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AN INVESTIGATION OF THE REPRODUCTIVE MODE OF THE PINFISH, *Lagodon rhomboides* Linnaeus (Osteichthys: Sparidae)

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ABSTRACT: The majority of sparids studied have shown evidence of hermaphroditism. The reproductive mode of the pinfish was investigated using museum and field collections of pinfish (n = 974) distributed in size from 13 to 276 mm SL. The observed female to male sex ratio of 1.3:1.0 was not significantly different from uniformity. Males were distributed in size from 63 to 252 mm SL ($\bar{x}$ = 127 mm); females were distributed from 57 to 276 mm ($\bar{x}$ = 119 mm). Individuals of undetermined sex occurred to 178 mm SL. Although the mean lengths of the sexes differed significantly, overlapping length-frequency distributions suggested gonochoristic development. Gonadosomatic indices (GSI) indicated spawning occurs between October and March in pinfish. Contrary to the predominance of hermaphroditism in sparids, histological investigation of the gonads of 106 specimens supported gonochorism as the reproductive mode in pinfish.

The diversity of reproductive "strategies" among sparids (Table 1) is unrivalled by any other perciform family with the possible exception of the serranids (Smith, 1975). Types of sparid reproductive modes include protandry, protogyny, non-functional hermaphroditism, and gonochorism. Evidence of simultaneous hermaphroditism is limited to a few isolated cases within populations (Waltz et al., 1982; Cody, 1989). Of 43 species examined to date, over 80% show evidence of sex change. Although the pinfish has been shown to be an important component species of estuarine fish communities of the eastern United States and the Gulf of Mexico (Stoner, 1980) information on its reproductive mode is sparse (Muncy, 1984).

Morphological descriptions of the sparid ovotestis indicate consistency in form (Kinoshita, 1936, 1939; D'Ancona, 1941, 1949a; Pasquali, 1941; Lissia-Frau 1966, 1968; Lissia-Frau and Casu, 1973; Mehl, 1973; Malo-Michelle, 1977; Coetzee, 1982; Waltz et al., 1982; Garratt, 1986). In general, testicular and ovarian portions are completely separated by connective tissue. This germinal configuration has been referred to by Sadovy and Shapiro (1987) as a "delimited" type. In protogynous individuals, testicular tissue becomes enlarged and envelops degenerating ovarian tissue which remains as a narrow strip on the medial surface of the gonad. Remnants of testicular tissue in protandrous individuals may be detected as longitudinal flaps positioned laterally on the ovary (D'Ancona, 1949a). The "delimited" type configuration of the sparid ovotestis has allowed sex-changers to be detected in many cases by gross visual inspection of the gonad rather than histological examination of gonadal structure (Penrith, 1972).

It has been established that most sparids are hermaphroditic and as such,

the failure to uncover evidence of hermaphroditism in a population should not be confused with the failure to accept hermaphroditism (or gonochorism) as a valid reproductive "strategy". Care should be taken with methodology so that if sex-changers are present in a population in low frequencies, they are likely to be detected. Caldwell (1957) believed that a size or sex-associated change in body shape may occur in pinfish but did not demonstrate such a relationship. Such a change in body shape may be associated with sex-change. Winstead (1977) examined the possible homology between cyst epithelial cells in pinfish testes and mammalian Sertoli cells. Although not alluded to in the study, isolated early stage oocyte-like cells were found in pinfish testes (Winstead, pers. comm.). Winstead's and Caldwell's observations in addition to the predominance of hermaphroditism as a reproductive mode in sparids were considered sufficient criteria to warrant examination of sex-change as a possible reproductive mode in pinfish. The hypothesis of hermaphroditism in the pinfish was tested using size distribution of the sexes and sex ratio data in addition to macrocscopic and histological examination of gonadal structure and maturation. The establishment of standardized criteria to detect hermaphroditism was also an objective of this study.

