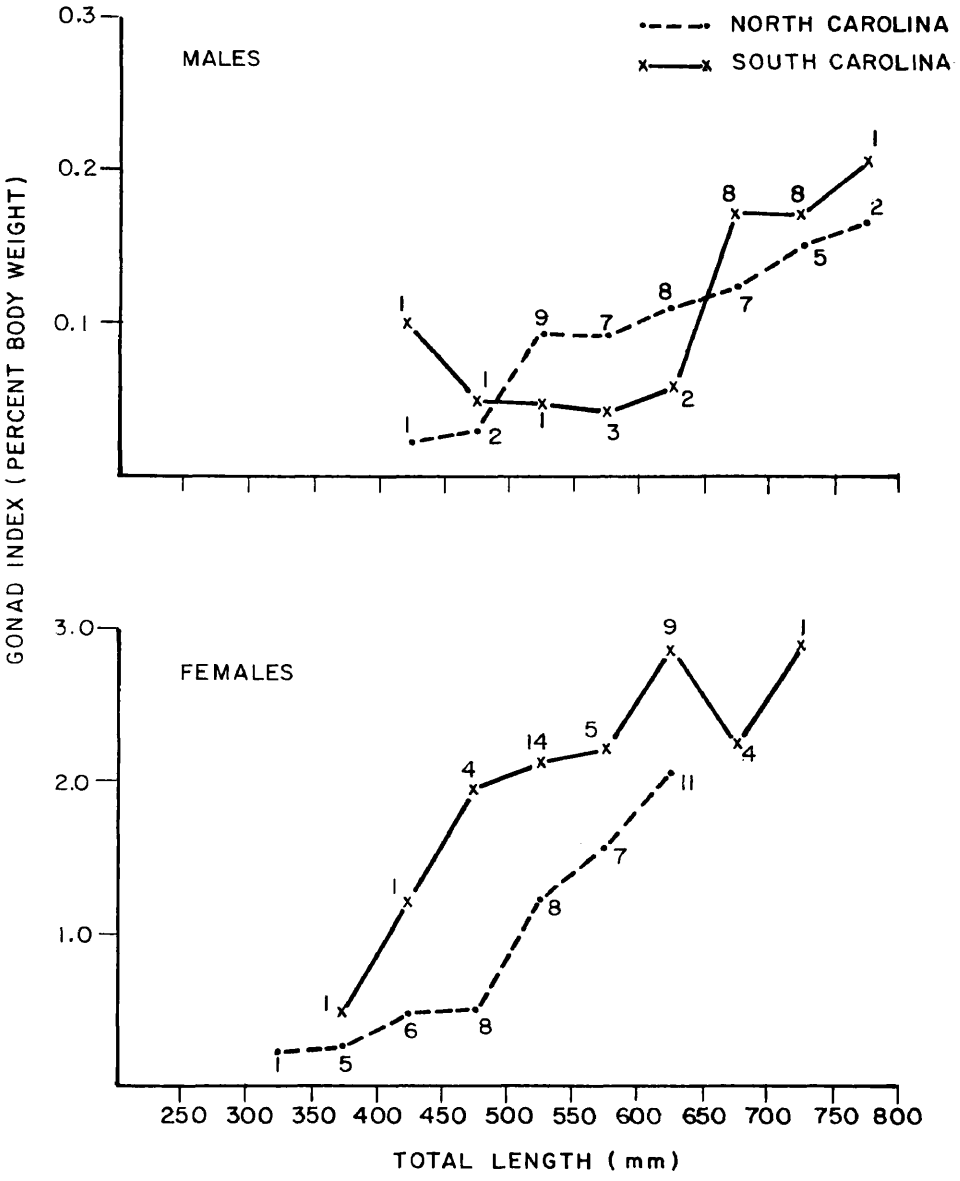

100
90
80
70
60
50
40
30
20
10
PERCENT
24 24 18
11
11
8
FEMALES
11
5
3 1 2 1 1 4 3
7 13 41
8
9 9
MALES
8
5
‹250 300 325 350 375 400 425 450 475 500 525 550 575 600 625 650 ›675
TOTAL LENGTH (mm)

Figure 9. Mean gonad indices plotted against total length (50 mm total length intervals) for male and female Caulolatilus microps from North and South Carolina.


NORTH CAROLINA
SOUTH CAROLINA
MALES
FEMALES
GONAD INDEX (PERCENT BODY WEIGHT)
0.3
0.2
0.1
3.0
2.0
1.0
250 300 350 400 450 500 550 600 650 700 750 800
TOTAL LENGTH (mm)

growth section) which could be due to a longer growing season and/or a greater food availability. Both situations impart an opportunity for greater caloric acquisition; subsequently, more metabolic energy is available for ovarian development (Bagenal, 1967; Gonor, 1972).

Male gray tilefish show little gross testicular development under 500 mm TL. Macroscopically, 50% were considered immature between 500 and 525 mm TL and 100% maturity was attained above 600 mm TL (Figure 8). No age 4 male was considered mature and a majority had not matured until their sixth year. Off North Carolina the first notable increase in testicular index occurred in fish from 500 to 550 mm (Figure 9). There was a consistent increase in gonad complement with increasing total length.

Histological examination of testicular tissue from fish 390 to 500 mm TL (n = 11) revealed active spermatogenesis in fish that had previously been considered immature upon macroscopic inspection. Testes were very small (less than 0.08% body weight) and maroon in color. Whether this development represented precocious development or functional maturity could not be determined.

Gray tilefish captured off South Carolina exhibited a delay in testicular development with no substantial change in gonad index until fish reached 650 mm TL (Figure 9). This pattern of gonad development could suggest size selection by spawning females and/or greater availability of larger males. This is common for protogynous hermaphroditic and gonorchistic labrids (Robertson, 1972; Olla and Samet, 1977), serranids (Smith, 1965) and scarids (Warner and Downes, 1977). The larger males found off South Carolina (see age and growth

section) could have behaviorally induced a delayed maturity (decreased spermatogenesis) in larger males than observed in gray tilefish off North Carolina.

Selectivity for larger males by spawning females could be related to the maintenance of territories by prospective mates (Ghislen, 1969; Warner, 1975; Choat and Robertson, 1975; Olla and Samet, 1977). Malacanthids are noted burrow inhabitants. M. plumeri has been observed hovering above burrows in pairs (Dooley, 1974) and displaying aggressive territorial behavior towards intruders (Clifton and Hunter, 1972; Clarke et al., 1977). Hopholatilus sp. B has been seen inhabiting burrows in pairs (Dooley, 1974). L. chameleonticeps enters burrows when disturbed (Freeman and Turner, 1977). The gray tilefish exists where a lifestyle of close association with burrows could be sustained or similar behavior patterns developed.

Seasonality of Spawning

Gonad indices are useful indicators of the time and duration of reproductive cycles (Gonor, 1972; Grimes, 1976; Manooch, 1975; Merriner, 1976). Gonad index values determined for 138 female and 101 male gray tilefish (Figure 10) and plotted as monthly means (excluding immature specimens) show peaks occurring in May and September for both sexes in North Carolina collections. High index values in May correspond with the greatest incidence of nearly ripe and ripe individuals (Figure 11). The decreased mean index value in June relates, in part, to a sampling bias from capture of more small fish in earlier stages of gonad development. There were several very ripe females taken in June. The lower mean index values from June through August reflect the diverse spectrum of gonadal conditions

Figure 10. Monthly mean gonad indices for male and female *Caulolatilus microps* from North and South Carolina.

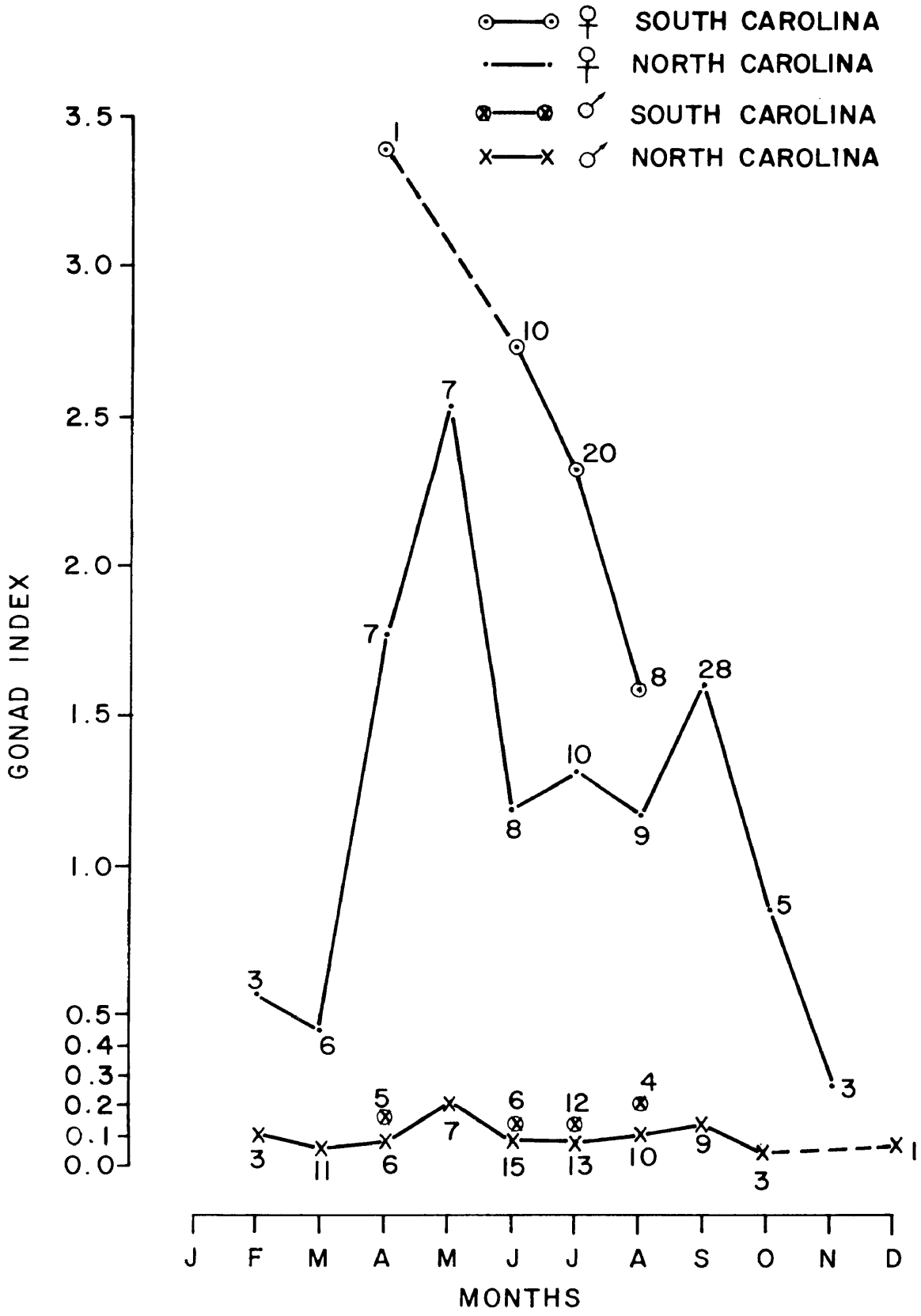
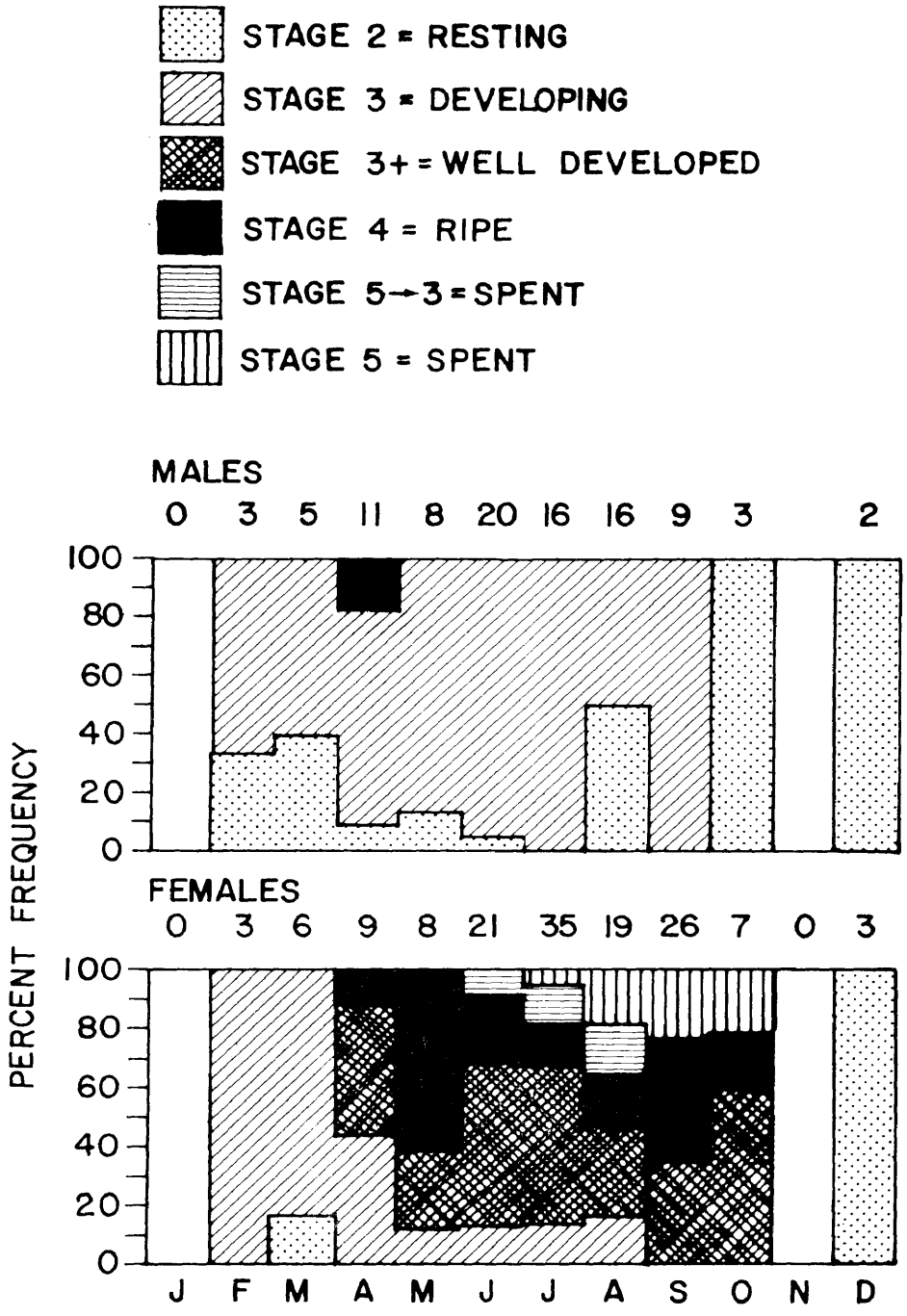

SOUTH CAROLINA ♀
NORTH CAROLINA ♀
SOUTH CAROLINA ♂
NORTH CAROLINA ♂
GONAD INDEX
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.4
0.3
0.2
0.1
0.0
J F M A M J J A S O N D
MONTHS

Figure 11. Percent frequency histograms of gonad developmental stages for each month for male and female *Caulolatilus microps*.

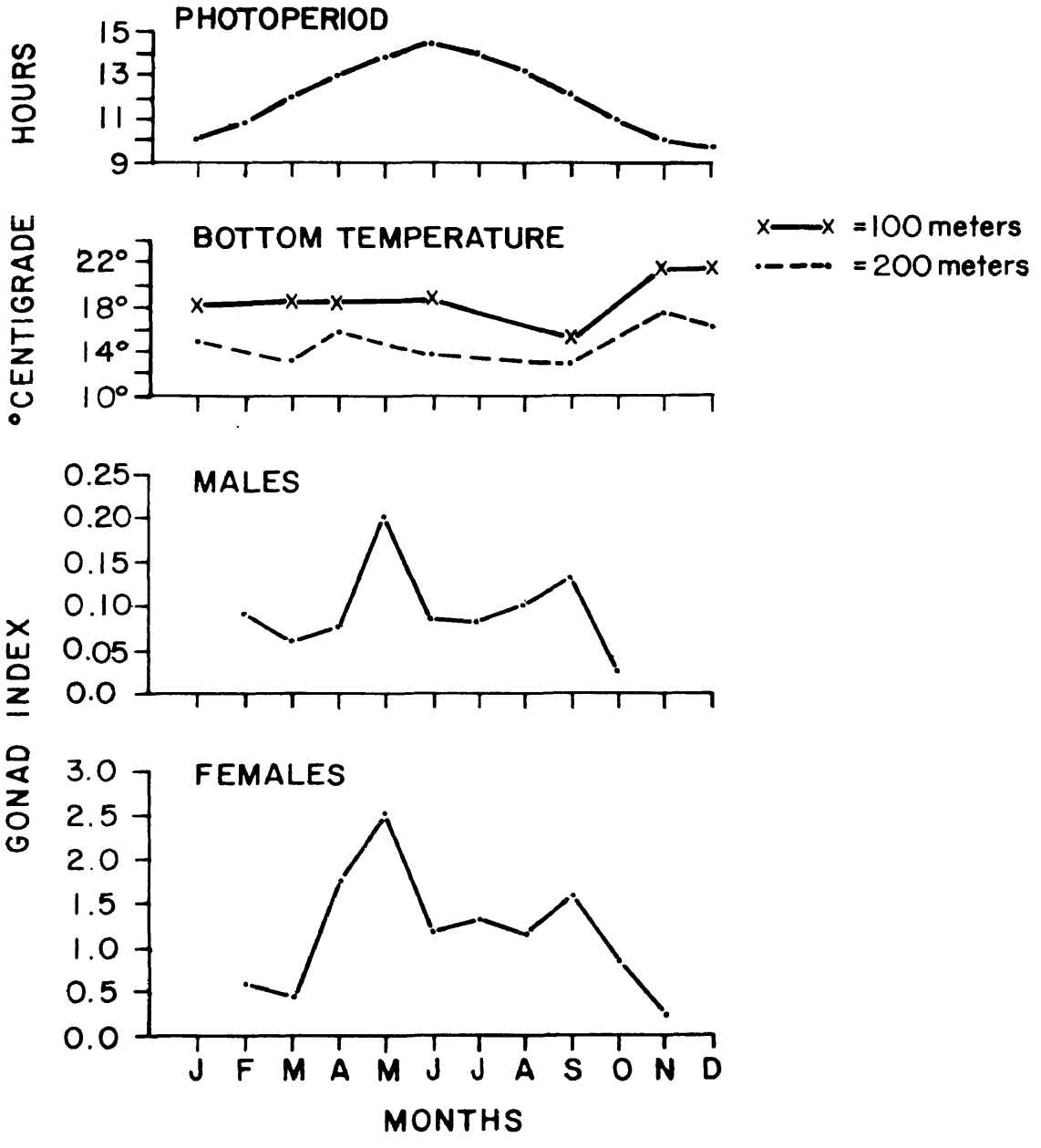

STAGE 2 = RESTING
STAGE 3 = DEVELOPING
STAGE 3+ = WELL DEVELOPED
STAGE 4 = RIPE
STAGE 5→3 = SPENT
STAGE 5 = SPENT
MALES
0 3 5 11 8 20 16 16 9 3 2
FEMALES
0 3 6 9 8 21 35 19 26 7 0 3
PERCENT FREQUENCY
100
80
60
40
20
0
J F M A M J J A S O N D

observed. A final synchrony among spawning tilefish in September concurs with the higher incidence of well developed gonads. Low index values from October through March reflect a period of gonad recovery and early development.

