ONTOGENY OF THE SEXUALLY DIMORPHIC SONIC MUSCLE IN THREE SCIAENID SPECIES

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APPROVAL SHEET

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Abstract

The ontogeny of the swimbladder and sexually dimorphic sonic muscles were examined in three sciaenid species - croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*) and weakfish (*Cynoscion regalis*). In croaker, both sexes possessed the sonic muscles, but they grew larger and heavier in males than in females. Muscle development began at the same standard length in both sexes (45 mm S.L.) when the fish were approximately 4 to 5 months old and the gonads were starting to develope, but before the onset of gametogenesis. Spot sonic muscle occured only in males and first appeared at 105 mm S.L. at approximately 6 to 7 months of age, before maturation of the gonads. Weakfish sonic muscle was present in males only, and first appeared at 119 mm S.L. at approximately 11 months of age, concurrent with gonadal maturation. Sonic muscle development was synchronous with the growth of the gonads in all three species. Swimbladders grew larger in male croakers than in females, but there was no sexual difference in swimbladder size in spot or weakfish.

ONTOGENY OF THE SEXUALLY DIMORPHIC SONIC MUSCLE IN THREE SCIAENID SPECIES

Introduction

The family Sciaenidae is among the largest of sound producing fishes with some 150 species within 30 genera (Ono and Poss, 1981). Sound production in sciaenids occurs through contraction of extrinsic muscles lateral to the swimbladder which originate on the central tendon overlying the dorsal surface of the swimbladder and insert, via connective tissue, to the lateral wall of the body cavity (Tower, 1908). Contractions of the sonic muscles cause the swimbladder walls to vibrate, producing the characteristic sound (Tower, 1908). Differences in swimbladder shape may be responsible for the different frequencies of sound produced in various sciaenid species (Chao, 1978) although no experimental work has been done. Swimbladders range from a simple carrot shape (Leiostomus xanthurus) to a similar carrot shape with additional diverticula (Micropogonias undulatus) to the two-chambered swimbladders of Stellifer and Bairdiella (Chao, 1978).

Most species are sexually dimorphic with sonic muscle occuring only in males: weakfish (Cynoscion regalis) and related species (C. nebulosis and C. jamaicensis), silver perch (Bairdiella chrysoura), the ground drummer (B. ronchus), the star drum (Stellifer lanceolatus), and spot (Leiostomus xanthurus) (Fish and Mowbray, 1970). An exception is the croaker (Micropogonias undulatus) in which both males and females

possess the muscle. Tower (1908), however, observed a much thicker and heavier drumming muscle in the male, suggesting differences in sound production. Sciaenid species of the genera Menticirrhus and Lonchurus have greatly reduced or degenerate swimbladders and can produce no sound in this manner.

The sexual dimorphism of sonic muscle is not restricted to sciaenid fishes. Male haddock (Melanogrammus aeglefinus) have larger sonic muscles than females especially during the spawning season (Templeman and Hodder, 1956). Sexual dimorphism also occurs in the bladder muscles of some species of ophidioids and macrourids. Males of some oviparous ophidioids have drumming muscles while the females' muscles are vestigial or absent (Marshall, 1967). Males of Barathrodemus manatinus a deep-sea ophidioid, possess two pairs of muscles while the female has only one pair (Carter and Musick, 1985). Further, Fine (1975) demonstrated sexual dimorphism in the rates of growth of swimbladders in toadfish, with those of males growing faster than those of females. Sound production in toadfish has also been shown to vary sexually. Although both sexes possess the intrinsic swimbladder muscle, only males produce the courtship boatwhistle call (Gray and Winn, 1961). Males also are more prone to grunt throughout the year, though females do participate in this vocalization (Gray and Winn, 1961). Thus, the sonic muscle of these species, like those of the Sciaenidae, apparently play a role in reproductive behavior.

Sound production in sciaenids occurs most prevalently during reproductive periods (Dijkgraaf, 1947; Fish, 1954; Fish and Cummings,

1972; Takemura et al., 1977; Guest and Lasswell, 1978), although the sounds produced are not necessarily a direct part of reproduction. For instance, vocalizations are produced by males in response to the presence of conspecific males during pairing in Corvina nigra (Dijkgraaf, 1947), and are produced by male weakfish (Cynoscion regalis) when pursued or captured by experimenters (Fish, 1954). Thus, sounds may be generated in response to territorial aggression, avoidance, or stress. In other species, the production of sound appears to be part of courtship behavior. Male red drum (Sciaenops ocellata), for example, produce their most intense sounds just before spawning (Guest and Lasswell, 1978).