MATERIALS AND METHODS

Specimens were obtained from catalogued collections of the University of South Alabama, Mobile, Alabama; the Florida State Museum, University of Florida, Gainesville, Florida; University of West Florida Ichthyology Collection, Pensacola, Florida; and from uncataloged collections of the Department of Biological Sciences, Florida State University, Tallahassee, Florida. In addition, hook-and-line and beach seine specimens were collected from the Northwest coast of Florida. Larger pinfish were acquired from day-cruise headboats and longliners operating 17-25 km offshore from Panama City and Destin, Florida. These specimens were fixed in 10% Formalin for up to 72 hours and subsequently transferred to 40% Isopropanol for storage.

Standard length (SL) and body depth (BD) were measured to the nearest mm. Body weight was measured in grams and gonad weight was measured to the nearest mg. Sex was determined by gross inspection of the gonad. Gonads were classified according to the criteria of Orange (1961): stage 1S - gonads elongate and ribbonlike in appearance, sex, not discernible by gross inspection; stage 1 - elongate, sex recognizable by color and textural differences; stage 2 - slightly enlarged, ova not visible to the naked eye corresponding to an early maturation phase; stage 3 - late maturation phase, individual ova distinguishable; stage 4 - ripe ova loose from follicles; stage 5 - undergoing atresia, resorption evident.

Entire gonads were extracted from 537 individuals and stored in 40% isopropanol. Subsamples of the extracted gonads for each month were examined histologically. A base sample of 72 gonads consisting of three ovaries and three testes representing small (mean SL = 87 mm), medium (mean SL = 115 mm), and large (mean SL = 145 mm) individuals from each month was supplemented with additional tissue, comprised of 34 gonads from months preceding and following the peak spawning period. An estimate of spawning period was made from calculation of gonadal index (GSI), where GSI = (wet gonadal weight / wet body weight) X 10^2. Descriptive terminology for oogonial and spermatogonial development followed Hayashi (1972), Coetzee (1983),

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and Selman and Wallace (1986).

Transverse sections 6μm - 10μm were taken from anterior, medial, and posterior portions of the gonad. Entire gonads from 10 specimens were serially sectioned. In larger individuals where serial sectioning of the gonad was not practical, 5 mm - 7 mm cubes were removed and embedded for sectioning. Dehydration and infiltration followed criteria described by Humason (1972) for paraffin embedding. Sections were progressively stained in hematoxylin (gills formulation 2) and counterstained in eosin-y. Statistical analysis was performed using SAS (Helwig and Council, 1979).

RESULTS

A total of 974 specimens were distributed from 13 mm to 276 mm SL. Females comprised 31% (n = 304) and males 24% (n = 233) whereas immatures accounted for almost 45% (n = 437) of the total sample. Females and males were distributed from 57 mm to 276 mm and 63 mm to 252 mm SL respectively (Figure 1). Although the size distributions of the sexes overlapped considerably (with the exception of immature specimens), a one-way ANOVA revealed a significant difference in means ($F = 303.7$, df = 2, $p < 0.0001$). A Student-Newman-Keuls test grouped immatures, females and males separately ($\alpha = 0.05$). The mean SL of females was 119 mm compared to a mean SL of 127 mm for males. A female to male sex ratio of 1.3:1 was not significantly different from uniformity (Chi Sq. = 4.69, df = 1, NS).

A comparison of SL/BD ratios was made to look for sex-related "shape" differences. A one-way ANOVA also tested differences in the mean ratio of SL to BD between males, females, and immatures. Significant differences between the three "classes" were found ($F = 21.03$, df = 2, $p = 0.0001$). Although no significant difference was found between females (SL/BD = 2.44) and males (SL/BD = 2.47), immature specimens (SL BD = 2.37) were found to differ significantly from both males and females using a Student-Newman-Keuls test ($\alpha = 0.05$).

Poor fixation and preservation of some of the specimens made thorough analysis of gross gonadal morphology and development difficult. For this reason, descriptions of gonadal morphology and development were only briefly summarized. In appearance, the pinfish gonad was elongate and bilobed, positioned dorsal to the intestine, with each lobe attached anteriorly to the body wall. The lobes united posteriorly, anterior to the genital opening. In immature specimens, the gonad was thread-like. In developing females it was larger and thicker than in similar-sized males, in which the testes were thin and ribbon-like. Vascularization was also more evident in the ovary. Spent ovaries were sack-like and grey in preserved specimens. Immature (stage 1S) gonads were encountered up to a size of 178 mm SL in 44.9% of the sample. Most specimens attaining a size of 100 mm SL showed macroscopic evidence of gonadal maturation (stage 1). Females sampled from March to September generally had stage 1 and stage 2 gonads. Stage 3 gonads were present only in small numbers in females from late July through February. Individuals having stage 3 and stage 4 gonads were common in collections from October to March. Females with stage 4 gonads were collected from December through April, but were uncommon.