Photoperiod, water temperature and food availability are important exogenous cues aiding teleosts to temporally optimize and synchronize spawning in offshore waters (Nikolsky, 1963; deVlamming, 1972; Cushing and Walsh, 1976). Gonadal activity of the gray tilefish begins during the period of most rapidly increasing photoperiod. Termination of gonadogenesis correlates with the point of decreasing photoperiod (Figure 12). Considering the erratic nature of bottom water temperature overlying the shelf-edge zone, it seems reasonable that spawning would be attuned to the more conservative environmental factor. The initiation of annual gonadal development has been correlated with photoperiod for several inhabitants of the shelf-edge community, including the red porgy (Manooch, 1975) and red grouper (Moe, 1969). The protracted spawning season of vermilion snapper is correlated with both photoperiod and water temperature (Grimes, 1976). Its occurrence over the continental shelf increases its susceptibility to seasonal temperature variations.

Protracted spawning seasons seem to be characteristic of caulolatilids and possibly branchiostegids. Female C. chrysops had developing ovaries from April through October and one ripe female was captured in May. L. chameleonticeps spawns from mid-March through mid-September (Freeman and Turner, 1977). Extended spawning seasons are reported for C. princeps (Fitch and Lavenberg, 1971; Schultz, pers. comm.) and C. affinis (Dooley, 1974) in the Pacific Ocean.

Figure 12. Mean gonad indices for male and female Caulolatilus microps from North and South Carolina for each month compared with photoperiod and bottom temperatures.


PHOTOPERIOD
HOURS
15
13
11
9
BOTTOM TEMPERATURE
°CENTIGRADE
22°
18°
14°
10°
x—x = 100 meters
·- - - = 200 meters
MALES
GONAD INDEX
0.25
0.20
0.15
0.10
0.05
0.0
FEMALES
3.0
2.5
2.0
1.5
1.0
0.5
0.0
J F M A M J J A S O N D
MONTHS

Frequency distributions of ova diameter provide details of seasonal development and spawning patterns (Clarke, 1934; Hickling and Rutenberg, 1936; Moe, 1969; Beaumarraige, 1973; deSilva, 1973; Grimes, 1976). Ova diameter frequencies (in ocular units, ou) were plotted by monthly collection (Figure 13) and designated ovarian developmental stages (Figure 14).

A residual stock of previtellogenic oocytes (stage II, 4-10 ou) was present as a source for further ova development in all maturing female gray tilefish. Their abundance was probably underestimated due to the packed nature of the ovigerous lamellae. Early vitellogenic oocytes (stage III, 10-18 ou) occurred in mature ovaries during all months sampled except December; only immature fish were available from December samples. Stage III oocytes represented the most mature oocyte retained in ovaries after the spawning season (rather than undergoing atresia). Stage III oocytes maintained consistent abundance from February through July which suggests a continuous progression of developing ova from the residual stock (stage II) through this stage. Vitellogenic ova (stage IV, 18-45 ou) occurred in ovaries from March through October and exhibited a broad size distribution through most of the period. Frequency modes of late stage IV ova (30-45 ou) in May, July and September-October coincided with peaks in gonad index. In April, June, and August size frequencies were more evenly distributed. Small numbers of mature ova (stage V - 45-70 ou) were collected in the ovarian lumen of ripe females captured in May through August. Ovaries with internal hemorrhaging and/or containing atretic stage V oocytes in June, July and August were mostly large fish which were continuing vitellogenesis.

Figure 13. Frequency distribution of ova diameters in two ocular unit intervals based on two Caulolatilus microps from North Carolina for available months.

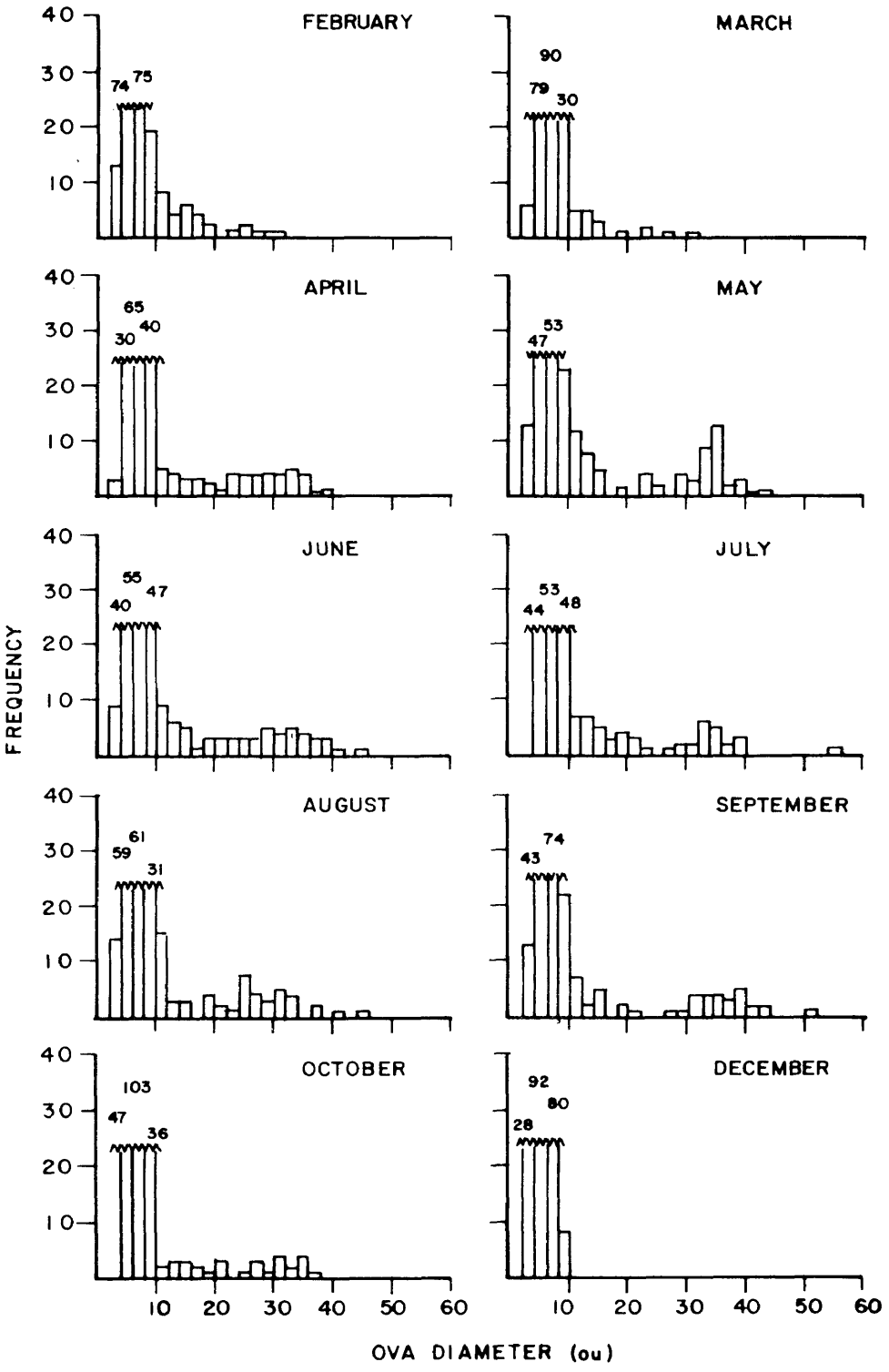
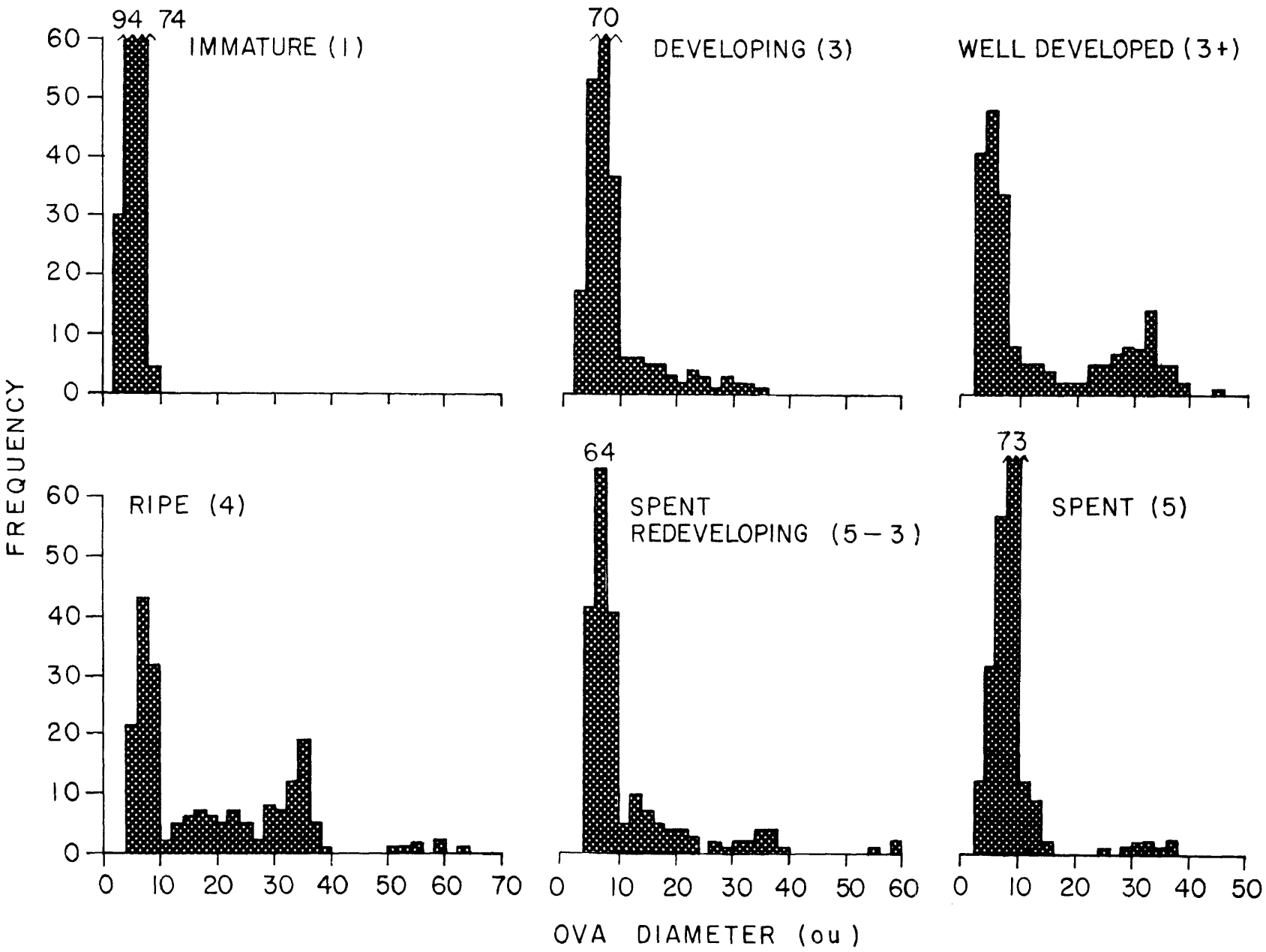

FEBRUARY
74
75
MARCH
90
79
30
APRIL
65
30
40
MAY
53
47
JUNE
55
40
47
JULY
53
44
48
AUGUST
61
59
31
SEPTEMBER
74
43
OCTOBER
103
47
36
DECEMBER
92
80
28
40
30
20
10
FREQUENCY
10
20
30
40
50
60
OVA DIAMETER (ou)

Figure 14. Frequency distribution of ova diameters in two ocular unit intervals based on two Caulolatilus microps from North Carolina for designated ovarian developmental stages.


94 74
IMMATURE (1)
70
DEVELOPING (3)
WELL DEVELOPED (3+)
64
RIPE (4)
SPENT
REDEVELOPING (5–3)
73
SPENT (5)
FREQUENCY
0 10 20 30 40 50 60
0 10 20 30 40 50 60 70
0 10 20 30 40 50 60
0 10 20 30 40 50
OVA DIAMETER (ou)

Vitellogenic activity in female gray tilefish is a continuous developmental process. From April through October several batches of late stage IV oocytes occurred while early vitellogenic oocytes (stage III) were being generated in the same ovaries. Size frequency distributions of ova within the developmental stages of ovaries (Figure 14) confirmed continual development of eggs; ripe females contained an abundance of well developed oocytes (late stage IV) and fully matured eggs (stage V) together with a progression of early developing oocytes.

Multimodal ova size distributions are characteristic of fishes that spawn several times during a protracted spawning season; a continuous maturation of residual, previtellogenic ova is inferred with no sharp distinctions between residual and maturing eggs (Clarke, 1934; Hickling and Rutenberg, 1936; Roede, 1962; Moe, 1969; Warner, 1975; Grimes, 1976). Ovarian development during a shorter spawning season would result in a more distinct separation of mature and maturing oocytes from the residual stock (Hickling and Rutenberg, 1936). Histologically, continuous ovarian development was evident in the ovigerous lamellae of gray tilefish (Figure 2D).

Testicular development followed an analogous continuous state of spermatogenesis at the cyst-tubule level from March through October off North Carolina (Figures 3 and 4). Males maintain a year round state of readiness at the testicular level. Testes from March collections were dormant or just beginning activity at the cyst-tubule level yet collections of residual spermatozoa were present in the collecting tubules from earlier spermatogenesis (Figure 3A & 4A).

Multiple spawning (=fractional spawning, Nikolsky, 1963) appears to be the mode of reproduction for branchiostegids. Female C. chrysops captured off North Carolina contained ova size distributions similar to those of gray tilefish. Multi-modal ova size distributions have also been described for L. chameleonticeps (Freeman and Turner, 1977; Morse, pers. comm.), B. wardi and B. serratus (Dooley, 1974; Dooley and Paxton, 1975). The origin and center of distribution of branchiostegids in tropical waters (Dooley, 1974) would account for this type of seasonal ovarian development. Multiple spawning as a reproductive strategy is prevalent in tropical waters and developed from the occurrence of optimal conditions for larval survival almost year-round (Lagler et al., 1953; Nikolsky, 1963).

Multiple spawning during a protracted season imparts several advantages to tilefish populations. First, it provides a greater probability for the production and release of pelagic eggs during periods of optimal temperature, food availability and favorable currents. The influence of currents upon the transport of pelagic eggs and larvae is particularly relevant to gray tilefish since the early developmental stages are susceptible to transport away from suitable habitat by the Gulf Stream. If spawning is partially directed toward maintenance of regional populations (Marshall, 1966), then fractional spawnings would increase the likelihood for the occurrence of passive life stages during favorable transport conditions. Velocity of the Florida Current decreases with distance from its axis (between the 100 and 1000 fathom curves in Raleigh and Onslow Bay) and it tends offshore during the summer (Stefansson and Atkinson, 1967). This summer meandering offshore could intermittantly reduce the

effective current encountered by gray tilefish larvae. Counterclockwise gyres deflected by Cape Lookout and Diamond Shoals would increase retention of locally spawned fish in North Carolina waters (Stefansson and Atkinson, 1967). Second, multiple spawnings optimize the chances of favorable conditions existing for survival of dispersed progeny (Cushing and Walsh, 1976). The repopulation of the New England area by L. chameleonticeps after the massive mortality of 1882 (Collins, 1884) was probably related to larval recruitment from southern populations. Shelf-edge finfish populations off the Carolinas are partially, if not entirely, supported by larvae from southern populations (Powles, unpub. manuscript; Huntsman and Manooch, 1978). Third, multiple spawnings can augment the individual female's reproductive potential by increasing the opportunity for mating with different males, thus contributing to population heterozygosity, while also increasing their potential annual fecundity (deSilva, 1973).

Fecundity

Fecundity can be defined as the number of eggs spawned by an individual in a season (Bagenal, 1967). Determination of gray tilefish fecundity posed problems of underestimation (by excluding previtellogenic oocytes that would develop later in the season) and overestimation (if all early vitellagenic oocytes were not released that season).

The annual fecundity estimate included eighteen well developed (stage 3+) and ripe (stage 4) fish captured off North and South Carolina from late April through mid-June. Fecundity was correlated with both length and weight (Figures 15 & 16) and expressed by the relationships:

Figure 15. Relationship between fecundity and length for Caulolatilus microps collected off North and South Carolina during May and June. Fecundity estimates for fish captured in July and September are also plotted.