The histology and ultrastructure of the sonic muscle was investigated in weakfish (Cynoscion regalis) by Ono and Poss (1981). Swimbladder muscle fibers average 29.6 $\pm$ 5.3 um in diameter with myofibrils radially arranged around a core of densely packed mitochondria, glycogen, and sarcoplasmic reticulum. Most myofibrils have a consistent width with some bifurcating as they extend from the center to the periphery. Mitochondria occur both in the central cisternae of the muscle fiber and surrounding the myofibrils. Innervation occurs through an apparently variable number of segmental nerves associated with spinal nerves 3 or 4 to 9, 10, or 11 (Ono and Poss, 1981). Although the gross morphology of the swimbladder and sonic muscles of a number of sciaenids has been examined (Marshall, 1962; Chao, 1978; Ono and Poss, 1981;), no one has formally investigated the ontogeny of the sonic muscles. Many fish species go through a juvenile

phase in which they possess gonads that are not morphologically distinguishable as to sex. Since sonic muscles in most sciaenids are a secondary sex character present only in the males, it is an interesting question as to what stage of development these muscles differentiate in.

The purpose of this study are to examine and quantify growth of both the sonic muscles and swimbladder, to determine the size at which the sonic muscle becomes visually evident in three sciaenid species - croaker (Micropogonias undulatus), spot (Leiostomus xanthurus) and weakfish (Cynoscion regalis), and to correlate these data with state of gonadal differentiation. Additionally, the study attempts to determine whether the muscles of male croaker grow larger and heavier than those of females as suggested by Tower (1908).

Materials and Methods

Three species of sciaenids (Micropogonias undulatus, Leiostomus xanthurus, Cynoscion regalis) were collected in trawls from the York River and Chesapeake Bay and from off the coast of North Carolina. Specimens were preserved in 10%, neutral, buffered formalin and later measured for standard length (S.L.), weight, swimbladder weight, sonic muscle weight, and muscle length and width. Selected gonadal tissues were embedded in paraffin, sectioned at 7 um, and stained with hematoxylin and eosin in order to assess degree of maturation. Maturation of sectioned gonadal tissue was determined through reference to Overstreet (1983). Immature individuals were sexed macroscopically through differences in morphology of the gonad. Immature testes were cylindrical in shape and consistently thin along their length. Ovaries were thicker in diameter but truncated to a much shorter length.

Dissections of the swimbladder and observations on the presence or absence of the sonic muscle were performed macroscopically. Sonic muscle was first separated from the lateral wall using a blunt probe and scalpel and extracted along with the swimbladder from the body cavity. Muscle tissue was then separated from the central tendon overlying the swimbladder. Muscle and aponeurosis could be differentiated by coloration and texture. Swimbladders and sonic muscles were weighed to 0.1 mg with a Metler B5 balance and muscle length and width were measured to 0.1 mm with a ruler. Measurements of length and width were made on both sonic muscles, one of which lies on

either side of the swimbladder. Length was defined as the anterior - posterior axis. The length and width of both right and left sonic muscle and other data are presented in Appendices A through C.

The data were used to determine when swimbladder muscles first appear and to document the development of the muscle with respect to time. Regressions of sonic muscle weight and swimbladder weight against body weight were calculated as were regressions of sonic muscle weight against gonad weight, and body weight against standard length. Evaluation of differences between male and female croaker muscles was performed by analysis of covariance using a computer program written by Joseph L. Russo following statistical procedures outlined by J.H. Zar (1974). An analysis of covariance was also utilized to evaluate swimbladder weight differences between males and females of all three species. Analyses of regressions of spot and weakfish data were performed using the Statistical Package for Social Sciences (SPSS) program.

Results

In all three species the sonic muscle was first observed as a thin, clear mass attached to and projecting from the central tendon which overlies the dorsal surface of the swimbladder. As development of the muscle proceeded, the width of the muscle extended farther down the sides of the abdominal cavity until it met or approached the ventral surface of the body cavity. The muscle's length was established soon after the muscle initially appeared and extended along most (approximately 3/4) of the surface of the swimbladder. The ratio of muscle length to swimbladder length remained constant with continued growth of the fish. Croaker muscle extended along both sides of the abdominal wall from the swimbladder to the ventral surface where both halves of the muscle met and attached to the abdominal wall by connective tissue. The connective tissue was visible as a lateral white band on each half of the muscle upon dissection, having been severed as the ventral surface of the body cavity was opened. As the sonic muscle thickened with growth, color changed slightly from a transparent or cloudy white to a red or brown-red hue. Spot sonic muscle did not extend to the ventral midline of the body cavity as in croaker. Instead, the muscle reached down to only about 3/4 of the abdominal wall, and was much thinner than croaker muscle. Spot sonic muscle was transparent or cloudy white in small individuals to a very light red in larger specimens. Weakfish muscle, similar to spot sonic