Gonadosomatic index (GSI) data were summarized for the sexes in Figure 2. Noticeable peaks in GSI occurred for both males and females in the months of February. Variance was relatively high for the months of October, December,

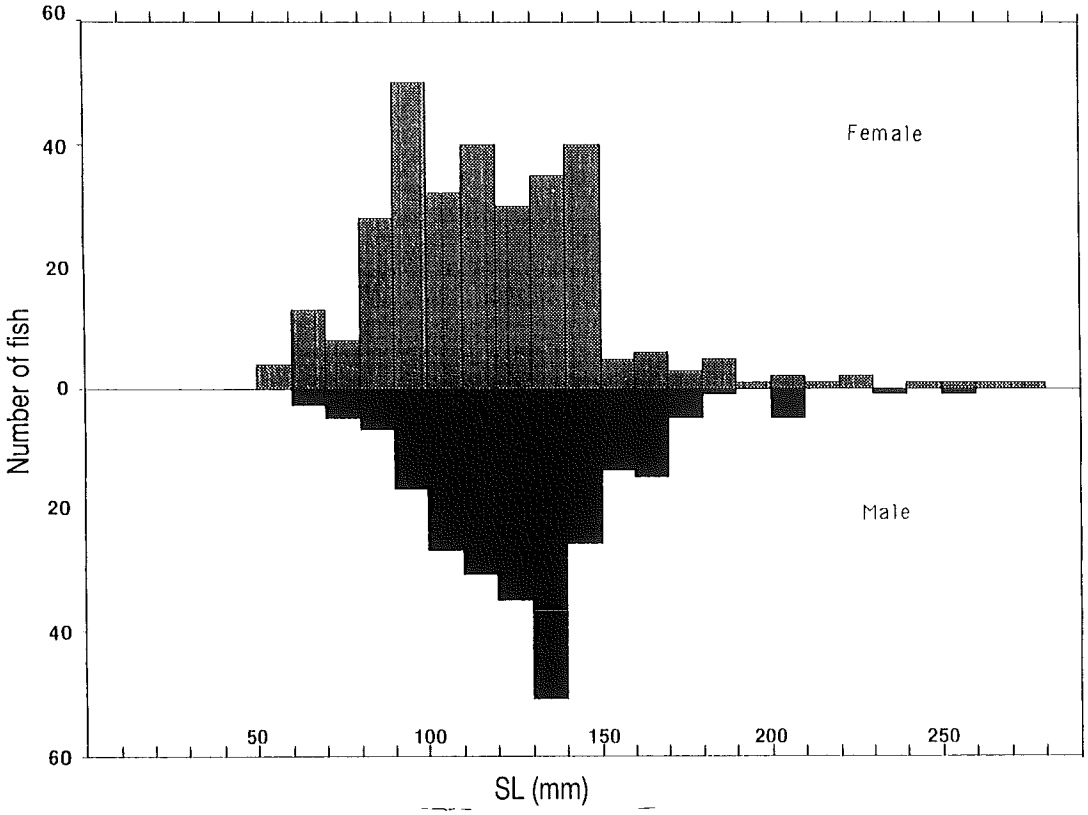


Figure 1. Length frequency distribution of male and female pinfish, measured as standard length (SL).