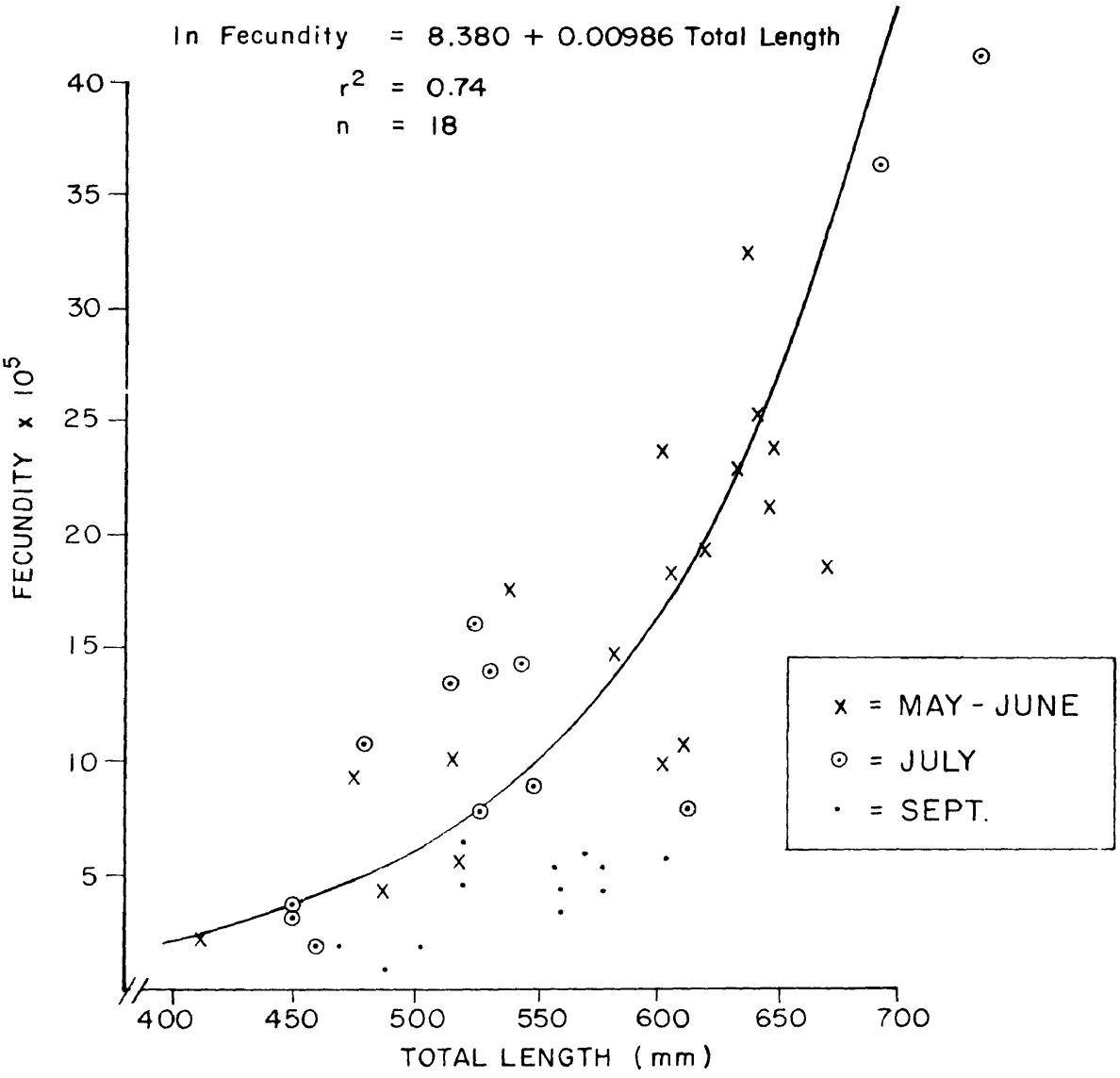
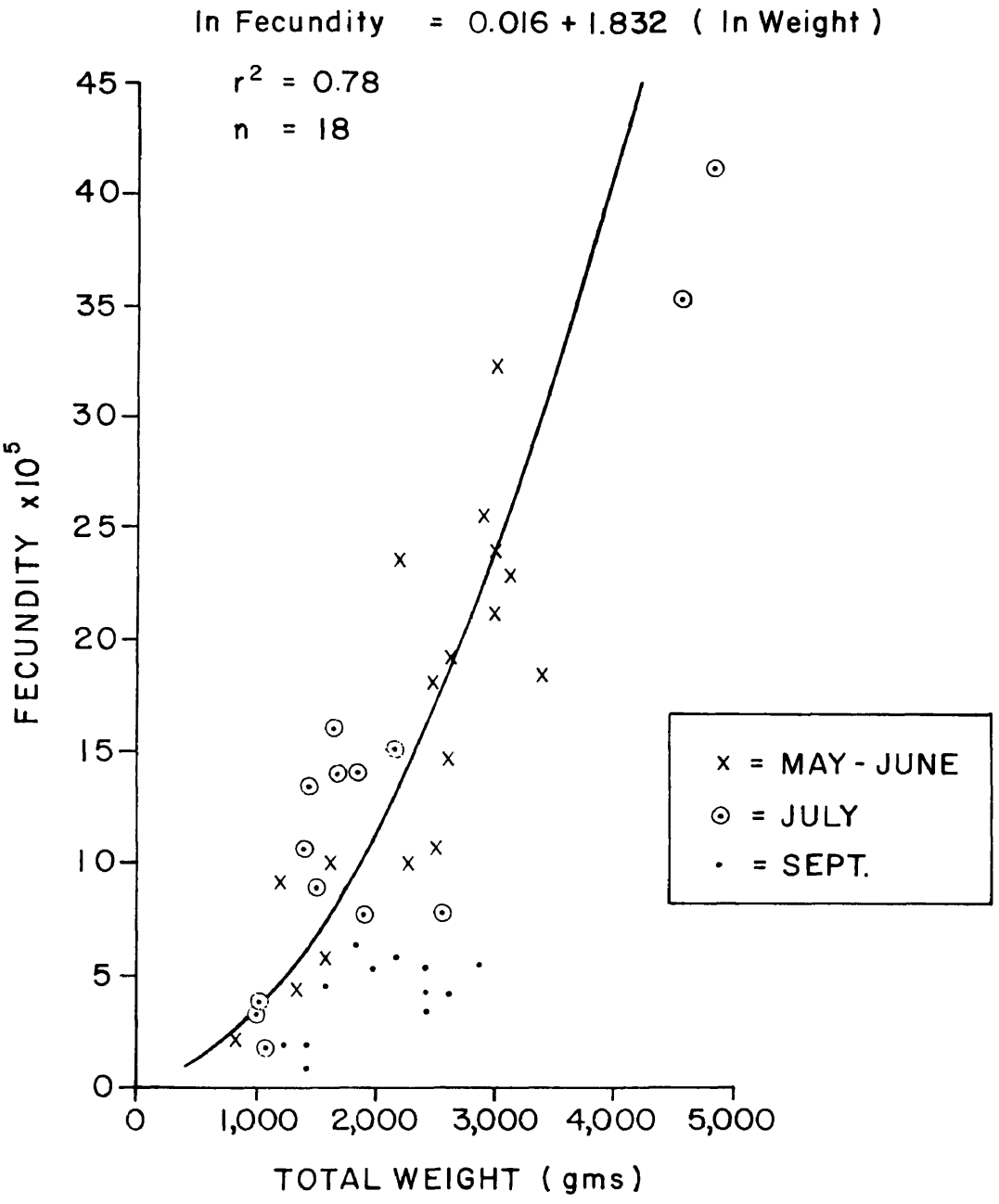

ln Fecundity = 8.380 + 0.00986 Total Length
r^2 = 0.74
n = 18
FECUNDITY x 10^5
40
35
30
25
20
15
10
5
400
450
500
550
600
650
700
TOTAL LENGTH (mm)
x = MAY - JUNE
⊙ = JULY
· = SEPT.

Figure 16. Relationship between fecundity and weight for *Caulolatilus microps* collected off North and South Carolina during May and June. Fecundity estimates from fish captured in July and September are also plotted.


ln Fecundity = 0.016 + 1.832 (ln Weight)
r² = 0.78
n = 18
FECUNDITY x10⁵
45
40
35
30
25
20
15
10
5
0
0
1,000
2,000
3,000
4,000
5,000
TOTAL WEIGHT (gms)
x = MAY - JUNE
⊙ = JULY
• = SEPT.

$$\ln \text{Fecundity} = 8.380 + 0.00986 \text{ Total Length}$$

$$r^2 = 0.74$$

$$\ln \text{Fecundity} = 0.016 + 1.832 \text{ (ln Weight)}$$

$$r^2 = 0.78$$

Fecundity values for 11 well developed and ripe females captured in July off South Carolina were consistent with the above fecundity relationships. Some of the larger fish in the group had probably spawned earlier that season. The continuum of developing ova apparently generated a mid-season batch of eggs which was equal to an earlier spawn.

Well developed and ripe gray tilefish captured in September off North Carolina (469 to 603 mm TL) had one-half to one-third fewer ova (Figures 15 & 16) as a result of reduced development of previtellogenic oocytes after July.

Fecundity estimates from specimens collected in May-June and July suggests the attainment of a maximum ova carrying capacity. Reduced fecundity of gray tilefish in September would be an energy conserving adaptation since stage III and early stage IV ova would not be released later that year (Alexander, 1975).

SUMMARY

Oogenesis and vitellogenesis proceed through five co-occurring morphological stages in the ovigerous lamellae of developing ovaries. Mature ova (785-910 μ) are released from ovigerous folds and collect in the ventral ovocoel.

The testicular counterpart of the ovigerous lamellae are the seminiferous tubules. Their structure is essentially a one spermatogonium - one cyst thick matrix, ringlike in cross-section, with a central lumen for collection of spermatozoa. Spermatogenesis occurs within the cysts, all constituents developing at an equal rate from one spermatogonium. Analogous to the continuum of ova maturation, development of cysts within the seminiferous tubules is staggered and tubules are generally composed of all developmental stages. Seminiferous tubule longevity is greater than one year.

Seminiferous tubules function in the drainage of spermatozoa from the testes. While developing they migrate medially and eventually merge with collecting tubules for the transfer of spermatozoa. Spermatozoa are then channeled posteriorly and ventrally through a network of secondary and primary collecting tubules to the sperm ducts.

Three of five juvenile gray tilefish examined had ovotestes. The ontogeny of the testes progressed by the proliferation of testicular mesothelium within the ovigerous lamellae. The mesothelium contained

primary spermatogonia which were forming spermatogenic tubules and initiating spermatogenesis. The ovarian stage was evidenced by residual and atretic oogonia and oocytes along the distal tunic epithelium.

Females were dominant within the 300 to 500 mm TL size classes. Between 500 to 600 mm TL a 1:1 sex ratio prevailed. Males were increasingly dominant in gray tilefish 600 mm or greater.

Transitional gonads were observed only in the juvenile life stage. Solitary previtellogenic oocytes were observed in the connective tissue or collecting tubules in 8 mature testes. These could be related to a recent ovarian stage, hence protogynous hermaphroditism on a functional level may exist in gray tilefish. However, the residual oocytes could also be attributed to residual gonocytes from a previous juvenile ovarian stage. The disproportionate number of males in fish larger than 600 mm TL would then be attributable to faster growth and greater longevity.

Female gray tilefish generally mature after their fourth or fifth years (~435 mm TL), after which ovarian development (expressed as percent body weight) increases consistently with increased length. Female gray tilefish from South Carolina waters produced a relatively greater gonad quantity, suggesting more favorable environmental conditions.

Male testicular development was somewhat delayed and proceeded actively after age 5 or 6 (>500 mm TL). Spermatozoa were present in tubules of 400-500 mm TL specimens but significant increases in testicular production (gonad index) did not occur until fish were 500-600 mm TL.

Mature females produce several batches of eggs during a protracted spawning season. Continuous development of previtellogenic oocytes occurs from March through August with mature ova present in the ovary from May through September.

Testicular development is synchronized with ovarian cycles: spermatozoa occurred in seminiferous and collecting tubules in March prior to onset of active spermatogenesis and during the spawning season spermatogenesis proceeded continuously at the cyst-tubule level.

Gonad index for male and female gray tilefish indicated peak spawning periods in May and September. Gonadogenesis is initiated in March and continues through October. Gonadal development is correlated with photoperiod. Spawning probably occurs earlier (in April) off South Carolina.

Fecundity of 18 female gray tilefish ranged from 207,000 to 4,100,000 vitellogenic eggs and was correlated with length ($r^2 = 0.74$) and weight ($r^2 = 0.78$). Fecundity was estimated by the relationships:

$$\ln \text{Fecundity} = 8.380 + 0.00986 \text{ total length}$$

$$\ln \text{Fecundity} = 0.016 + 1.832 (\ln \text{Weight})$$

Fecundity estimates were of equal magnitude from specimens captured in May-June and July because of the continued oogenesis and vitellogenesis through July. Fecundity estimates from specimens collected in September were 1/3 to 1/2 less than May or July estimates. These estimates corresponded with modes in the ova diameter frequencies and indicated decreased vitellogenesis after July.

SECTION II: AGE, GROWTH AND MORTALITY

INTRODUCTION

The age and growth of the gray tilefish, Caulolatilus microps, is undescribed in the literature. Fitch and Lavenberg (1971) reported ocean whitefish, Caulolatilus princeps, from four to thirteen years old over a total length range of 302 to 645 mm TL. Freeman and Turner (1977) estimated lengths of northern tilefish, Lopholatilus chamaeleonticeps, for ages through 40 years based on otoliths, but did not validate the formation of an annulus. Hayashi's (1976a, b) reports on red tilefish, Branchiostegus japonicus japonicus, are the only detailed age and growth studies of a branchiostegid. He validated otoliths as an aging structure and derived growth models for both sexes.

In the management of a fishery, three important parameters necessary for an understanding of the population dynamics of a species are age, growth, and mortality. The objectives of this section relative to C. microps are to: (1) validate the use of otoliths as an aging structure; (2) describe their age and growth with respect to empirical lengths/age, back-calculated lengths/age, and derivation of theoretical growth equations; (3) define the length-weight relationships by area and sex; (4) illustrate the size and age composition of the recreational fishery catch; and (5) estimate total mortality.

METHODS AND MATERIALS

Sample Collections

Gray tilefish and Atlantic golden-eyed tilefish were obtained primarily from experimental hook and line fishing trips aboard the R/V Onslow Bay off Cape Lookout, North Carolina. Specimens were also acquired through the National Marine Fisheries Service's (NMFS) port sampling activities covering headboats which operate in North and South Carolina waters. Attempts were made to obtain specimens each month, but the seasonal nature of the headboat fishery and sea conditions off North Carolina precluded substantial winter collections.

Otoliths

Otoliths were selected as the most reasonable structure for aging gray tilefish because: (1) scales are regenerated (Dooley, 1974); (2) otoliths were available from NMFS sampling; and (3) initial observations revealed a readable pattern of concentric rings.

Fish collected on experimental fishing trips were returned to the laboratory for dissection. Length, weight, stomach, and gonads were obtained from all specimens. The cranium was cut open with a hacksaw. The right and left sagittae were removed with forceps from the otic capsules and placed in labelled vials which contained glycerine for clearing.

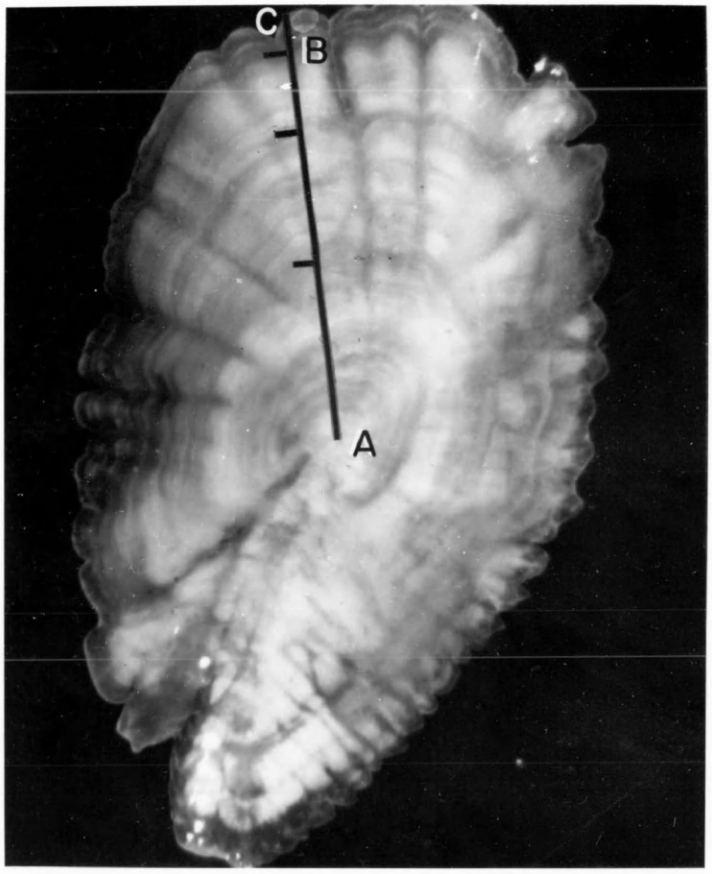
Otoliths were immersed in a petri dish containing glycerine and viewed over a dark background with a binocular dissecting scope

at a magnification of 10X. Illumination was provided by an overhead bright light (reflected light).

Measurements of seasonal growth rings were taken along the most dorsal radii extending from the nucleus to the posterior dorsal corner of the sagitta (Figure 17). Circuli were most distinguishable within the posterior region where maximum outward radiation from the nucleus occurred. The hyaline (dark) zones were generally narrower than the opaque zones and were considered annuli. The first two annuli were relatively wide with indefinite boundaries. When the inner margin of the succeeding fast growth zone was not distinct, I measured to a point halfway between the opaque zones. Otherwise, all measurements of annular growth were taken to the inner edge of the opaque zones. Marginal increments were measured from the inner margin of the last opaque zone to the edge of the sagitta using a magnification of 20X (Figure 17).

Annuli were counted and measured twice; if these did not correspond, a third reading attempt was made. Disagreement after three readings precluded use of that fish in age and growth analysis.

Figure 17. A left otolith of from an age 3 Caulolatilus microps exhibiting measurements taken. (The lateral concave surface is up.) Abbreviations: A, focus or nucleus; AC, otolith radius and line of annular measurements; BC, marginal increment; dark bars indicate annuli.