muscle, extended ventrally to only about 3/4 of the surface of the abdominal wall. The two halves originated, as did spot and croaker muscle, on the dorsal surface of the swimbladder from a common aponeurosis. The sonic muscle of weakfish was thick, similar to croaker, and deep red in hue.

I did note a difference in sound producing capabilities between croaker, spot and weakfish. When captured, croaker actively vocalized and the abdominal cavity vibrated noticeably. Sounds produced were loud and continued throughout measurement and weighing. Spot, however, could not be heard vocalizing unless held close to the ear and vibrations of the abdominal cavity could be felt, but only slightly. The weaker sounds produced in spot are probably due to the smaller size of the sonic muscle as compared to croaker. In fish of comparable weights, spot muscle is much lighter than that of croaker. Weakfish also produced intense sound, as might be expected from the thickness of their muscle.

Croaker

Ninety-eight croaker, collected from the last of April through July, 1984, ranged in standard length (S.L.) from 43 to 190 mm. Sonic muscles were not observed in a male and female at standard lengths of 43 mm and 44 mm respectively. The smallest individuals with swimbladder muscles were a male and a female of 45 mm S.L. with sonic muscle weights of 0.4 mg and 1.3 mg respectively (Appendix A). The

muscles at this stage of development were extremely thin and too small to measure macroscopically, but were discernable from the aponeurosis primarily through differences in texture and color. The largest sonic muscles taken from a female were found in a fish of 188 mm S.L. and weighed 1.74 g. A larger female of 190 mm S.L. had a muscle weight considerably lighter at 1.61 g. The largest sonic muscles taken from a male weighed 2.11 g from a specimen of 184 mm S.L.

In the earliest stages of development of the swimbladder muscle (body weights up to 60 g) there was no significant difference in weight of muscle between males and females (Fig. 1; Table 1). (Comparative length measurements of all body weights given in text can be found in Fig. 3.) Regression lines were not significantly different ($F=2.6762$; $df=1,63$; $p=0.1068$). Equation of best fit line for females was: Muscle weight = -0.0419 + 0.0099(Body weight); and for males was: Muscle weight = -0.0531 + 0.0110(Body weight). As the body weight of the fish increased above 60 g, however, the sonic muscle of males grew at a faster rate and became larger and heavier than that of females (Fig. 2). An analysis of covariance was performed on body weights ranging from 50 to 105 g (Table 1). Regressions for males and females differed significantly ($F =9.8345$; $df=1,24$; $p=0.0044$). Thus, the size of male sonic muscle exceeded that of the female over body weights of from 50g to 105g. Regression lines for all data points (up to 168 g) were also significantly different ($F=53.3584$; $df=1,92$; $p=0.0001$). Equation of best fit line for females was: Muscle weight = -0.03563 + 0.0096(Body weight); and for males was: Muscle weight = -0.1074 + 0.0135(Body

weight) (Table 1). Differences in growth of the muscle with respect to sex can also be seen in larger specimens by comparing measurements of length and width (Appendix A).

Initiation of sonic muscle growth was concurrent with gonadal development (Fig. 4 and 5) and there was a significant correlation between gonad growth and sonic muscle growth in males and females (R^2= 0.934 in females; R^2= 0.785 in males). Muscle development began at 1.8 g in males and 1.9 g in females. At that same body weight, the gonads were just beginning to increase in weight. Thus, at weights below 1.8 or 1.9 g, muscle weights were not observed and gonad weights were near zero. At very nearly the same point at which the rate of gonad growth increased, sonic muscle development was initiated. The gonads continued maturing at a rate which was in synchrony with that of the sonic muscle.

Select gonadal tissue was sectioned and examined histologically to determine the presence or absence of gametogenesis. A male at 109 mm S.L. (Fig. 6-1) and a female at 93 mm S.L. (Fig. 7-1) were both found to be immature - gametogenesis was not yet occuring. At the opposite extreme, a male of 182 mm S.L. was observed to be undergoing active spermatogenesis with all stages of spermatazoa present (Fig. 6-2). A female of 188 mm S.L. was just undergoing development of oocytes (Fig. 7-2). Although sonic muscle developes along with gonadal development, the muscles differentiate long before sexual maturity.