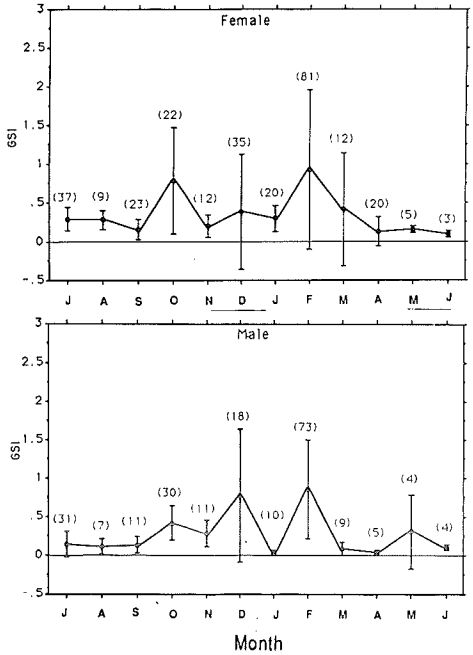
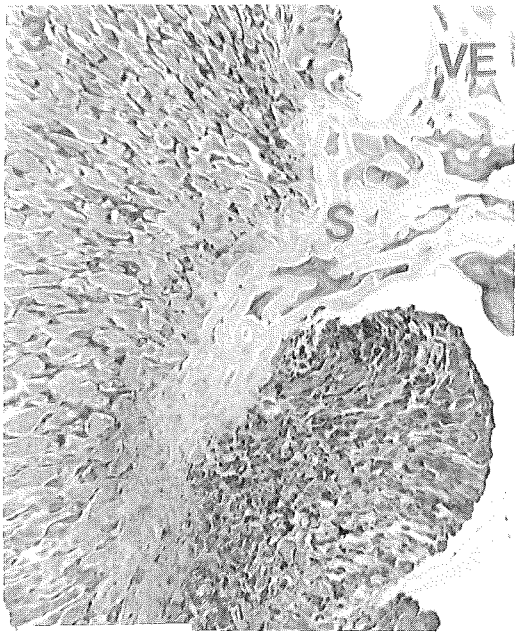
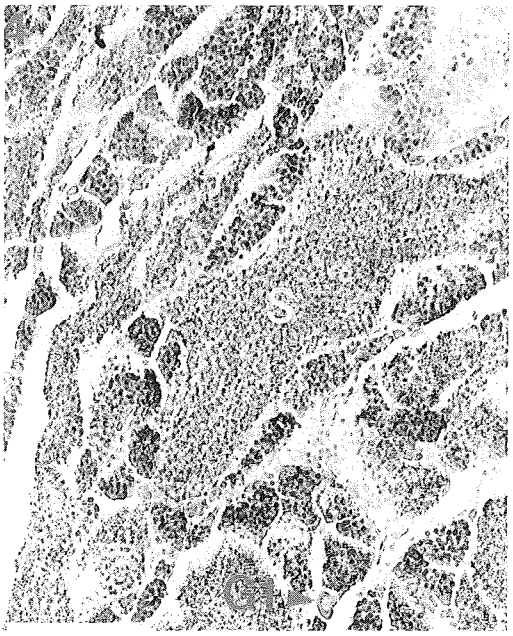


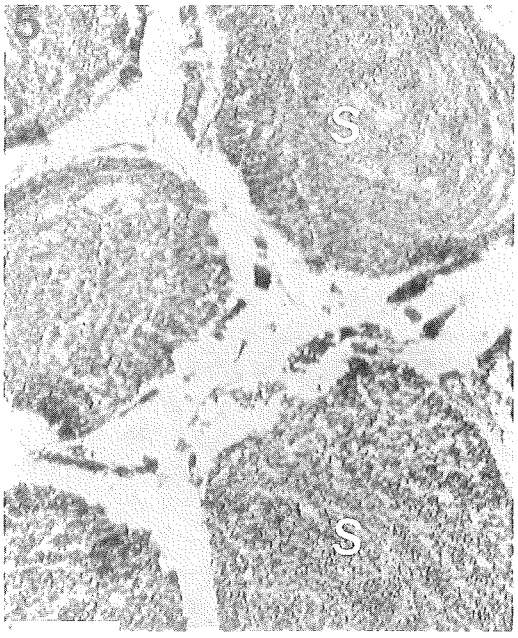
Figure 2. Monthly progression of pinfish ovarian and testicular condition based on mean gonadosomatic index (GSI). Error bars represent 1 standard deviation, number of specimens are shown in parenthesis.