C
B
A

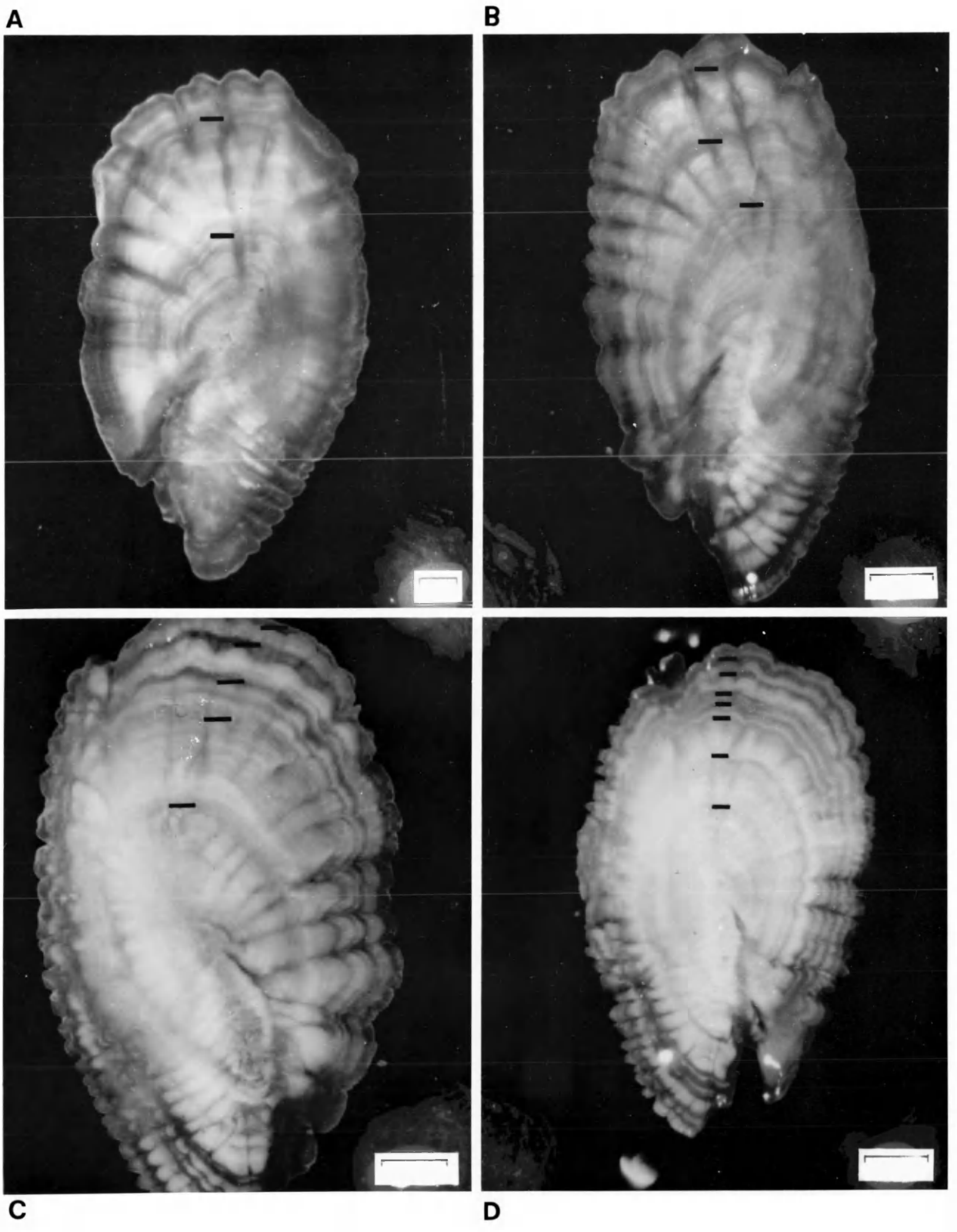
RESULTS AND DISCUSSION

Otolith Description and Growth

The sagitta of C. microps is eliptical, laterally compressed and moderately concave (Figure 18). Its height is about two-thirds its length. The posterior quarter is the area of maximum outward radiation and is bordered by the most evenly convoluted margin. Anteriorly, the margins become increasingly convoluted and fragile in older fish. The convex (medial) surface of the sagitta is smooth except for the sulcus acousticus. The concave surface bears a continuous pattern of alternating opaque and hyaline concentric rings.

The nature and composition of otolith growth rings has been discussed by numerous authors including Dannevig (1956), Irie (1955, 1960), Blacker (1969, 1974), Panella (1971, 1974) and Williams and Bedford (1974). Growth of the sagitta results from the deposition of aragonite crystals within an organic matrix, and corresponds to the endogenous and exogenous factors controlling the fish's growth. Fast growth (opaque) zones are characterized by larger, densely packed aragonite crystals within an organic matrix. Slow growth (hyaline) zones are composed of smaller microcrystals which allow more organic matter (concholin) within the interstitial spaces (Dannevig, 1956; Blacker, 1974). This translates into greater reflectivity of the fast growth zones and greater absorbtivity of the slow growth zones (Panella, 1971, 1974).

Figure 18. A. Otolith from Caulolatilus microps in age group 2, May, 270 mm TL. B. Otolith from a fish in age group 3, August, 387 mm TL. C. Otolith from a fish in age group 5, April, 435 mm TL. D. Otolith from a fish in age group 7, October , 626 mm TL. (scale = 1 mm)


A
B
C
D

The nucleus of the gray tilefish sagitta is a faint hyaline mark within a solid opaque band (Figure 18). The nucleus is surrounded by a hyaline zone which contains or grades into a series of thin (0.03 to 0.05 mm) opaque growth checks (generally 8-15 in number) which are most distinct posteriorly. A relatively wide hyaline zone (first annulus) is followed by another series of thin, opaque growth checks. These represent the second fast growth zone and grade into a solid opaque zone or remain distinct. The third fast growth zone is a solid opaque band and is comparatively reduced in width. Succeeding hyaline (slow growth) zones become equally narrow and distinct in older fish. A gradual reduction in fast growth zone width continues until they are not much wider than the hyaline zones in older fish.

The hyaline zone (= annulus) forms on the sagitta of C. microps between January and April. Its formation corresponds with the initiation of gonadal development which entails a sudden shift of metabolic energy from growth and maintenance and can result in its subsequent translation as a growth check (Hickling, 1933; Hartley, 1947; deBont, 1967; Moe, 1969; Panella, 1974). Formation of annuli prior to sexual maturity could arise from an innate physiological rhythm or feeding cycle attuned to photoperiod (Hartley, 1947; Panella, 1974; Grimes, 1976). Although the annual range of bottom temperatures along the shelf-edge zone off the Carolinas (4-5°C) is just equivalent to the minimum range which could induce decreased growth in fish (Chevey, 1933), I do not consider it as the critical factor triggering annulus formation by C. microps. Stephanson and Atkinson (1967) reported inconsistent bottom temperature variations which would not correlate with annulus formation between February and April.

Numerous false annuli were observed on the sagittae of C. microps (particularly females) and probably related to reproductive activity. These "spawning checks" were characterized by: (1) the presence of two or three slow growth checks within a fast growth zone after age four which would concur with multiple spawnings and attainment of sexual maturity; (2) occurrence along the margins from May through September corresponding with gonadal condition; (3) succeeding fast growth zone (the same year) replication of preceeding fast growth pattern (contour) and; (4) traceability around the sagitta of fish ages 4-6. Spawning check formation is analogous to annulus formation and induced by a shift in allocation of metabolic energy. The salience of spawning checks on otoliths of females is attributed to their greater relative gonadal production.

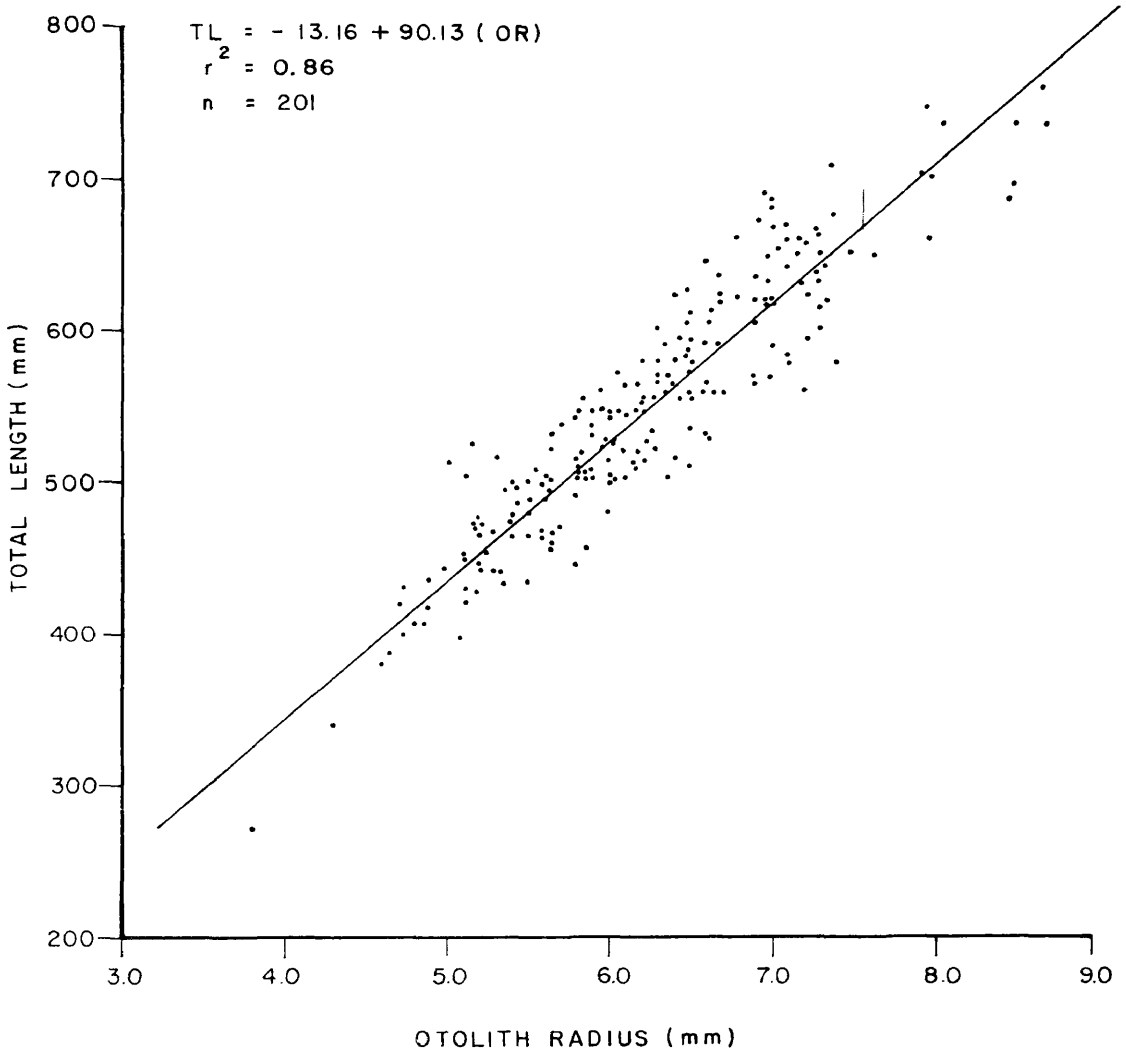
Validation of Otolith as Aging Structure

The criteria of Van Oosten (1929) and deBont (1967) were used for validation of otolith use in age and annual growth determinations.

Otolith presence during early development was assumed because they are necessary for orientation to the pelagic environment inhabited by larval fish (Williams and Bedford, 1974). Otolith persistence throughout life was also assumed since they are an integral part of the acousticosensory system.

The relationship between total length and otolith radius (OR) for 201 gray tilefish captured from 1973 to 1977 from North and South Carolina (inclusive of both sexes) is expressed by the geometric mean regression (Ricker, 1973) TL = -13.16 + 90.13 OR (Figure 19). The coefficient of determination (r^2 = 0.86) indicated a reasonably strong linear relationship between variables.

Figure 19. Scatter diagram and relationship of total length (mm) to otolith radius (mm) for Caulolatilus microps.


TL = - 13.16 + 90.13 (OR)
r² = 0.86
n = 201
800
700
600
500
400
300
200
TOTAL LENGTH (mm)
3.0
4.0
5.0
6.0
7.0
8.0
9.0
OTOLITH RADIUS (mm)

The smallest marginal increments consistently occurred between February and April (Figure 20) for all ages sampled. Hyaline zones were observed on the margins of sagittae from fish captured in February, March, and April. The initial formation of the opaque zones occurred along the posterior edge of the sagitta during this period. The gray tilefish from December collections had wide opaque zones which included the edge of the sagitta.

Body lengths of individual gray tilefish at earlier ages were obtained by the direct proportion back-calculation method of Lea (1910) and Van Oosten (1929): $L_n = \frac{S_n}{S} L$ with : L_n = total length at time of annulus formation; L = total length at time of capture; S_n = radius to respective annuli; and S = total radius of sagitta. The assumptions that tilefish (1) maintain essentially the same body contour throughout its life, and (2) otolith and the body growth are isogonic (Tesch, 1973; Everhart et al., 1975) were confirmed by linear relationships of length and weight ($r^2 = 0.96$), total length and standard length ($r^2 = 0.99$) and total fish length and sagitta radius ($r^2 = 0.86$). This model was selected without the use of a correction term (C) because the limited sample size under 400 mm TL could introduce a bias on the total length-otolith radius relationship, and particularly the y-axis intercept.

The mean back-calculated lengths for 97 females, 83 males, and 201 male and female gray tilefish are compared to the mean empirical lengths for each age (Tables 2-4, Figure 21). Empirical lengths (length at time of capture) were consistently higher for individual age groups, the difference within the limit of a seasons growth and related to the marginal increment.

Figure 20. Monthly mean marginal increments (in ocular units) for Caulolatilus microps.

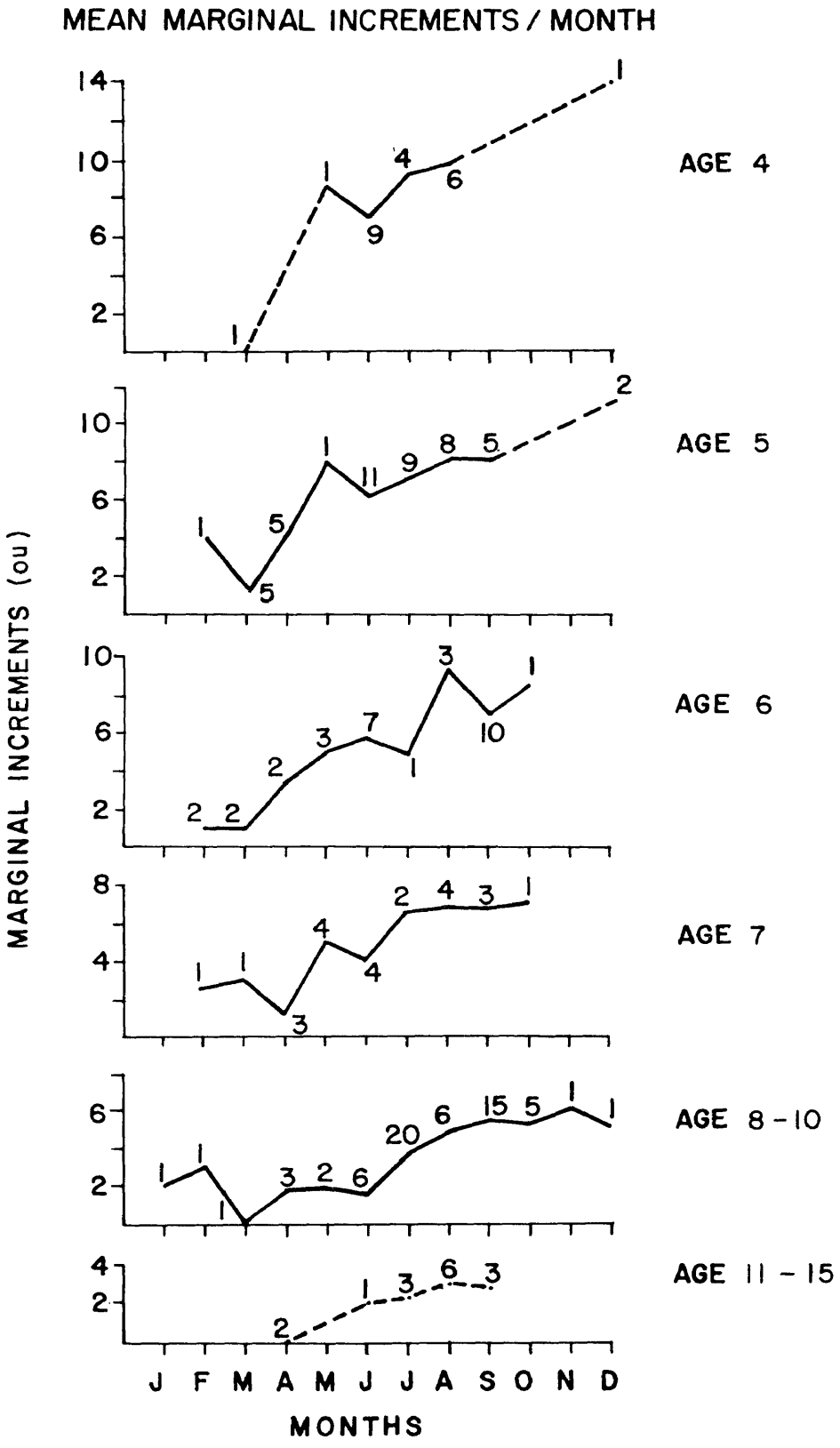

MEAN MARGINAL INCREMENTS / MONTH
MARGINAL INCREMENTS (ou)
AGE 4
AGE 5
AGE 6
AGE 7
AGE 8 - 10
AGE 11 - 15
J F M A M J J A S O N D
MONTHS

TABLE 2

MEAN BACK-CALCULATED TOTAL LENGTHS FOR 97 FEMALE CAULOLATILUS MICROPS

Age	Number of Specimens	Mean length at capture	Mean back-calculated lengths at successive annuli														
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	0																
2	1	341	151	262													
3	3	403	163	272	361												
4	16	450	165	263	356	412											
5	26	478	160	280	354	409	456										
6	16	512	164	281	345	400	447	484									
7	11	553	167	285	356	408	456	495	531								
8	11	569	147	265	338	393	438	481	517	549							
9	7	610	166	280	354	412	460	500	537	569	594						
10	4	621	149	267	351	407	446	482	518	550	578	605					
11	1	691	151	301	390	461	505	532	571	611	638	656	673				
12	0																
13	0																
14	0																
15	1	736	172	309	382	445	500	527	554	582	609	627	650	668	682	695	727
Weighted mean			161	279	352	407	453	490	528	559	594	617	661	668	681	695	727
Growth increment			161	118	73	55	46	37	38	31	35	23	44	71	13	14	32