Swimbladder weights were also tested by analysis of covariance (Fig. 8; Table 1.) to determine if differences existed between males

and females. Regression lines were significantly different ($F=11.7285$; $df=1,91$; $p=0.0009$). Equation of best fit line for females was: Swimbladder weight = -0.0149 + 0.0129(Body weight); and for males was: Swimbladder weight = -0.0676 + 0.0152(Body weight). Male swimbladders grew to a heavier size than those of females.

FIGURE 1. Regression of sonic muscle weight against body weight for male and female croaker of body weights less than 60 g.

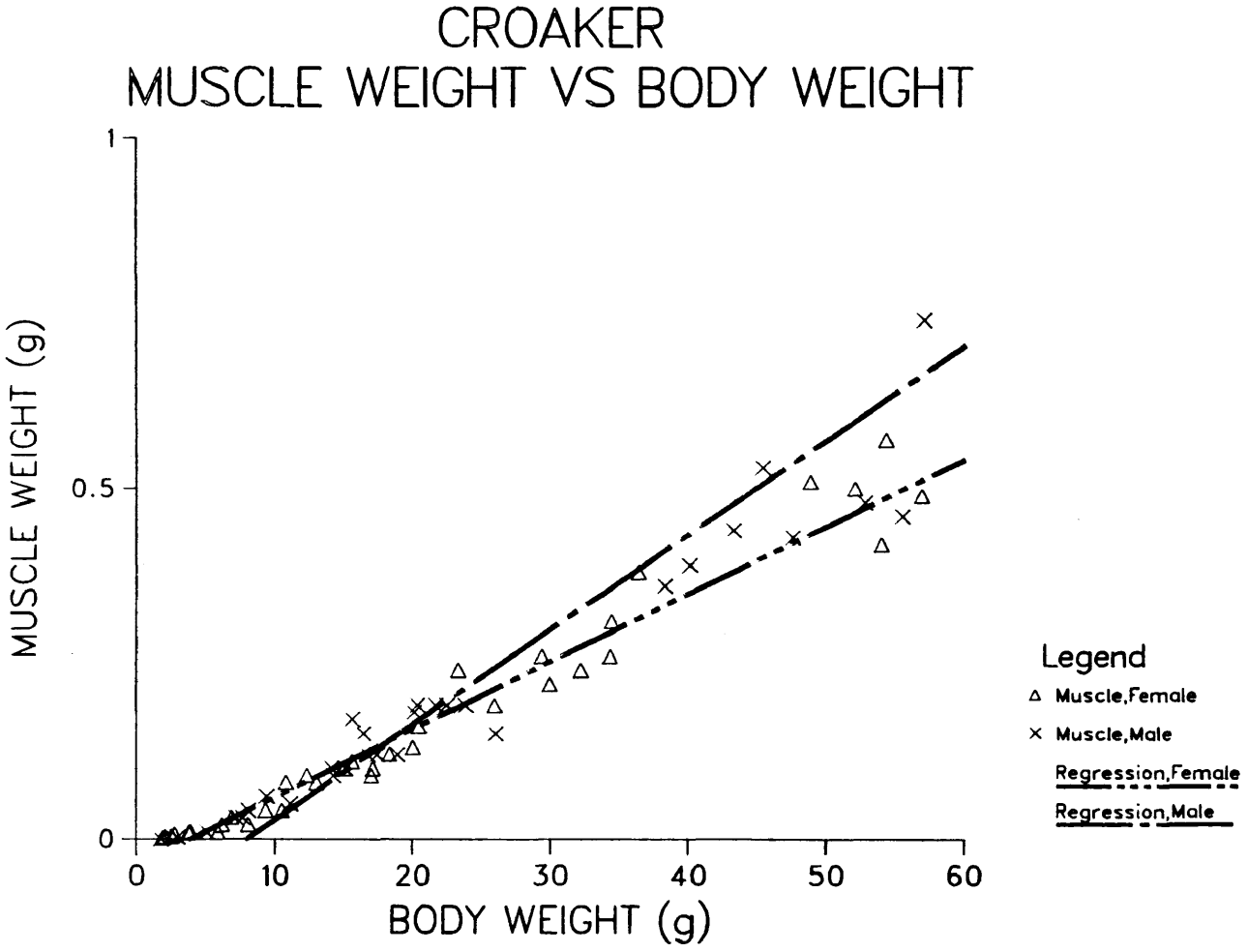

CROAKER
MUSCLE WEIGHT VS BODY WEIGHT
MUSCLE WEIGHT (g)
1
0.5
0
0
10
20
30
40
50
60
BODY WEIGHT (g)
Legend
Muscle,Female
Muscle,Male
Regression,Female
Regression,Male

FIGURE 2. Regression of sonic muscle weight against body weight for male and female croaker (including all specimens).