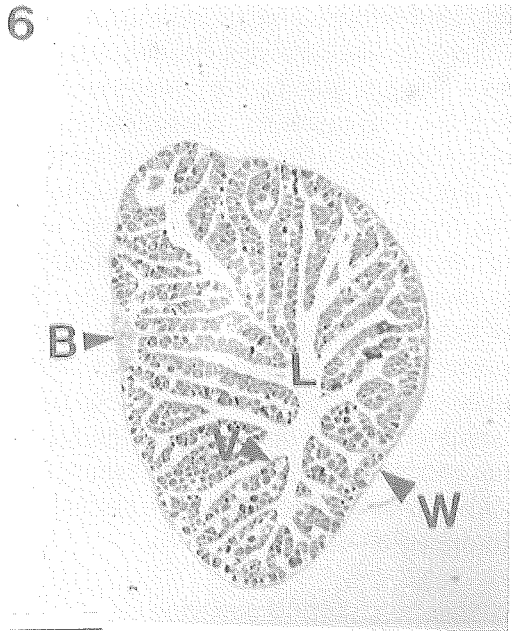
February and March in females while in males the months with the highest degree of variance were December, March, and May. Low variability in GSI values obtained for the months: April-September suggested spawning occurred from October through March in pinfish sampled.

Histological examination of pinfish gonads supported macroscopic descriptions and GSI results. The pinfish testis was comprised of a complex network of seminiferous tubules which emptied into vasa efferentia (Figure 3). Developing males from all months showed a limited degree of spermatogenesis (Figure 4). Ripe testis determined by gross examination displayed little spermatogenic activity; the crypts being either full of spematozoa, or partially evacuated (Figure 5). The pinfish ovary was found to consist of numerous ovigerous lamellae









Figures 3-6. 3. Lobular conformation of testis, showing seminiferous tubules leading to sperm duct via the vasa efferentia, scale = 1 mm. **4.** Cyst configuration of developing testis showing spermatozoa in lumina of tubules, scale = 0.05 mm. **5.** Reduction of spermatogenic activity in ripe testis, scale = 0.05 mm. **6.** Early phase oocytes in developing ovary, scale = 0.5 mm. B = blood vessel, G1 = gonial cell, L = ovarian cavity, V = ovigerous lamellae, S = spermatozoa, VE = vasa efferentia, W = ovarian wall.

projecting inward to the ovarian lumen from the tunica albuginea (Figure 6). The ovarian lumen continued posteriorly as the oviduct which was also recognizable in individuals determined to be immature by gross examination of the gonad. Developing ovaries contained mostly early phase oocytes in which the nucleoli lined the periphery of the nucleus (Figure 7). Primary yolk-vesicle oocytes were noticeably larger than perinuclear stage oocytes. There was, however, a wide range in cell diameter depending on the degree of yolk-vesicle formation (Figure 8). In early yolk-vesicle formation, two distinct bands of yolk-vesicles were visible; a circum-nuclear band of large vesicles and a row at the cell periphery. Secondary yolk-vesicle oocytes were characterized by a loss of the banding pattern found in primary yolk-vesicles and also by the thickening of the zona radiata (Figure 8). Tertiary yolk-vesicle oocytes were recognizable by the peripheral position of the nucleus, consolidation of secondary yolk globules, and a large lipid droplet replacing the migratory nucleus. The large central primary yolk was obscured. Secondary yolk-vesicle coalescence was clear (Figure 9). Although maturing oocytes were observed, histological sections were generally of poor quality. Of 52 ovaries examined, atretic oocytes were limited to ripe and maturing individuals (stage 4 and stage 5 ovaries) occurring from December through February (Figure 10).