TABLE 3

MEAN BACK-CALCULATED TOTAL LENGTHS FOR 83 MALE *CAULOLATILUS MICROPS*

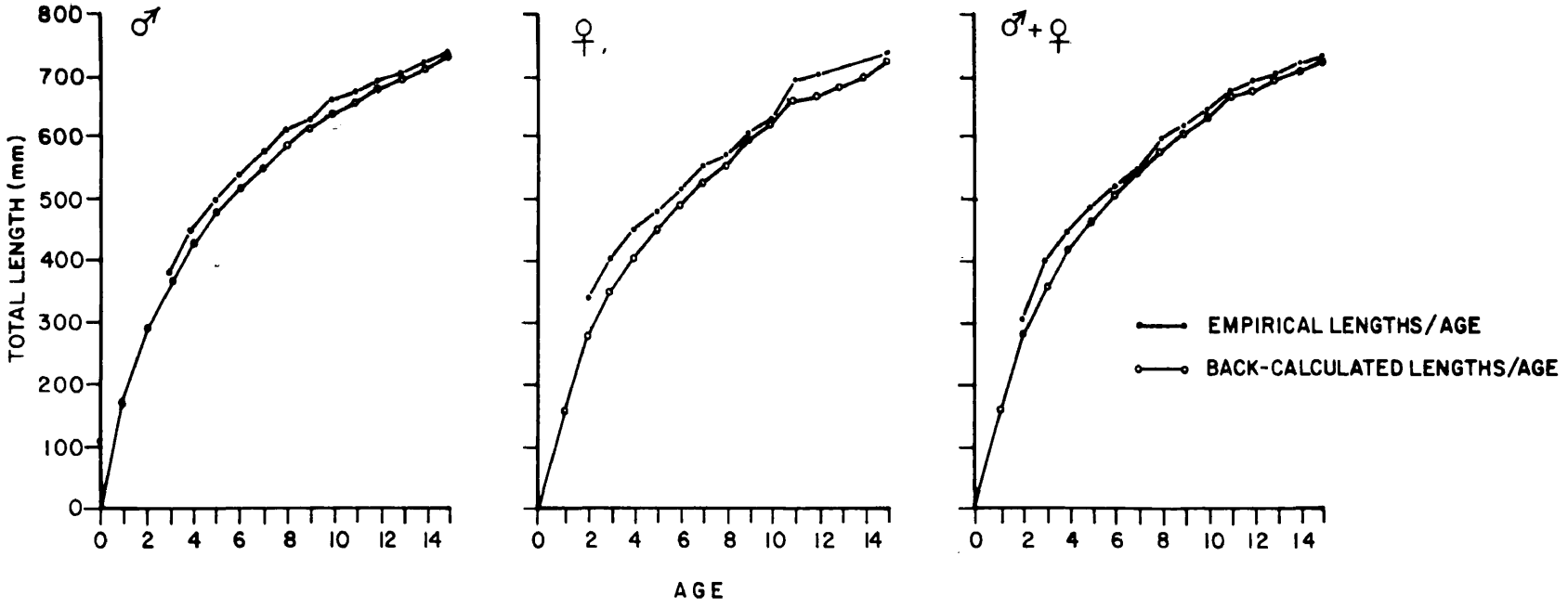
Age	Number of Specimens	Mean length at capture	Mean back-calculated lengths at successive annuli													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	0																
2	0																
3	1	382	150	282	349												
4	4	444	160	291	367	413											
5	15	495	168	288	362	419	470										
6	9	536	183	297	370	425	476	516									
7	7	571	165	290	367	432	481	516	549								
8	16	612	171	288	364	426	476	519	558	588							
9	4	625	173	289	357	425	475	516	555	586	613						
10	12	658	178	299	367	430	484	529	566	596	620	642					
11	3	672	202	320	389	455	490	526	557	590	611	633	656				
12	6	688	167	281	358	409	457	498	537	570	603	638	655	675			
13	2	698	156	276	376	447	497	533	569	599	621	643	662	683	698		
14	2	718	181	301	381	441	484	518	551	581	609	632	657	675	692	712	
15	2	728	136	242	316	279	434	487	527	563	598	622	649	674	695	712	727
Weighted mean			171	290	364	425	475	518	555	587	613	637	655	676	695	712	727
Growth increment			171	191	74	60	50	43	37	32	26	24	18	21	19	17	15

TABLE 4

MEAN BACK-CALCULATED TOTAL LENGTHS FOR 201 MALE AND FEMALE CAULOLATILUS MICROPS

Age	Number of Specimens	Mean length at capture	Mean back-calculated lengths of successive annuli														
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	0																
2	2	306	136	245													
3	5	402	161	278	360												
4	22	447	163	285	357	411											
5	44	487	164	283	358	414	463										
6	32	525	169	285	353	410	459	500									
7	19	548	166	285	358	415	463	501	536								
8	29	594	162	278	354	412	460	503	540	571							
9	13	619	166	279	355	416	464	507	544	577	605						
10	17	648	169	292	364	425	475	517	554	584	610	633					
11	4	677	189	315	389	456	494	527	561	595	618	639	661				
12	7	690	167	282	360	411	457	497	537	570	602	633	656	677			
13	2	698	156	276	376	447	497	533	569	597	621	643	662	683	698		
14	2	718	181	301	381	441	484	518	551	581	609	632	656	675	692	712	
15	3	731	148	264	338	401	456	500	536	569	602	623	649	672	691	706	727
Weighted mean			165	284	358	415	464	505	544	577	608	633	656	676	693	709	727
Growth increment			165	119	74	57	49	41	38	33	31	25	23	20	17	16	18

Figure 21. Graphs of mean back-calculated lenth at age versus mean empirical lengths at age for Caulolatilus microps females, males, and the sexes combined.


♂
♀
♂+♀
TOTAL LENGTH (mm)
800
700
600
500
400
300
200
100
0
0 2 4 6 8 10 12 14
AGE
EMPIRICAL LENGTHS/AGE
BACK-CALCULATED LENGTHS/AGE

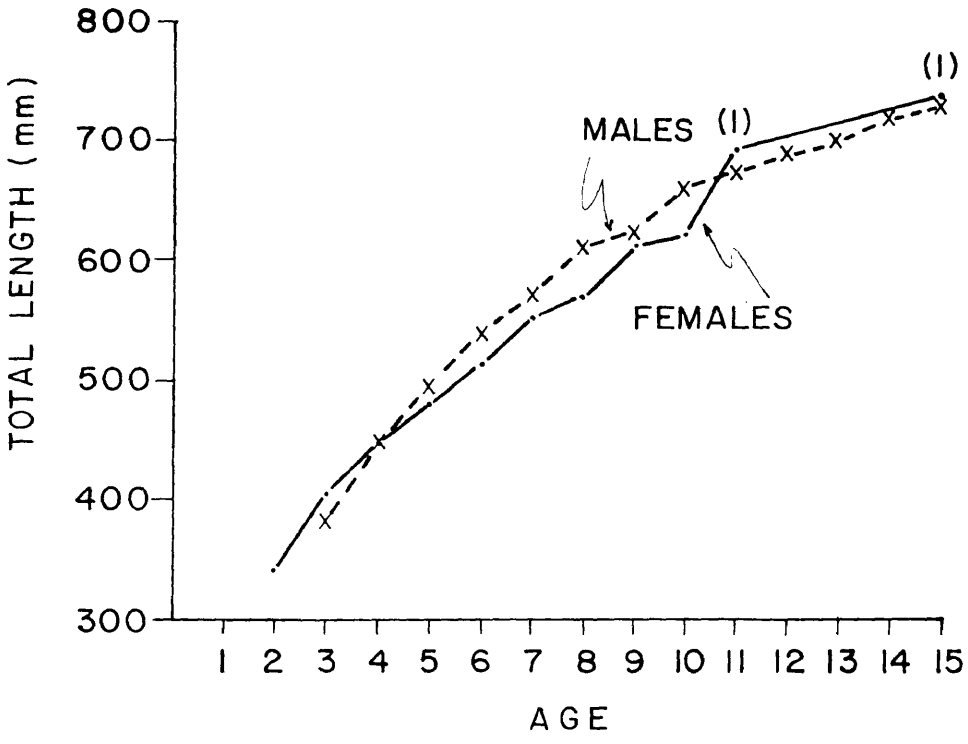
No age 1 gray tilefish were captured, but four museum specimens (165, 178, 184 and 202 mm TL) captured March 13, 1961 off North Carolina were examined. Total lengths of three of the four fell within the range of back-calculated lengths for age 1. The mean of the four (182.3 mm) was within one standard deviation (s = 21.6 mm) of the mean for the back-calculated lengths (sexes combined). Their date of capture was during the time of annulus formation thus strengthening the validity of the calculated lengths at age 1.

Empirical Lengths

Both sexes exhibited similar growth patterns: rapid growth during the first two years followed by gradually decreasing growth increments (Figure 22). Greater mean empirical length of males after age 4 result primarily from their faster growth rate between ages 3 and 6. The variation is attributable to earlier attainment of sexual maturity by females (age 4-5) and corresponding greater gonadal development. Males show appreciable gonadal development after age 5 though it is approximately 1/10 (by weight) less than females of comparable ages. The mean total length of males ($\bar{x}$ = 593.5 mm TL) exceeded that of females ($\bar{x}$ = 527.0 mm TL) captured off North and South Carolina. Hayashi (1976b, 1977) reported an analogous growth pattern for red tilefish in the East China Sea: consistently faster growth rate of males after age 1 due to attainment of sexual maturity by females at an earlier age.

Apparent differences in longevity between the sexes are suggested in my data but might be related to hook and line sampling bias. Males live at least fifteen years (n = 2, TL = 760, 696).

Figure 22. Mean empirical lengths at age for female versus male Caulolatilus microps.

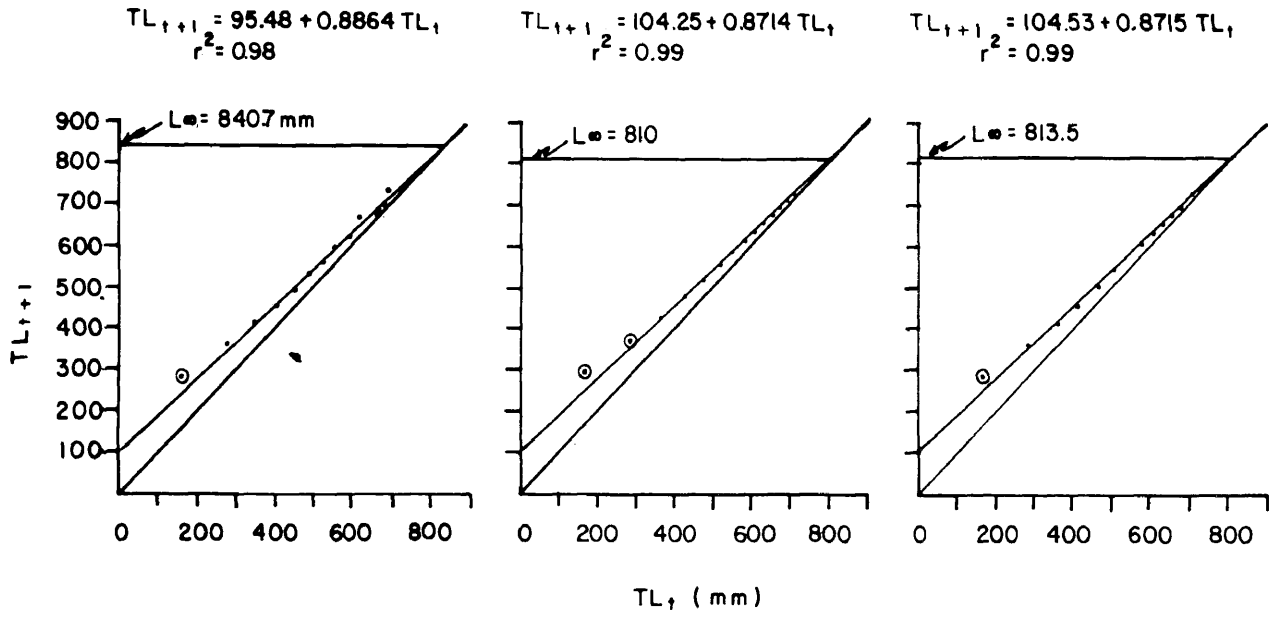

800
700
600
500
400
300
TOTAL LENGTH (mm)
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
AGE
MALES (1)
(1)
FEMALES

This could be an underestimation of longevity since at least three fish between 760 and 780 mm TL were captured by headboats off North Carolina and 32 fish over 700 mm TL were recorded from South Carolina. The oldest female from North Carolina collections was ten years old (TL = 670 mm) and no female over 700 mm TL was encountered. Female gray tilefish captured off South Carolina were larger (TL_{max} = 759 mm) and older (15 years) than those off North Carolina. Male C. chrysops ($TL_{\bar{x}}$ = 523 mm TL) were consistently larger than females ($TL_{\bar{x}}$ = 461 mm) (possibly attributable to sex reversal).

Theoretical Growth

Calculation of yield per recruit models is important in the evaluation of management strategies. Several integral parameters of these models can be determined by derivation of a theoretical growth curve such as that ascribed to von Bertalanffy (1938). This model describes growth of a fish in terms of a decreasing exponential function and provides a physiological basis for the mathematical representation of growth. The growth parameters obtained through computation are: L_∞, the asymptotic (mean maximum) length; K, the growth coefficient; and t_o, the hypothetical time at which a fish begins growth according to the growth curve (at rate K). Methods of Beverton and Holt (1957), as described by Ricker (1975), were employed to derive the growth curve parameters. The mean back-calculated lengths (97 females, 84 males and 201 male and female gray tilefish) were used (Tables 2-4). Functional regressions (Ricker, 1975) derived for Walford plots (Figure 23) provided initial estimates of k, the slope, and $L_\infty = \frac{\text{Y-axis intercept}}{1-k}$. The mean back-calculated

Figure 23. Walford growth transformations for Caulolatilus microps females, males and the sexes combined, with estimates of the asymptotic lengths.



⊙ excluded from regression calculation

lengths predicted for age 1 females, age 1 females and males (sexes combined), and age 1 and 2 males were not included in these calculations because of their position above (which tends to depress) the line established by the older age groups (Ricker, 1975). The resulting Walford estimates were:

	k	L_∞
Females	0.8864	840.7
Males	0.8714	810.7
Sexes combined	0.8715	813.5

The estimated asymtotic lengths for males and the sexes combined seem reasonable. The largest fish landed were 780 mm TL (n = 2). The higher estimate of L_∞ for females was attributable to the paucity of specimens aged in the larger size classes. If the mean back-calculated lengths for age 11-15 were deleted (n = 2), then the predicted value of L_∞ fell between 660 and 680 mm TL which was smaller than several females captured.

To estimate K and t_o, $\ln(L_\infty - L_t)$ was plotted against t (age) (Beverton and Holt, 1957) and predictive regressions were derived for the relationships (Figure 24). The lines have a slope equal to -K, and a Y-axis intercept equal to $\ln(L_\infty + Kt_o)$. The latter is then solved for t_o.

The von Bertalanffy theoretical growth equations are thus:

Males: $L_t = 810.7\ (1-e^{-0.139(t+1.19)})$

Females: $L_t = 840.7\ (1-e^{-0.119(t+1.31)})$

Sexes combined: $L_t = 813.5\ (1-e^{-0.137(t+1.03)})$

The calculated lengths for the theoretical models are compared with the empirical lengths in Figure 25 and with back-calculated and empirical

Figure 24. Graphs of $\ln(L_\infty - L_t)$ on age for Caulolatilus microps females, males and the sexes combined.

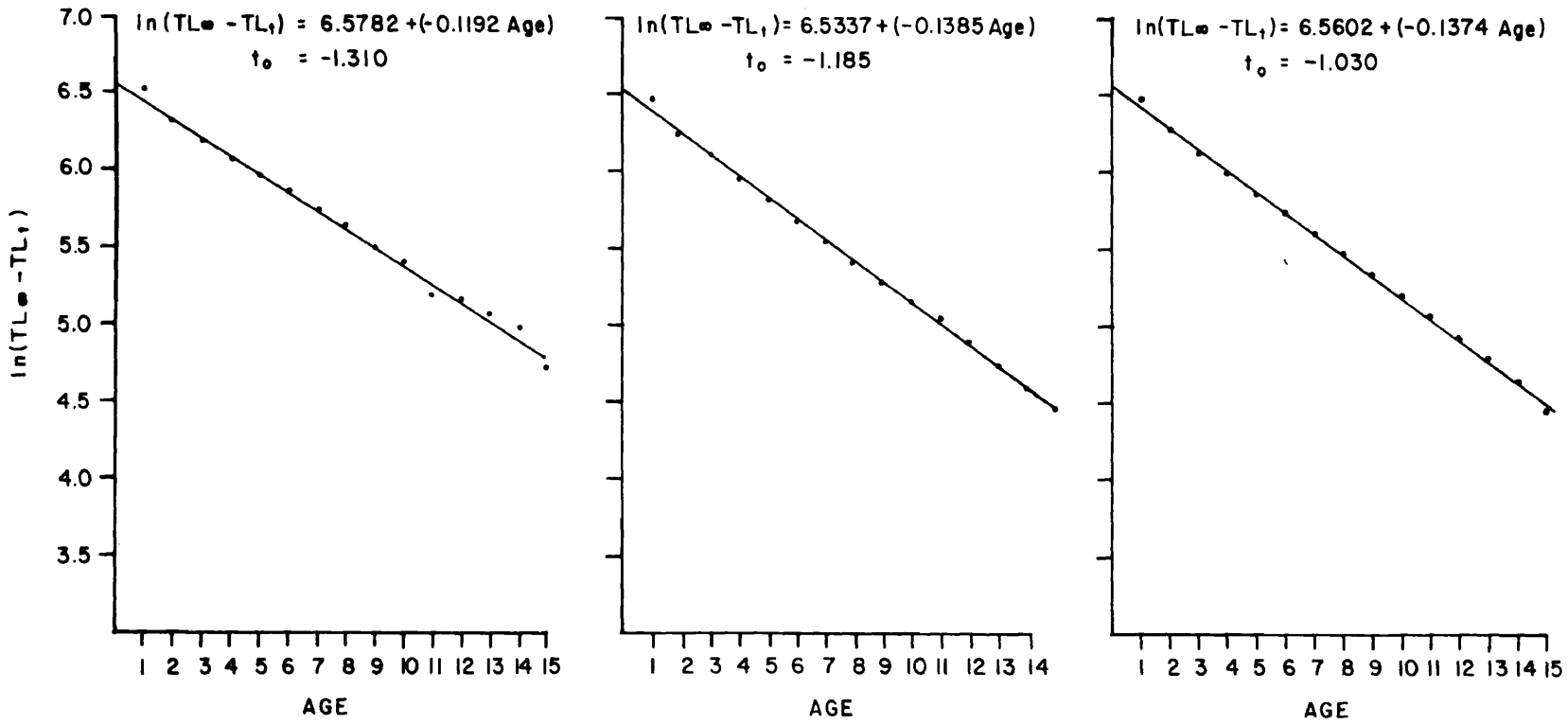

ln(TL∞ - TL$_t$) = 6.5782 + (-0.1192 Age)
t_0 = -1.310
ln(TL∞ - TL$_t$) = 6.5337 + (-0.1385 Age)
t_0 = -1.185
ln(TL∞ - TL$_t$) = 6.5602 + (-0.1374 Age)
t_0 = -1.030
ln(TL∞ - TL$_t$)
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
1 2 3 4 5 6 7 8 9 10 11 12 13 14
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
AGE
AGE
AGE

Figure 25. Graphs of theoretical lengths at age versus empirical lengths at age for Caulolatilus microps females, males and the sexes combined.