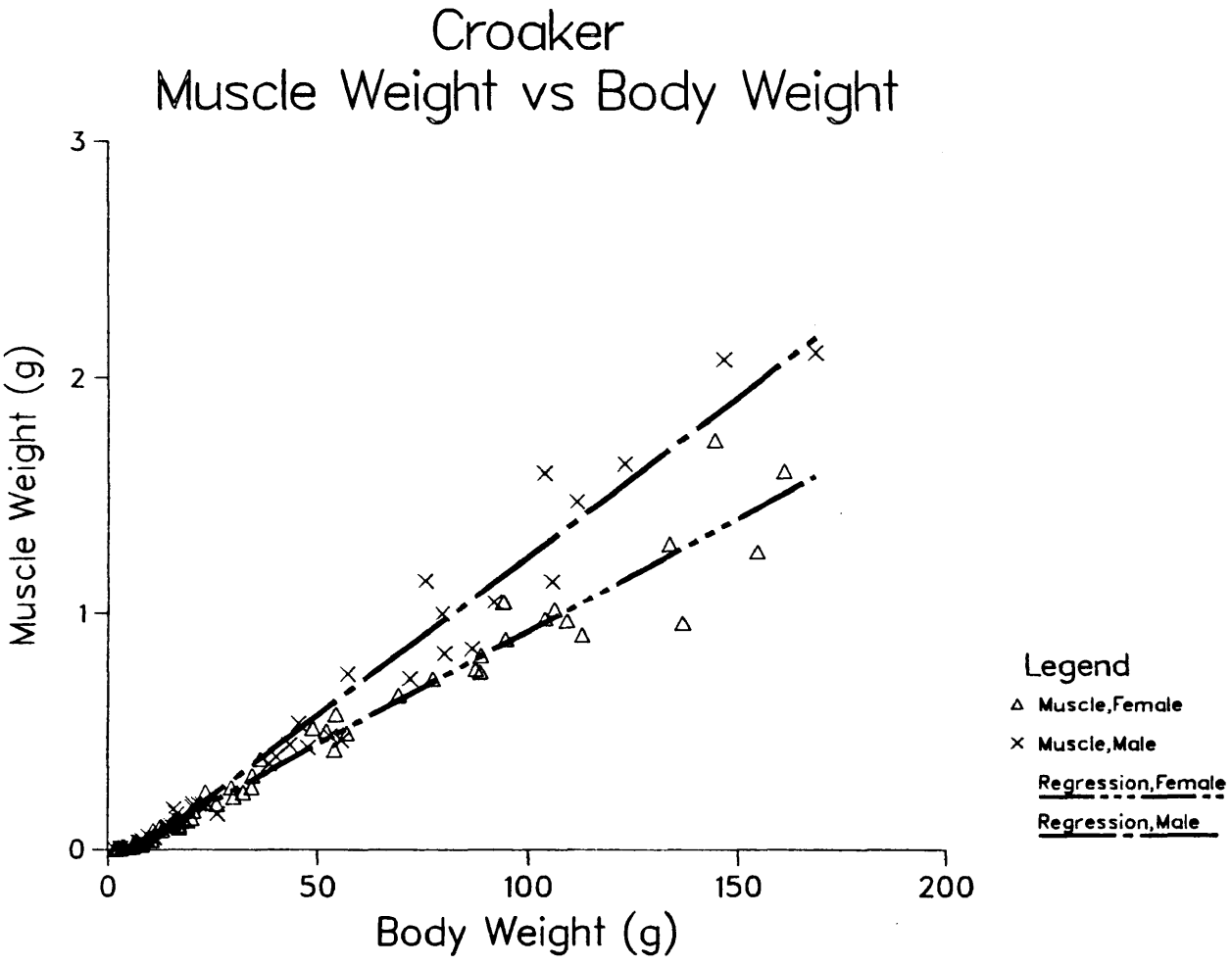

Croaker
Muscle Weight vs Body Weight
Muscle Weight (g)
Body Weight (g)
0
1
2
3
0
50
100
150
200
Legend
Muscle,Female
Muscle,Male
Regression,Female
Regression,Male

FIGURE 3. Regression of body weight against standard length for male and female croaker.