DISCUSSION

Features of population structure such as sex ratios and size differences of males and females have been widely used to detect hermaphroditism in teleost fishes (Sadovy and Shapiro, 1987). Female and male pinfish differed significantly in mean size, but, their respective size distributions overlapped considerably with neither sex dominating the larger or smaller size classes. A slightly skewed sex ratio of 1.3 females to each male did not represent a significant departure from the hypothesized uniformity. Sex ratios as low as 2:1 have been encountered for hermaphroditic species (Penrith, 1972) and as high as 6:1 for gonochoristic species (Dooley, 1978). The unreliability of of sex ratios as indicators of hermaphroditism was shown by Erickson and Grossman (1986) for the gonochoristic Atlantic tilefish, *Lopholatilis chamaeleonticeps* despite the dominance of smaller size classes by females. Sex ratio may also vary considerably from year to year. Manooch (1976) found that ratio of female to male red porgies varied from 1.9:1 to 3.3:1 within a three year period for fish caught in North Carolina. Inaccurate sex ratio data from population samples may be produced as a result of segregation of the size classes and sexes due to respective habitat preferences. Larger pinfish inhabit deeper water (Hastings et al., 1976) and in colder months there is a general offshore migration as inferred from the absence of larger size classes from shallow water (Orth and Heck, 1980; Nelson, 1979; Stoner and Livingston, 1984). As pinfish sampled were collected by a variety of methods over a number of years, and from a variety of habitats the effects of size-related (and sex-related, if present) habitat preferences should have been reduced. The sex ratio may be closer to uniformity as immature ovaries were easier to recognize than immature testes.

It is possible that discrete morphological differences may arise in fish undergoing sex change (or fish that have already changed sex) due to physiological adjustments associated with gonadal (ovotesticular) development similar to changes which occur in some developing or maturing individuals of a gonochoristic species. It was

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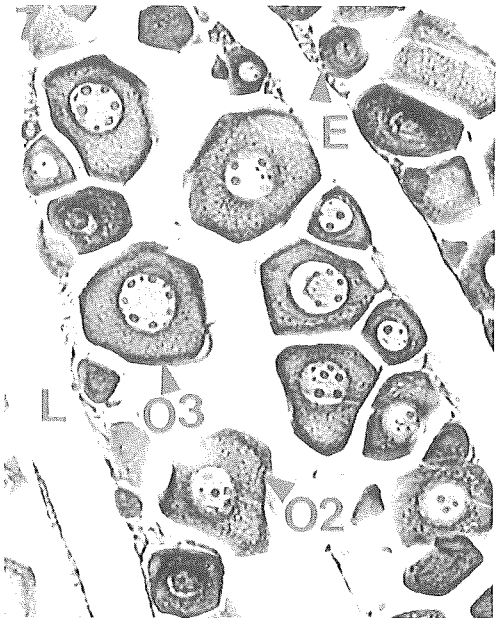