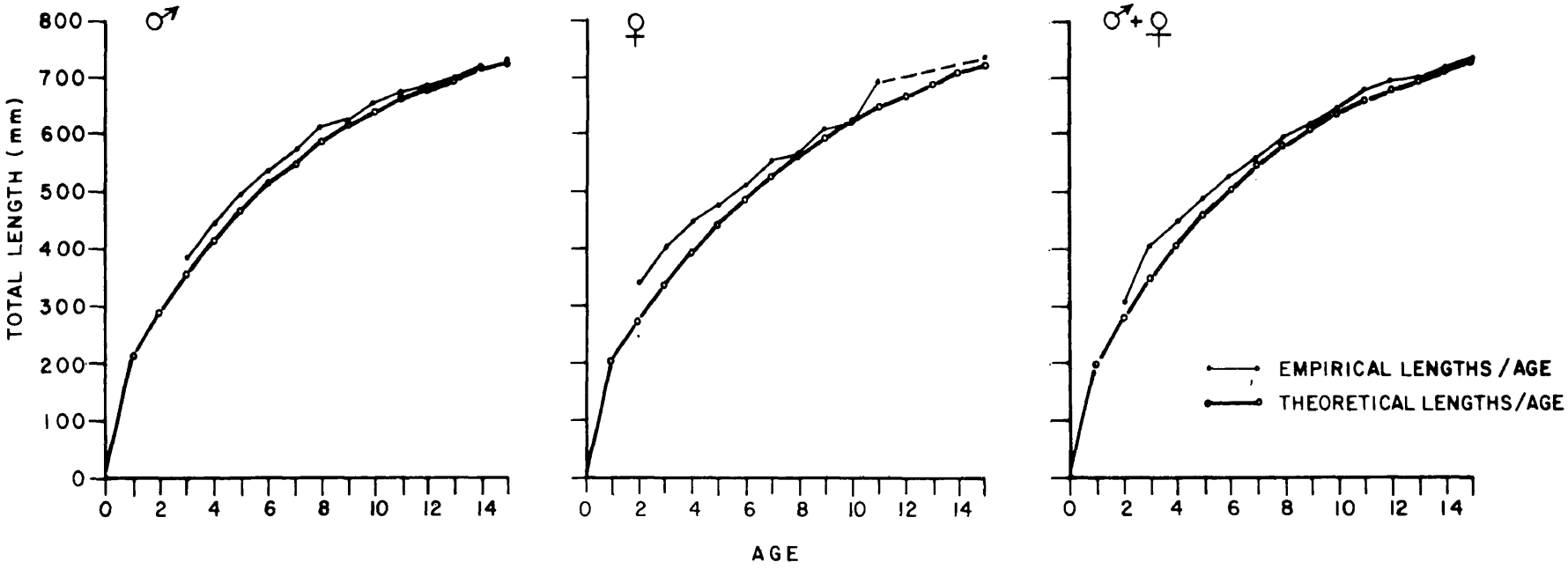

♂
♀
♂+♀
TOTAL LENGTH (mm)
800
700
600
500
400
300
200
100
0
0 2 4 6 8 10 12 14
AGE
EMPIRICAL LENGTHS / AGE
THEORETICAL LENGTHS/AGE

TABLE 5

COMPARISON OF THE MEAN EMPIRICAL TOTAL LENGTHS/AGE, MEAN BACK-CAULCULATED TOTAL LENGTH/AGE AND THEORETICAL TOTAL LENGTH/AGE FOR FEMALE AND MALE CAULOLATILUS MICROPS

	Females				Males			
Age	Number	Mean empirical length	Mean back-calculated length	Theoretical length	Number	Mean empirical length	Mean back-calculated length	Theoretical length
1			161	202			171	212
2	1	341	278	274			290	289
3	3	403	351	338	1	382	365	357
4	16	440	407	394	4	444	425	415
5	26	478	453	444	15	495	475	467
6	16	512	490	489	9	536	518	511
7	11	553	528	529	7	571	555	550
8	11	569	559	563	16	612	587	583
9	7	610	594	595	4	625	613	613
10	4	621	617	622	12	658	640	638
11	1	691	662	647	3	672	655	661
12			668	669	6	688	676	680
13			682	688	2	698	695	690
14			695	705	2	718	712	712
15	1	736	727	720	2	728	725	725

lengths in Table 5. The correlation between the different growth representations was close in both rate and magnitude.

Length and Weight Relationships

The relationship between body weight and total length for 601 gray tilefish is described by the functional regression:

$$\ln \text{Weight} = -12.286 + 3.142 \ln (\text{Total length})$$

$$r^2 = 0.96$$

Individual regressions (Figure 26) were derived for male and female gray tilefish captured off North Carolina:

Females: $\ln \text{Weight} = -11.495 + 3.024 \ln (\text{Total length})$

$$r^2 = 0.96$$

$$n = 120$$

Males: $\ln \text{Weight} = -10.948 + 3.297 \ln (\text{Total length})$

$$r^2 = 0.97$$

$$n = 113$$

An analysis of covariance (Snedecor and Cochran, 1967) detected no significant differences in residual variances ($P>0.50$) (Table 6) but did suggest significant differences between the regression coefficients ($P<0.01$). Under 600 mm TL the females exceed males in weight and over 600 mm TL males exceed females in weight/length. Length at maturity and gonad development in females probably causes the observed differences; mature ovaries ranged from 6 to 143 grams but mature testes only weighed 0.8 to 12.0 grams.

Individual length-weight relationships for North and South Carolina gray tilefish (Figure 26) are described by the functional regressions:

Figure 26. Weight-length relationships of Caulolatilus microps for: (1) females versus males (North Carolina only) and (2) North Carolina versus South Carolina (sexes combined).

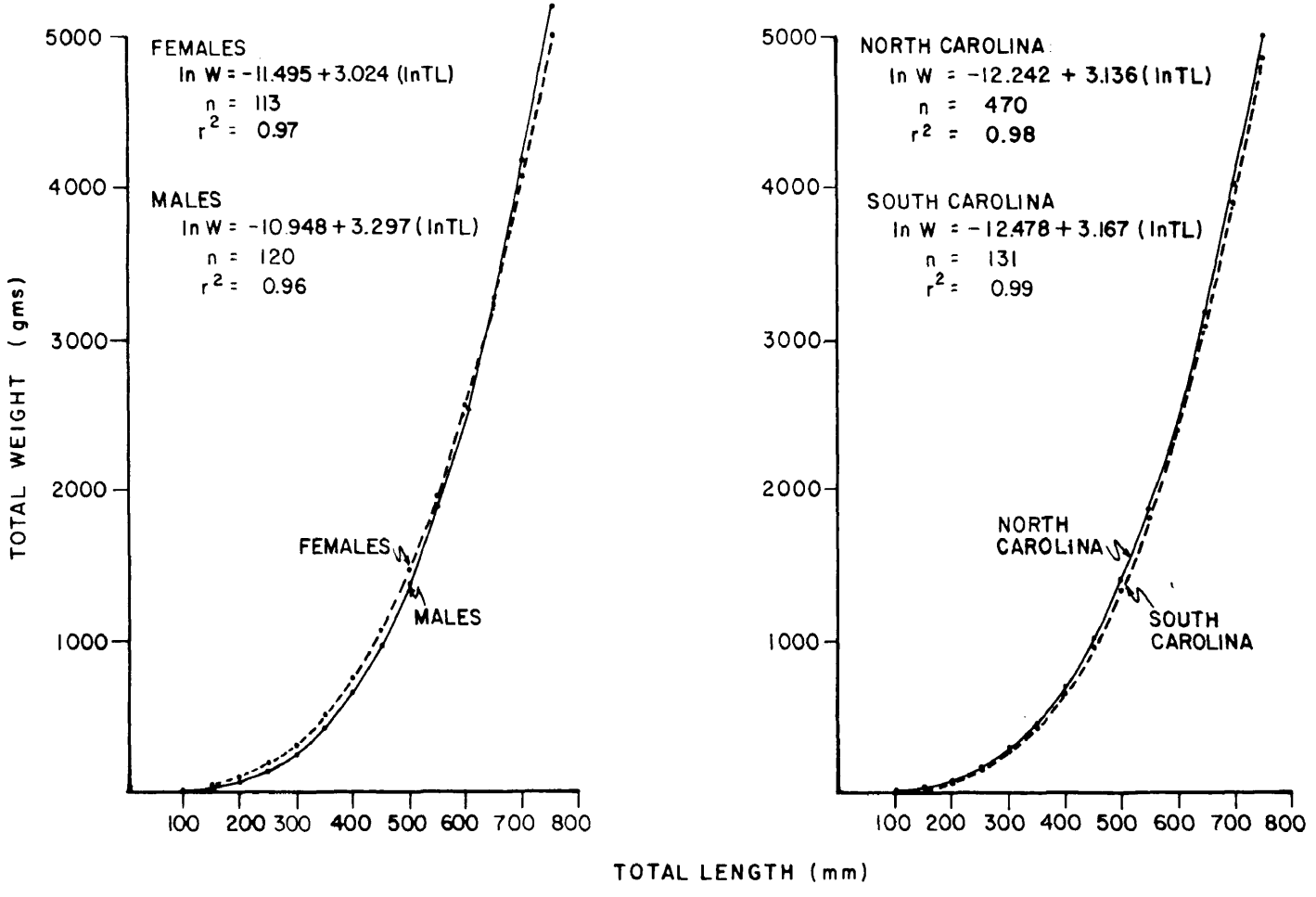

FEMALES
ln W = -11.495 + 3.024 (lnTL)
n = 113
r² = 0.97
MALES
ln W = -10.948 + 3.297 (lnTL)
n = 120
r² = 0.96
FEMALES
MALES
NORTH CAROLINA
ln W = -12.242 + 3.136 (lnTL)
n = 470
r² = 0.98
SOUTH CAROLINA
ln W = -12.478 + 3.167 (lnTL)
n = 131
r² = 0.99
NORTH CAROLINA
SOUTH CAROLINA
TOTAL WEIGHT (gms)
TOTAL LENGTH (mm)
1000
2000
3000
4000
5000
100 200 300 400 500 600 700 800

TABLE 6

ANALYSIS OF COVARIANCE FOR NORTH CAROLINA FEMALE AND MALE *CAULOLATILUS MICROPS*

WEIGHT-LENGTH RELATIONSHIPS

Source of Variation	df	Σx^2	Σxy	Σy^2	Regression Coefficient	Reduced SS	df	MS
Males	112	2.256	7.313	24.516	3.297	0.8083	111	0.00738
Females	119	2.439	7.2315	22.309	2.964	0.8733	118	0.00740
						1.6816	229	0.00734
Pooled, W	231	4.696	14.545	46.825		1.772	230	0.0077
					Difference between slopes =	0.0904	1	
Between B		0.882	2.747	8.105				
W+B	232	5.578	17.292	54.930		1.3220	231	0.00572
					Between adjusted means =	0.446	1	0.4459

Comparison of slopes: $F = 0.0904/0.00734 = 12.32$ (d.f. = 1,229) sig. $p<0.01$

N. Carolina: $\ln \text{Weight} = -12.242 + 3.136 \ln (\text{Total length})$

$r^2 = 0.98$

$n = 470$

S. Carolina: $\ln \text{Weight} = -12.478 + 3.167 \ln (\text{Total length})$

$r^2 = 0.99$

$n = 131$

Analysis of covariance (Table 7) revealed no significant differences in residual variances ($P>0.10$) or slopes ($P>0.50$). There were significant differences ($P<0.01$) in the elevations (adjusted means) of the regression lines which means that fish captured off North Carolina were significantly heavier than those of equivalent length captured off South Carolina.

The functional regression between standard length and total length (Figure 27) based on 95 gray tilefish captured off North Carolina in 1976 and 1977 was linear:

$$\text{Standard length} = -19.21 + 0.864 \text{ Total length}$$

$$r^2 = 0.99$$

Size and Age Composition

The length frequency distributions of gray tilefish for North Carolina ($n = 478$), South Carolina ($n = 174$) and the combined fisheries ($n = 652$) (including experimental fishing trips) (Figure 28) indicated that gray tilefish were generally not susceptible to capture by the hook and line fishery until they attain a size of 400 mm TL and they are fully recruited at total lengths of 500 to 525 mm. Only 4.6% of the total catch was under 400 mm TL while 23.8% were smaller than 500 mm. Through gear selectivity the recreational fishery

TABLE 7

ANALYSIS OF COVARIANCE OF NORTH AND SOUTH CAROLINA *CAULOLATILUS MICROPS*

WEIGHT-LENGTH RELATIONSHIPS (SEXES COMBINED)

Source of Variation	df	Σx^2	Σxy	Σy^2	Regression Coefficient	SS	df	Mean square
North Carolina	469	11.969	36.739	117.727	3.070	4.9492	468	0.0106
South Carolina	130	2.671	8.268	26.793	3.095	1.2017	129	0.0093
						6.1509	597	0.0103
Pooled, W	599	14.640	45.007	144.521		6.1523	598	0.0102
				Difference between the slopes		0.00139	1	0.00139
Between, B		1.348	3.637	10.024				
W+B	600	15.989	48.645	154.544		6.5454	599	0.0109
				Between adjusted means		0.3931	1	0.3931

Comparison of slopes: $F = 0.00139/0.0103$ 0.135 (d.f. = 1,597) N.S.

Comparison of elevations: $F = 0.3931/0.0102$ 38.54 (d.f. = 1,598) sig. $p<0.01$

Figure 27. Standard length-total length relationship for *Caulolatilus microps* from North Carolina (sexes combined).

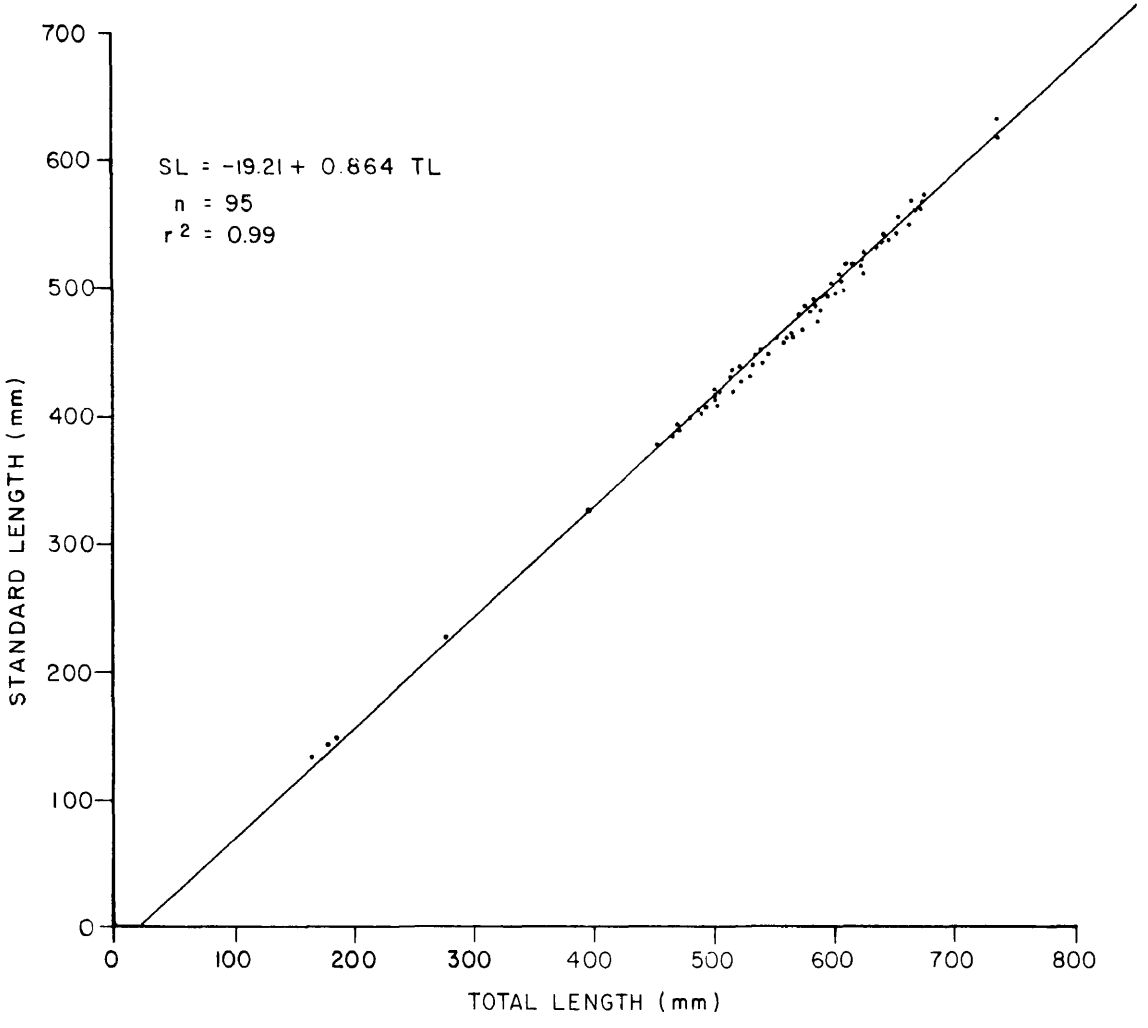
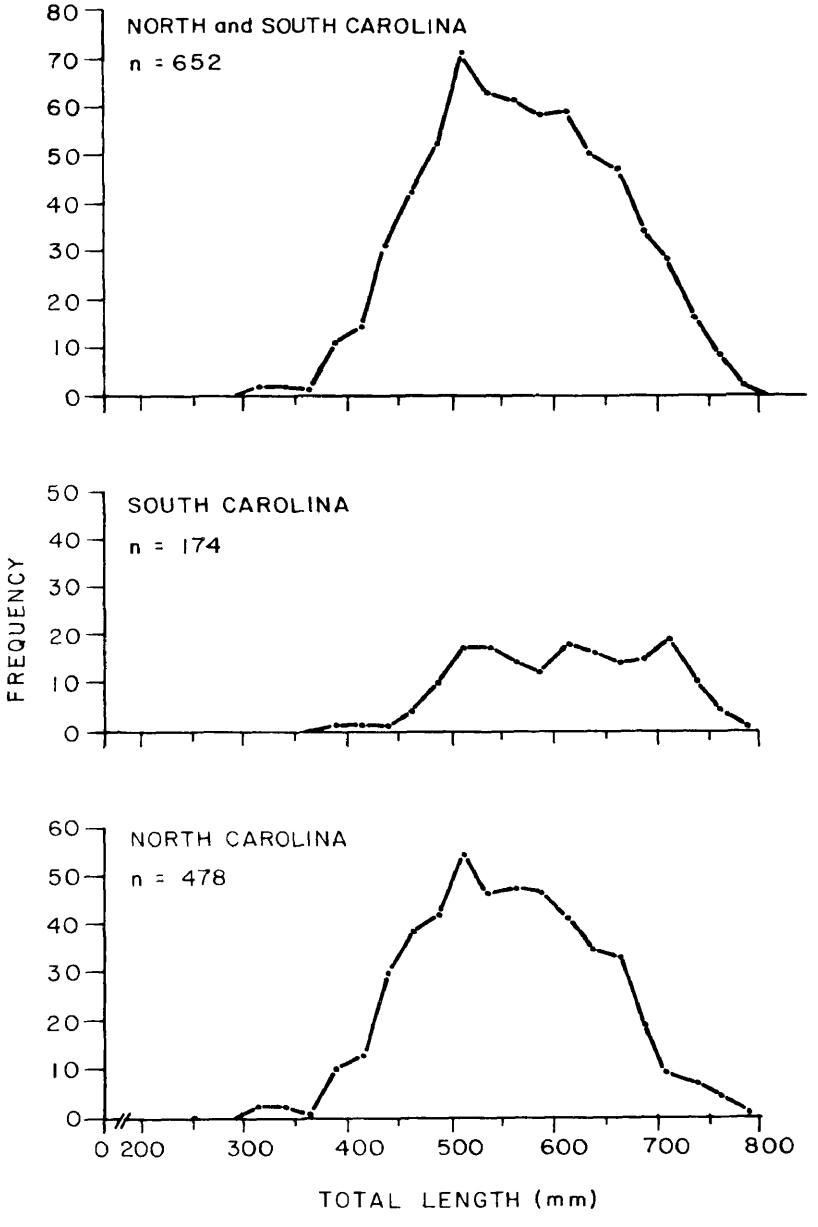

SL = -19.21 + 0.864 TL
n = 95
r 2 = 0.99
STANDARD LENGTH (mm)
TOTAL LENGTH (mm)
0
100
200
300
400
500
600
700
800

Figure 28. Length frequency distribution for North and South Carolina headboat and R/V Onslow Bay catches of Caulolatilus microps from 1972 to 1977.