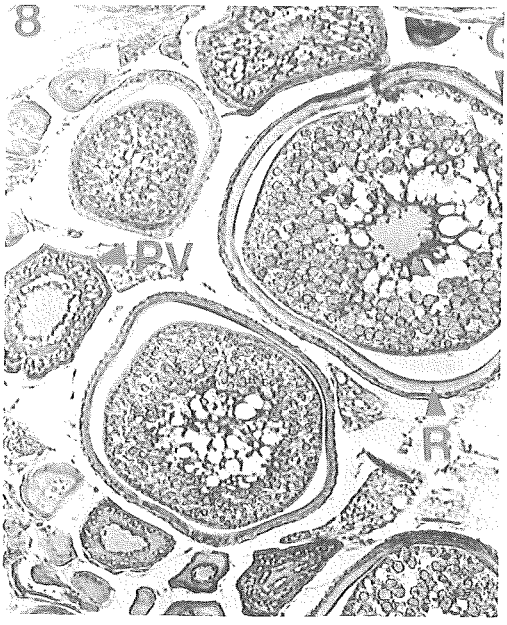

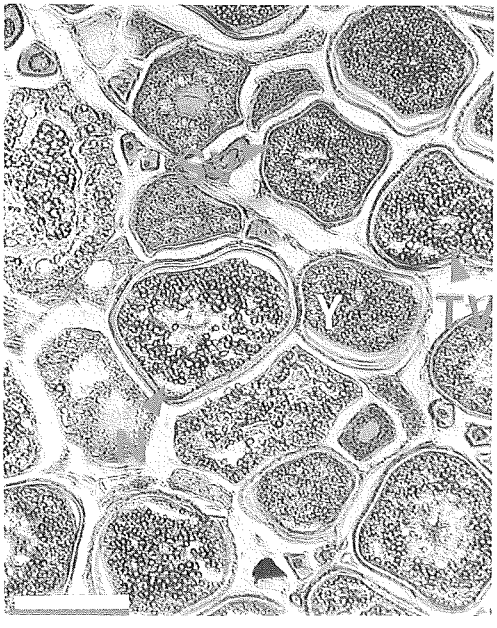

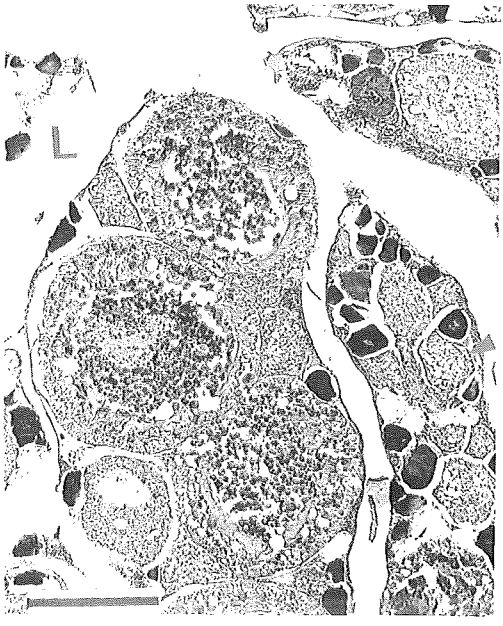

Figures 7-10. 7. Ovigerous lamellae of developing ovary, perinuclear oocytes with migrating nucleolus at periphery of nucleus, scale = 0.05 mm. **8.** Primary and secondary yolk vesicles (note double band of yolk globules in primary vesicle stage which is lost in secondary yolk vesicles), scale = 0.2 mm. **9.** Late maturation phase containing predominantly tertiary yolk vesicles (nucleus has migrated to periphery of cell, scale = 0.2 mm. **10.** Atretic oocytes (type-c) in ripe ovary, scale = 0.2 mm. L = ovarian lumen, E = germinal epithelium, G = zona granulosa, N = nucleus, O2 = secondary oocyte, O3 = late perinuclear oocyte, PV = primary yolk vesicle, R = zona radiata, SV = secondary yolk vesicle, TV = tertiary yolk vesicle, Y = secondary yolk globules,.

hypothesized here that individuals undergoing sex-change could account for suspected differences in pinfish shape. In general, teleost growth is allometric so SL/BD would not be expected to remain constant (Bookstein, et al. 1985). As SL/BD was significiantly smaller for immatures than males and/or females, this suggests that variation in pinfish shape is growth-related rather than sex-related. Measurement error must also be acknowledged as a potential influence. As a "ratio" was used to examine body shape, one may expect greater error among the smaller size classes. The mean size of the immature pinfish was 67 mm. We would have less confidence in results if smaller specimens were used to measure SL/BD. It is also possible that differences in "body shape" were not reflected in the the use of SL/BD. Results of a discriminant function analysis have shown that at least 14 morphometric variables were required before separation of the sexes was achieved with 95% confidence and no other class representing sex changers was detected (Cody, 1989).

GSI results supported the "suspected" winter-spawning of pinfish. A reduction in the number of larger pinfish observed in shallow waters during winter months (Nelson, 1979; Orth and Heck, 1980; Stoner and Livingston, 1984) has been attributed to prespawning migration and avoidance of temperature fluctuations associated with shallow water (Gunter, 1945; Joseph and Yerger, 1956; Moe and Martin, 1965; Hansen, 1970). Largest GSI values were found in October, December, February and March in females and December and February for males suggesting a protracted spawning period. However, as samples consisted of fish from a number of years and from a number of localities results may reflect year to year variation.

A major concern of this study was effective histological sampling. Care was taken to avoid "unnecessary" or redundant histology. The technique of using GSI data to identify the times of the year when sex change (if present) was most likely to occur we believe is sound. The months just prior to spawning, and directly after spawning (when the gonad undergoes the most amount of physical and physiological change) were more heavily sampled. Large cells resembling early stage oocytes were observed occasionally in testes but these may have been undifferentiated gonia.

In conclusion, pinfish gonadal structure was consistent with primary gonochorism being the dominant or expressed reproductive mode. It should be noted that this mode of reproduction represented an exception to the predominance of hermaphroditism within the family. Atz (1964) indicated that the sexual history of a single sparid had yet to be described adequately, and this is reflected in more recent conflicting evidence on sparid reproductive modes (Table 1). The lack of consistency in criteria used to determine the reproductive modes of species (added to confusion existing in sparid nomenclature) has made assessment of the diversity of sparid reproductive modes difficult. However, an increasing body of knowledge of reproductive strategies is becoming available so that interspecific comparisons may provide some explanation for the apparant preponderance of hermaphroditism relative to gonochorism in sparids. It will be interesting to see if future studies can relate differences in reproductive mode to ecology, behavior, and phylogeny.

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Table 1. Summary of sparid reproductive modes: + refers to conflicting evidence on reproductive mode, and * refers to incomplete or inconclusive evidence.

Species	Reprod. Mode	Reference
Acanthopagrus australis	Protandry	Pollock, 1985
Acanthopagrus bifasciatus	Gonochorism	Druzhenin, 1975
Acanthopagrus cuvieri	*Rudimentary*	*Hussain et al., 1981*
Archosargus probatocephalus	Rudimentary	Render & Wilson, In press
Boops boops	Protogyny +	Lissia-Frau, 1968
Boops salpa (Box salpa)	Protandry +	Lissia-Frau, 1966; Joubert, 1981
Boopsoidea inornata	Gonochorism	Penrith, 1972
Calamus leucosteus	Protogyny	Waltz et al., 1982
Calamus proridens	Protogyny*	Cody, 1989
Cheimerius nufar	Rudimentary	Coetzee, 1982
Chrysoblephus cristiceps	Protogyny	Robinson, 1976
Chrysoblephus gibbiceps	Gonochorism	Penrith, 1972
Chrysoblephus laticeps	Protogyny	Penrith, 1972
Chrysoblephus punicius	Protandry	Garratt, 1986
Chrysophrys major	Protogyny +	Huang et al., 1974
Dentex dentex	Gonochorism	D'Ancona, 1949b
Dentex gibbosus	Protandry	Bonnet, 1969
Diplodus annularis (Sargus annularis)	Protandry* +	D'Ancona, 1949a; Salekhova, 1961
Diplodus puntazzo (Puntazzo puntazzo)	Rudimentary +	D'Ancona, 1949b; Faranda et al., 1985
Diplodus vulgaris (Sargus vulgaris)	Rudimentary +	D'Ancona, 1949b
Lagodon rhomboides	Gonochorism	Cody, Present study
Lithognathus lithognathus	Rudimentary	Mehl, 1973
Oblada melanura	Rudimentary +	D'Ancona, 1949b
Pachymetopon grande	Gonochorism	Penrith, 1972
Pagellus acarne	Protandry*	Reinboth, 1962
Pagellus centrodontus	Functional	Williamson, 1911
Pagellus erythrinus	Protogyny	D'Ancona, 1949b
Pagellus mormyrus (Lithognathus mormyrus)	Protandry +	D'Ancona, 1949b
Pagrus auriga	Protogyny	Alekseev, 1982
Pagrus ehrenbergi	Protogyny	Alekseev, 1982
Pagrus orpheus	Protogyny	Alekseev, 1982
Petrus rupestris	Gonochorism	Penrith, 1972
Pterogymnus laniarius	Conochorism +	Penrith, 1972
Rhabdosargus globiceps	Gonochorism	Penrith, 1972
Sargus sargus (Diplodus sargus)	Protandry +	Reinboth, 1962
Sparus aries (Acanthopagrus aries)	Protandry*	Kinoshita, 1939
Sparus auratus (Chrysophrys aurata)	Protandry	Pasquali, 1941; D'Ancona, 1949b
Sparus caerulostictus	Protogyny	Bonnet, 1969
Sparus latus (Acanthopagrus latus)	Protandry*	Kinoshita, 1939
Sparus longispinis (Mylio macrocephalis)	Protandry*	Kinoshita, 1936; Okada, 1965 a,b,c,
Spondyliosoma cantharus (Cantharus cantharus)	Protogyny	Bonnet, 1969
Spondyliosoma emarginatum	Gonochorism	Penrith, 1972
Talus tumifrons	Protogyny	Aoyama, 1955

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