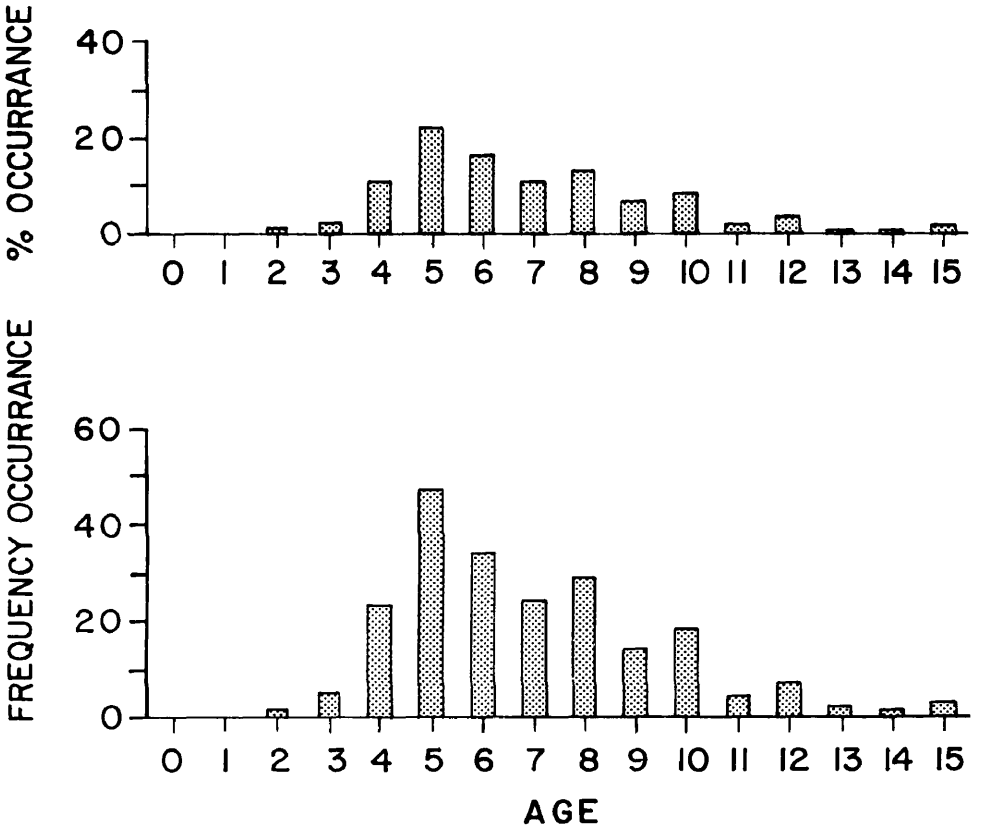

NORTH and SOUTH CAROLINA
n = 652
SOUTH CAROLINA
n = 174
NORTH CAROLINA
n = 478
FREQUENCY
TOTAL LENGTH (mm)
0 200 300 400 500 600 700 800

favors the survival of gray tilefish beyond sexual maturity. Females average 400-425 mm TL and males average approximately 500 mm TL at maturity.

Gray tilefish are recruited to the North and South Carolina recreational fisheries within the same size range (350-500 mm TL). However, disproportionally more large fish are captured off South Carolina. The mean total length ($\bar{x}$ = 609.3 mm) exceeded that of gray tilefish caught off North Carolina ($\bar{x}$ = 554.4 mm). Where as 31% of the gray tilefish recorded from North Carolina waters exceeded 600 mm and 4.4% were 700 mm TL or larger, 55.7% and 19.5% of the fish captured in South Carolina waters exceeded the same lengths, respectively. This anomaly could result from: (1) more favorable conditions (temperature, food availability) off South Carolina which enhance growth rate and/or longevity, or (2) greater fishing pressure off North Carolina.

The age composition of the gray tilefish catch indicates full recruitment by age 5 (empirical TL = 487 mm) (Figure 29). This age group comprised 22% of the catch. The weighted mean age at recruitment is 4.53 years based on a weighted probability appropriate to the ages captured up until and including the age of full recruitment (Huntsman pers. comm.). Recruitment ages of other species exploited by the recreational fishery are: red porgy, Pagrus pagrus, fully recruited by age 5, mean age of recruitment 4.1 to 4.3; vermilion snapper, Rhomboplites aurorubens, recruited between age 3.5 and 3.8; red snappers, Lutjanus sp., are recruited by age 6; Myctoperca and Epinephelus groupers recruited from 3.5 to 6.5 years old; (Huntsman, pers. comm.).

Figure 29. Age composition of North and South Carolina headboat and R/V Onslow Bay fishing catches of Caulolatilus microps.


% OCCURRANCE
40
20
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
FREQUENCY OCCURRANCE
60
40
20
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
AGE

Mortality

Mortality estimates are an essential component in the generation of yield per recruit models. Estimation of survival rates (S) can be derived from age frequency distributions by calculating the rate of decline of individuals from the descending leg of the catch curve (Ricker, 1975; Everhart et al., 1975) and mortality (A) is obtained as 1-S = A.

As a data base for survival estimates, the percent of each age group within 25 mm TL intervals was calculated from the length frequency distribution of fish aged (Figure 30). With these values, the age frequency distribution represented in the length frequency distribution of C. microps captured from 1972 to 1977 by recreational and exploratory fishing (Figure 28) was estimated. The result was an age frequency distribution and catch curve (Figure 31). This method reduced bias imposed by the limited sample of older fish and allowed an accurate representation of mortality based on the recreational fishery data set.

Methods of determining survival rates included those of Beverton and Holt (1957), Jackson and Heincke (as cited by Everhart et al., 1975), Robson and Chapman (1961) and incorporated both ages 5 and 6 as the age of full recruitment. Comparison of Robson and Chapman's "best estimate" with Heincke's estimate (Robson and Chapman, 1961) indicated a significant difference (χ^2 = 13.43 and 9.96) for both sets of data. This implies one or more of the assumptions in the models were not met: year class size or survival rates are not constant or all age groups are not equally vulnerable to the fishing

Figure 30. Length frequency distribution within individual age groups for 212 Caulolatilus microps.

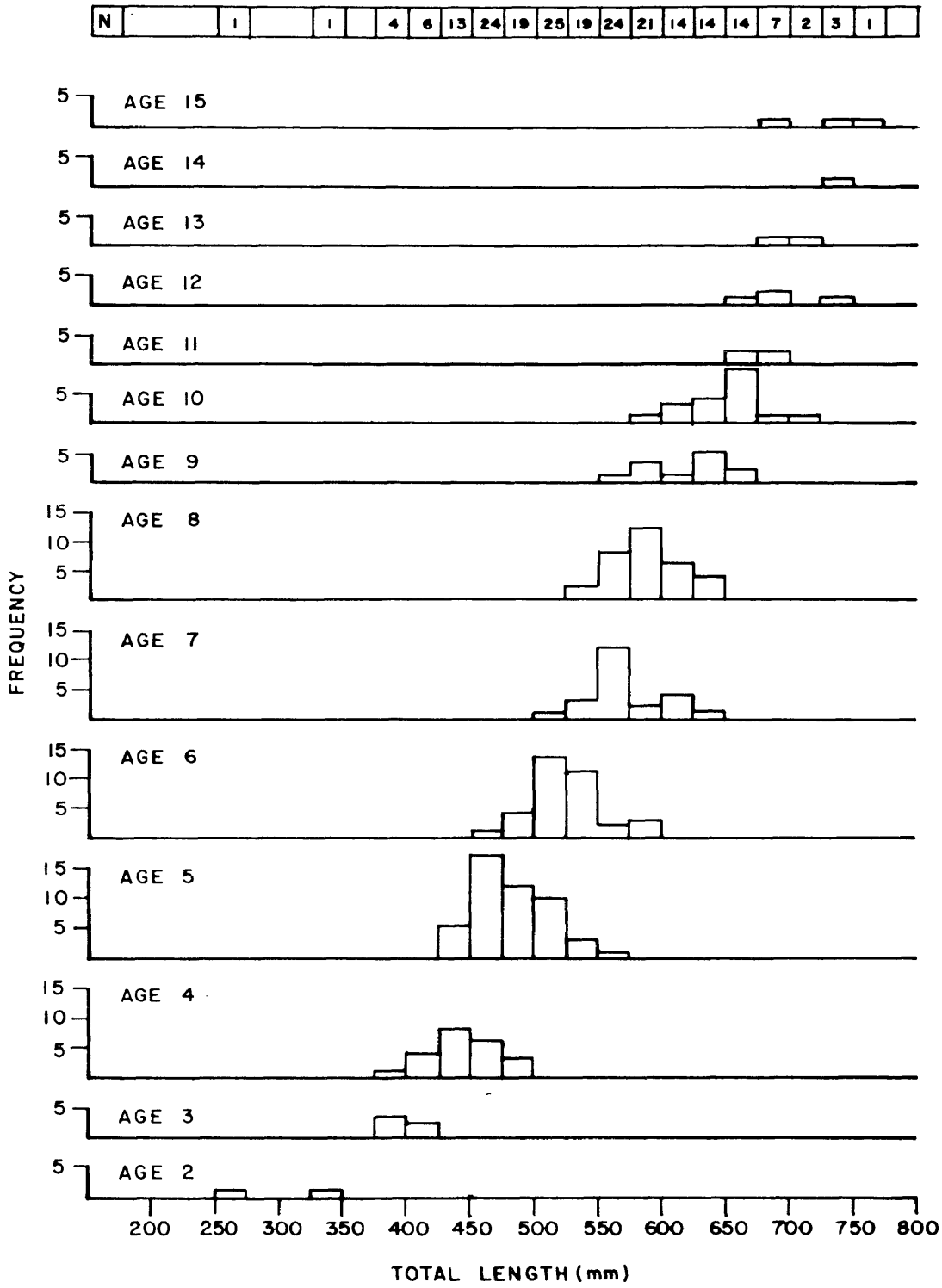
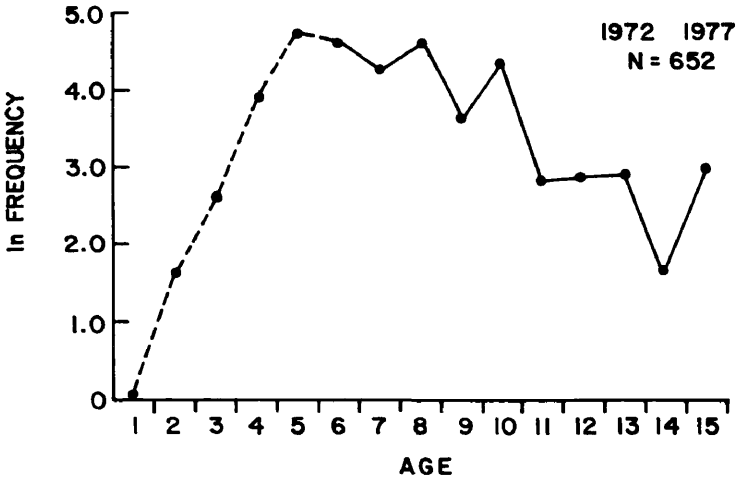
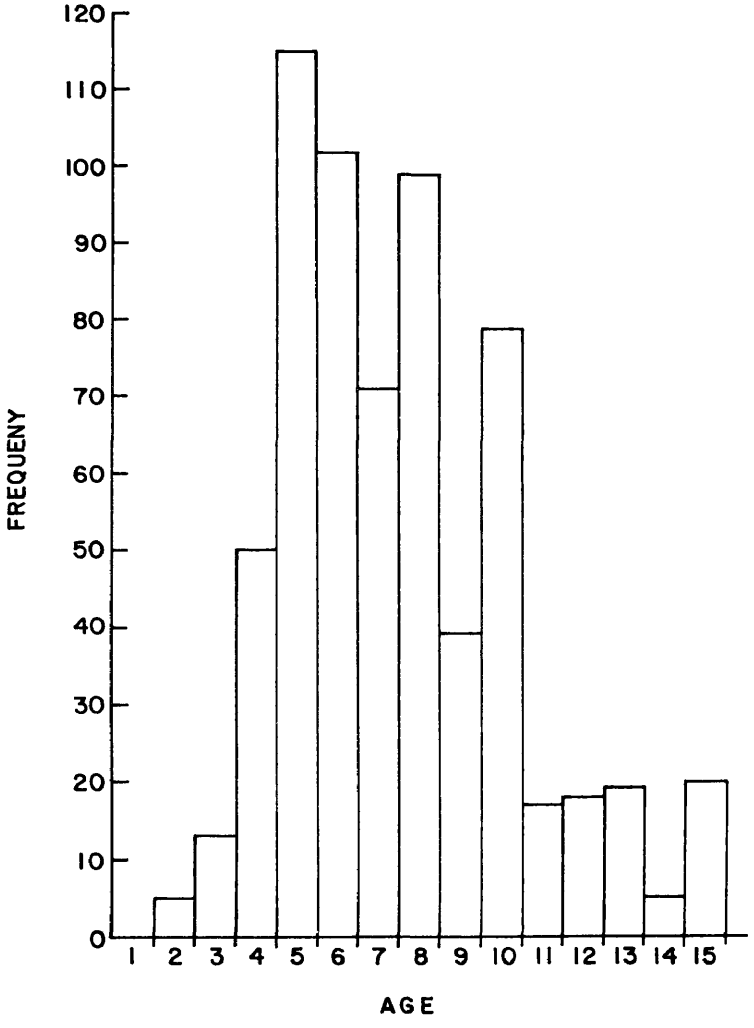

N
1
1
4
6
13
24
19
25
19
24
21
14
14
14
7
2
3
1
AGE 15
AGE 14
AGE 13
AGE 12
AGE 11
AGE 10
AGE 9
AGE 8
AGE 7
AGE 6
AGE 5
AGE 4
AGE 3
AGE 2
5
15
10
FREQUENCY
200
250
300
350
400
450
500
550
600
650
700
750
800
TOTAL LENGTH (mm)

Figure 31. Predicted age frequency distribution based on the length frequencies of Caulolatilus microps captured by the headboats and R/V Onslow Bay, 1972 to 1977.


1972 1977
N = 652
ln FREQUENCY
5.0
4.0
3.0
2.0
1.0
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
AGE


FREQUENY
120
110
100
90
80
70
60
50
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
AGE

gear (Robson and Chapman, 1961). Each of these possibilities is feasible in the case of C. microps. Further consideration excludes age 5 from mortality estimates.

The concurrance of the "best estimate" with the slope of the descending leg of the catch curve suggested 0.27 was the most reasonable estimate of total mortality (Z) (Table 8). Conceivably, this is a low mortality estimate if larger fish are increasingly vulnerable to the fishing gear. However, C. microps is a relatively slow growing, long lived species which after age 4 or 5 would probably not be subject to high natural predation. Fishing pressure on the shelf-edge community is light at present. There were less than 5000 gray tilefish captured off North and South Carolina during the 1975 season. Natural mortality probably accounts for most of total mortality in the expression Z=F+M, since fishing mortality (F) is relatively small. The predicted values of total instantaneous mortality (Z=0.32) is close to estimates of natural mortality for black sea bass, Centropristis striata (Mercer, 1978).

TABLE 8

TOTAL ANNUAL MORTALITY ESTIMATES FOR CAULOLATILUS MICROPS

(AGE 6 AND OLDER)

Method of Calculation	Formula	Total Annual Mortality (A)	Total Instantaneous Mortality (Z)
Jackson (Everhart et al., 1975)	$S = \frac{N_2+N_3+....Nr}{N_1+N_2+....Nr-1}$	0.18	0.20
Heincke (Everhart et al., 1975)	$S = \frac{\Sigma N-N_o}{\Sigma N}$	0.22	0.25
Robson & Chapman (1961)	$S = \frac{T}{\Sigma n+T+1}$	0.27	0.32
Beverton & Holt (1957)	A = slope of catch curve	0.27	0.32

where:

S = annual survival rate
A = 1-S = total annual mortality
$N_1, N_2, ...$ = number of fish in age groups 1,2....
N_o = number of fish in youngest age group
Nr = number of fish in oldest age group
ΣN = total number of fish in all age groups
$T = N_1 + 2N_2 + 3N_3... + rN_r$
$Z = -\log_e S$ = total instantaneous mortality rate

SUMMARY

Otoliths were proven to be valid structures for the aging of the gray tilefish considering:

1. the implicit early origin and constancy of the sagitta throughout the fish's life.

2. the linear relationship between growth of sagitta radius and total length.

3. the formation of an annulus at approximately the same time each year for all age groups sampled (lowest mean monthly marginal increments occurred between January and April).

4. the close correlation between empirical and back-calculated total lengths within age groups, the observed differences within the range of growth expected for that cohort during the year captured.

Annulus formation between January and April was correlated with innate physiological rhythms related to the onset of gonadal maturation and increasing photoperiod. Annuli were observed as narrow hyaline bands under incident (reflected) light. Fast growth zones were wider opaque (white) bands which decrease in width with age. Spawning zones were observed as multiple narrow hyaline bands which corresponded with attainment of sexual maturity and multiple spawnings.

The direct proportionality method of Lea (1910) was employed to derive the back-calculated lengths for earlier ages. This method was considered acceptable because: (1) gray tilefish maintained a general constancy in body contour throughout life and (2) growth rates of otolith radius and total length were isogonic.

Mean back-calculated lengths showed faster growth by males than by females. The differences in growth increments were particularly evident at ages 4 through 7.

Comparison of mean empirical total lengths of male and female gray tilefish revealed greater average lengths for males between the ages of 5 and 8 which corresponded to the increased energy demands of ovarian development. The mean empirical total length of males ($\bar{x}$ = 593.5 mm) exceeded that of females ($\bar{x}$ = 527.0 mm).

Both empirical and back-calculated total length data showed growth to be most rapid during the first year and decreasing in subsequent annual growth increments.

The von Bertalanffy (1938) theoretical growth curve was fitted to the mean back-calculated total lengths. The relationships are:

Both sexes: $L_t = 813.5\ (1-e^{-0.137(t+1.03)})$

Females: $L_t = 840.7\ (1-e^{-0.119(t+1.31)})$

Males: $L_t = 810.7\ (1-e^{-0.139(t+1.19)})$

There was a close agreement between the predicted total lengths from the theoretical growth models and the mean empirical lengths for the respective age groups.

Length and weight relationships of gray tilefish were expressed by functional regressions for: (1) sexes combined; (2) males and females (North Carolina only) and; (3) area of capture (sexes combined). Significant differences between the sexes ($P<0.01$) were attributed to differences in relative gonad weight. Gray tilefish from North Carolina waters were heavier than those of equal length captured off South Carolina ($P<0.01$).

Gray tilefish were first available to the recreational fishery at age 3 but the mean age of recruitment was 4.53 years. They were fully recruited by age 5; this age group comprised the greatest component of the catch (22%). Maximum longevity was at least 15 years for both males and females.

Gray tilefish above a total length of 400 mm are recruited into the recreational fishery. Full recruitment occurs for fish 500 to 525 mm TL. Size composition of the gray tilefish catch in North and South Carolina revealed nearly twice as many fish greater than 600 mm TL and four times as many fish greater than 700 mm TL captured off South Carolina.

Total annual mortality estimates were derived using a predicted age composition based on the length frequency distribution. The most reasonable estimate was 0.27 using age 6 as the age of full recruitment. A hook and line fishing selectivity could favor the capture of larger fish and thus cause annual mortality to be underestimated.

SECTION III: FOOD HABITS

INTRODUCTION

An analysis of feeding habits can provide insight into community relationships and species adaptability to different habitats. The feeding habits and preferences of the gray tilefish, Caulolatilus microps, are not well documented. Dooley (1974) suggested they are strict benthic predators by listing decapod crustaceans, echinoderms, molluscs, polychaetes, and ascideans as food items. He also reviewed the food organisms found in the digestive tracts of ocean whitefish, C. princeps, northern tilefish, Lopholatilus chameleonticeps, Branchiostegus wardii, and B. serratus. Fitch and Lavenberg (1971) briefly discussed the prey organisms in stomachs of C. princeps. Freeman and Turner (1977) gave a detailed review of tilefish food habits in their biological synopsis of L. chameleonticeps. Food studies of fish which co-occur with C. microps include the red porgy, Pagrus pagrus (Manooch, 1975) and the vermilion snapper, Rhomboplites aurorubens (Grimes, 1976).

This section provides a qualitative description of the foods consumed by gray tilefish off North and South Carolina.

METHODS AND MATERIALS

Collection of Specimens

Digestive tracts of gray tilefish were obtained primarily from experimental fishing trips aboard the R/V Onslow Bay (NMFS, Beaufort, N.C.) from 1973 through 1977. Ancillary specimens were acquired from port sampling collections of headboat catches from Cape Hatteras, N.C. to Charleston, S.C., and during an extended exploratory fishing trip aboard the R/V Eastward in May, 1975. All gray tilefish were captured by hook and line fishing in depths ranging from 40 to 130 fathoms. The alimentary tract was removed by severing anterior to the stomach and at the distal end of the intestines. These were stored in labelled jars with 10% formalin.

Analysis of Digestive Tract Contents

Intestinal and stomach contents were separated by taxon and measured volumentrically in graduated cylinders. Familial and specific identifications were facilitated with the aid of various texts including: fish: Randall (1968), Bohlke and Chaplin (1970), Walls (1975); invertebrates: Williams (1965), Gosner (1971), and Perez-Farfante (1977). Specific identifications of invertebrates were made by B. L. Wenner (decapods), D. Weston (molluscs, gastropods, echinoderms), G. Gaston (annelids).

The majority of the gray tilefish (>90%) regurgitated their stomach contents during capture due to the depths and speed of ascent. Consequently, most of the foods reported here came from intestinal contents and were often in advanced states of digestion. This imparts a bias in favor of less digestible food components such as exoskeletons, shells and other hard parts of organisms and inorganic materials. The emphasis of this discussion will primarily relate to the qualitative aspects of the gray tilefish's feeding habits.

RESULTS

The stomachs and intestines of 123 gray tilefish contained representatives of seven phyla (Table 9) with arthropods, echinoderms, molluscs, annelids and chordates dominating. A minimum of 34 invertebrate families and 8 species of fishes occurred. Major taxonomic groupings of prey and other items found in the intestines (n=82) and stomachs (n=10) of gray tilefish were quantified for relative frequency and volume (Table 10). The number of fish in which a specific food type was dominant was tabulated; the dominant food item was defined as that organism which comprised the largest total volume within an intestine or stomach sample.

Decapod crustaceans are the most prevalent organisms in the diet of C. microps; they occurred in 78.1% of the intestines and 60% of the stomachs. Eight families and at least 11 species of reptantian decapods were present in 59.8% of the intestines and comprised 21.6% of the total volume. They exceeded all equivalent taxa in both categories. The most important crabs were the portunids (especially P. spinicarpus), callapids and porcellanids (particularly Ranilia muricata). Crabs ranged in size from several young Anasimus latus (carapace widths and lengths <5 mm) to R. muricata (25 mm wide, 50 mm long carapace). Identified crabs were tropical or subtropical organisms whose distribution extends south from Cape Hatteras or Cape Lookout into the Caribbean or Gulf of Mexico (Williams, 1965).

TABLE 9

LIST OF ORGANISMS FOUND IN THE DIGESTIVE TRACTS OF *CAULOLATILUS MICROPS*

- Bryozoa
  - 2 unidentified pieces
- Mollusca
  - Gastropoda
    - Turridae
    - Notacidae
      - *Polinices* sp. (*P. lacteus* or *P. uberinus*)
  - Bivalvia
    - Pholididae
  - Cephalopoda
- Annelida
  - Polchaeta
    - Aphroditidae
    - Sigalionidae
      - *Leanira* sp.
    - Glycerida
    - Goniadidae
      - *Goniada teres*
    - Sabellariidae
    - Oenone
      - *Oenone fulgida*
    - Eunicidae
    - Arabellidae
      - *Drilonereis* sp.
- Sipuncula
- Arthropoda
  - Crustacea
    - Cirripedia
      - several unidentified shells
    - Malacostraca
      - Stomatopoda
        - *Squilla* sp.
    - Decapoda
      - Natantia
        - Panaeidae
          - *Solenocera mesopina*
          - *Solenocera* sp.
          - *Mesopenaeus tropicalis*
        - Caridea
          - Alepheidae
          - Pasiphaeidae
            - *Leptochelia bermudensis*
          - Processidae
            - *Processa* sp.

- Reptantia
  - Porcellanidae
    - *Ranilia muricata*
  - Calappidae
    - *Calappa angusta*
    - *Calappa* sp.
    - *Osachelia* sp.
  - Majidae
    - *Anasamus latus*
  - Parthenopidae
    - *Parthenope* sp.
  - Portunidae
    - *Portunus spincarpus*
    - *Portunus* sp.
  - Paguridae
    - *Pagurus* sp.
  - Albunidae
    - *Albunea* sp.
  - Iliacanthidae
    - *Iliacantha* sp.
  - Munidae
    - *Munida* sp.

Echinodermata

- Holothuroidea
  - *Pentamera pulcherina*
  - unidentified specimens
- Echinoidea
- Asteroidea
  - *Astrophyton muricatum*
  - *Astroporpa annulatus*
  - *Ophiophragmus pulcher*

Chordata

- Osteichthyes
  - Muraenidae
    - *Gymnothorax* sp.
  - Ophidioidei
    - *Rissola emarginata*
  - Synodontidae
    - *Synodus* sp.
  - Serranidae
    - *Centropristis* sp.
  - Bothidae
  - Scorpaenidae
  - Batracoidea
    - *Porichthys porosissius*

TABLE 10

RELATIVE FREQUENCY OF OCCURRENCE, VOLUME AND DOMINANCE OF ORGANISMS FOUND IN THE INTESTINES AND STOMACHS OF *CAULOLATILUS MICROPS*

Food Item	Intestines (n=82) Percent Frequency	Percent volume (ml)	Dominant food	Stomachs (n=10) Frequency	Percent volume	Dominant food
Invertebrates	96.3	92.5		100.0		
Annelida						
Polychaeta	31.7	3.9	5	20.0	2.2	
Sipuncula	12.2	5.6		20.0	1.2	
Mollusca	25.6	3.9	5	10.0		
Gastropoda	12.2	1.1	2			
Bivalvia	17.1	0.6	2	10.0	<.1	
Cephalopoda	3.7	2.2	1			
Arthropoda						
Crustacea	81.7	27.4	31	60.0	64.3	5
Cirripedia						
Stomatopoda	15.9	2.4	1			
Decapoda	78.1	25.0	30			
Natantia	41.5	3.4	7	60.0	60.4	4
Reptantian	59.8	21.6	23	20.0	3.9	1
Callapidae	9.8	1.8	4			
Portunidae	17.6	6.3	10			
Porcellainidae	11.0	5.1	4			

TABLE 10 (continued).

Food Item	Intestines (n=82) Percent Frequency		Percent volume (ml)		Dominant food	Stomachs (n=10) Frequency		Percent volume	Dominant food
Echinodermata	36.6		12.4		12	10.0			
Holothuroidea		13.4		3.8	4				
Echinoidea		23.2		4.5	7				
Asteroidea		17.1		2.3	1		10.0	<.1	
Urochordata									
Ascidiacea	20.7		14.2		10				
Vertebrata									
Fish	22.0		2.6		5		80.0	32.2	5
Miscellaneous	50.0		30.0		14	10.0			
Shell hash		43.9							
Coral rubble		22.0				10.0		.1	
Sand		29.3							

As a group they inhabit sand, coral sands, mud, coral or shell bottoms (Williams, 1965; Gosner, 1971).

Shrimp were the second most frequently occurring organisms in gray tilefish intestines (41.5%), but were relatively unimportant volumetrically (3.4%). The frequency of occurrence of shrimp in the stomachs (60%) was second only to fish and volumetrically shrimp exceeded all other taxa. This anomaly was due to the presence of extremely large quantities (6, 67, 112, and 133 ml) of Leptochelia bermudensis in four fish stomachs. These are small, semi-tropical shrimp (5 to 10 mm long) which undergo extensive diurnal migrations (Chace, Jr., 1972). They were probably engulfed from dense aggregations hovering above the bottom. The small volume of shrimp remaining in the intestines could be a result of rapid digestion.

Echinoderms were present in 36% of the intestines and represented 12.4% of the volume. Sea urchins were the most prevalent echinoderm (23%) and probably represent an even greater relative volume in the diet since I found only small broken shell fragments. Holothurians were usually found nearly intact. Brittle stars were also found in the intestines as test fragments: one specimen of Ophiophagamus pulcher represents the northern distributional record for the species (D. Weston, pers. comm.).

Polychaetes occurred in 31% of the intestines and were the dominant food item in five fish. Two species of Aphroditidae were identified; these are typically muddy bottom dwellers (Gosner, 1971). The most prevalent polychaetes were from the tubiculous families Eunicidae and Sabellaridae. Tubes of sand, shell rubble or mud with extended setae were generally all that remained.

Ascidians occurred in 20.7% of the intestines, comprised 14.2% of the volume, and were the dominant food item for 10 gray tilefish. They were present as transparent, gelatinous masses which were apparently more resistent to digestion than other non-skeletal body parts. These were probably colonial tunicates (Manooch, pers. comm.).

Molluscs were also a substantial component of the diet of gray tilefish; 12.2% of the intestines contained small gastropods and 17.1% contained small bivalves.

Shell hash, coral rubble and sand occurred in 50% of the intestines and comprised 30% of all observed matter. Its recurrence together with the sessile ascidians, polychaetes, bivalves and sipunculids is strong evidence of benthic browsing by gray tilefish.

Fish or fish parts (essentially spines, otoliths or vertebrae) were identifiable in only 22% of the intestines and accounted for 2.6% of the total volume. Fish were present in 80% of the stomachs and comprised 32% of the total volume of food items. The eight genera included three strict benthic types (Gymnothorax sp., Synodus sp., Bothus sp.). The remaining genera generally maintain close association with the substrate. The largest items found in the stomachs of gray tilefish were a cusk eel, Rissola sp. (220 mm TL, 82 ml), several moray eels and lizard fish (135 to 185 mm TL).

Partitioning the prey items of C. microps by fish size (100 mm total length increments) suggested shifts in food preferences (Table 11); essentially a selection for larger prey organisms by

TABLE 11

RELATIVE FREQUENCY OF OCCURRENCE AND DOMINANCE OF ORGANISMS FOUND IN INTESTINES AND STOMACHS OF *CAULOLATILUS MICROPS*, PARTITIONED BY 100 MM SIZE CLASSES (400 TO 800 MM TL)

Food Item	Percent Frequency	Dominance	Percent Frequency	Dominance	Percent Frequency	Dominance	Percent Frequency	Dominance
TL	400-500 mm		501-600 mm		601-700 mm		701-800 mm	
N	17		36		31		8	
Annelida								
Polychaeta	17.6		38.9	3	32.3	2	25.0	
Sipuncula	17.6		13.9		6.4		25.0	
Mollusca	35.2		27.7	2	19.4		12.5	
Gastropoda	17.6	1	16.7	2	12.9	1		
Bivalvia	23.5		11.1		6.4		12.5	
Cephalopoda	5.9				3.2			
Arthropoda								
Crustaceans	82.4	11	83.3	11	83.9	17	75.0	3
Cirripeda	5.9		2.8					
Stomatopoda			11.1		19.4	1	25.0	
Decapoda	76.4	7	83.3	11	67.7	17	75.0	3
Natantian	58.8	2	58.3	4	29.0	3	12.5	
Reptantian	58.8	5	41.7	7	48.4	9	75.0	3
Callapid	11.8	1	5.5	2	9.7	1	12.5	
Portunid	23.5	3	19.4	4	16.1	4	12.5	
Porcellainid			5.5		9.7	2	50.0	3

Table 11 (continued).

Food Item	Percent Frequency	Dominance	Percent Frequency	Dominance	Percent Frequency	Dominance	Percent Frequency	Dominance
Echinodermata	52.9	2	77.2	7	35.4	2	12.5	1
Holothuroidea	5.9	1	16.7	3	9.7		12.5	
Echinoidea	29.4		25.0	4	12.9	2	12.5	1
Asteroidea	23.5	1	16.7		12.9			
Unochordata								
Ascideacea	17.6	1	13.9	4	19.4			
Pices	17.6	2	27.7	2	32.3	4	37.5	3
Misc.	58.8	2	38.9	4	48.3	7	37.5	3
shell hash	47.1		33.3		35.5		37.5	
coral rubble	17.6		13.9		22.6		25.0	
sand	23.5		19.4		32.3		37.5	

larger gray tilefish. The importance of fish increased from 17.6% occurrence in 400 to 500 mm gray tilefish to 37.5% in the 700+ mm fish. Decapod crustaceans were the most persistent prey category through all size groups. The preference for larger prey by larger tilefish was shown by a decline in relative importance of shrimp with a concurrent increase in the larger crabs, notably Ranilia muricata. Molluscs and echinoderms decreased in relative importance in the diet of larger gray tilefish, while annelids, sipunculids, and ascidians remained consistent sources of nutrition.

DISCUSSION

The gray tilefish is an omnivorous, opportunistic predator which feeds on a heterogeneous mixture of organisms. This feeding strategy is exhibited by other high order predators comprising the shelf-edge community (Manooch, 1975; Grimes, 1976; Freeman and Turner, 1977) and coral reefs (Randall, 1967; Moe, 1969). Red porgies, P. pagrus, consume an equally heterogeneous mixture of organisms with decapod crustaceans the dominant prey. The diversity of prey in the diet of gray tilefish and red porgies probably reflects the localized faunal assemblages rather than a specific preference for certain food items (Manooch, 1975).

The omnivorous nature of the gray tilefish was proven by the presence of five or more phyla in 34.2% of the intestinal tracts. One individual (525 mm TL) consumed several portunid crabs, an unidentified crab, medium sized shrimp, barnacles, sea urchin, gastropods, several polychaetes, a sipunculid, a colonial tunicate, along with shell hash, sand and pebbles. Their opportunistic habit and disregard for a size or type of organism was exemplified by a 616 mm specimen whose stomach contained two lizard fish, Synodus sp., (135 and 140 mm TL) and 67 ml of Leptochelia bermudensis (<10 mm body length).

Dooley (1974) asserted that gray tilefish are strict benthic browsers. This is essentially correct but the occurrence of epibenthic prey noted in this study suggests facultive benthic

browsing. Gray tilefish maintain a close association with the substrate when feeding as evidenced by sessile benthos (ascidians, bivalves, tubiculous polychaetes and sipunculids) and slow moving or obligate benthos (predatory polychaetes, echinoderms, gastropods) consumed by all fish sizes examined. Even the fishes ingested by gray tilefish maintain close contact with the substrate (synodontids, muraenids, Porichthys sp., bothid). However, gray tilefish are able swimmers and feed epibenthically since prey items such as L. bermudensis, portunid crabs, Rissola emarginata, natantian decapods and the juvenile Centropristis sp. are not obligate benthic organisms.

Gray tilefish have morphological adaptations for active benthic browsing: terminal mouth and somewhat pointed snout which would facilitate the extraction of organisms from crevices and holes in the irregular substrate; and upper and lower jaws have single rows of moderately large canines around a medial patch of villiform teeth which would aid in the grabbing, tearing and/or scraping of sessile and benthic organisms from the substrate.

The omnivorous benthic browsing exhibited by C. microps is the pervarsive mode of feeding for branchiostegids. Golden-eyed tilefish, C. chrysops (340-545 mm TL, n = 8) exploit the same prey resources off North and South Carolina as do C. microps, including: shrimp, sea urchins, bivalves, polychaetes, with lesser amounts of brittle stars and holothurians; but the individual prey items are smaller. C. princeps inhabits rocky bottoms in the north eastern Pacific; B. wardi and B. serratus are known from the outer portions of the Australian coral reefs; L. chameleonticeps occurs over the mud bottoms of the outer continental shelf and upper slope regions

and at the heads of submarine canyons of the mid and northeast Atlantic. In all cases tilefish reportedly consume a heterogeneous mixture of macro-invertebrates with crustaceans as the principal component and fishes a secondary component (Fitch and Lavenberg, 1971; Dooley, 1974). The generalized feeding of gray tilefish and other branchiostegids thus facilitates their utilization of the diverse invertebrate assemblages associated with reef, high relief and rocky substrates. This feeding strategy reduces the energy expended by individual fish searching for specific food items in an area where individuals of any taxa may be limited and it enhances their adaptability to exploit regional faunal changes.

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VITA

Jeffrey L. Ross

Born in Forest Hills, New York, May 14, 1951. Graduated from W. Trespar Clarke High School, Westbury, New York, June, 1969. Received B.A. degree in Zoology from Ohio Wesleyan University, Deleware, Ohio, June, 1973.

In September of 1974, entered School of Marine Science, College of William and Mary as a graduate research assistant working toward a M.A. in Marine Fisheries Science.