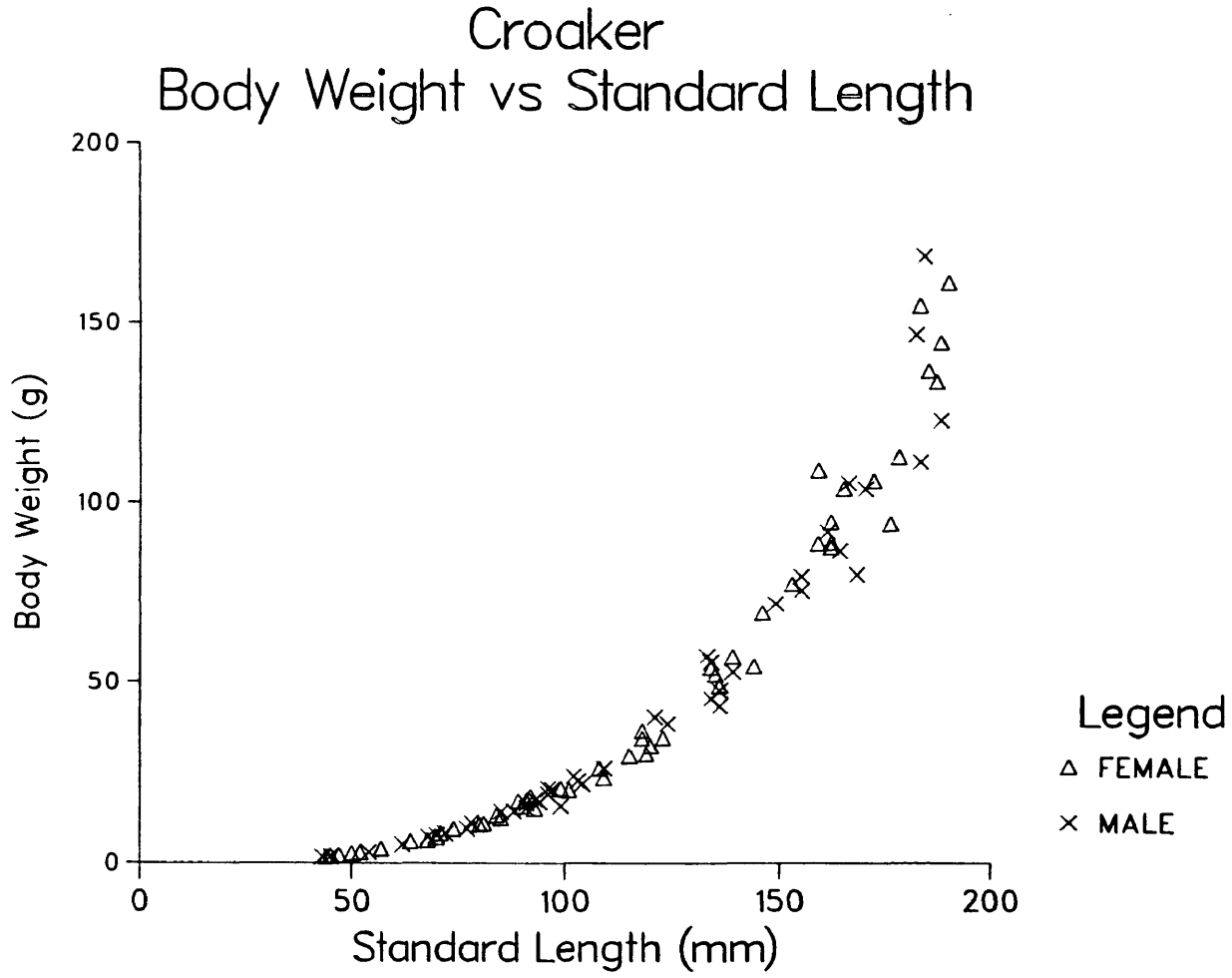

Croaker
Body Weight vs Standard Length
Body Weight (g)
200
150
100
50
0
0
50
100
150
200
Standard Length (mm)
Legend
FEMALE
MALE

FIGURE 4. Regression of sonic muscle and gonad weight against body weight in male croaker.

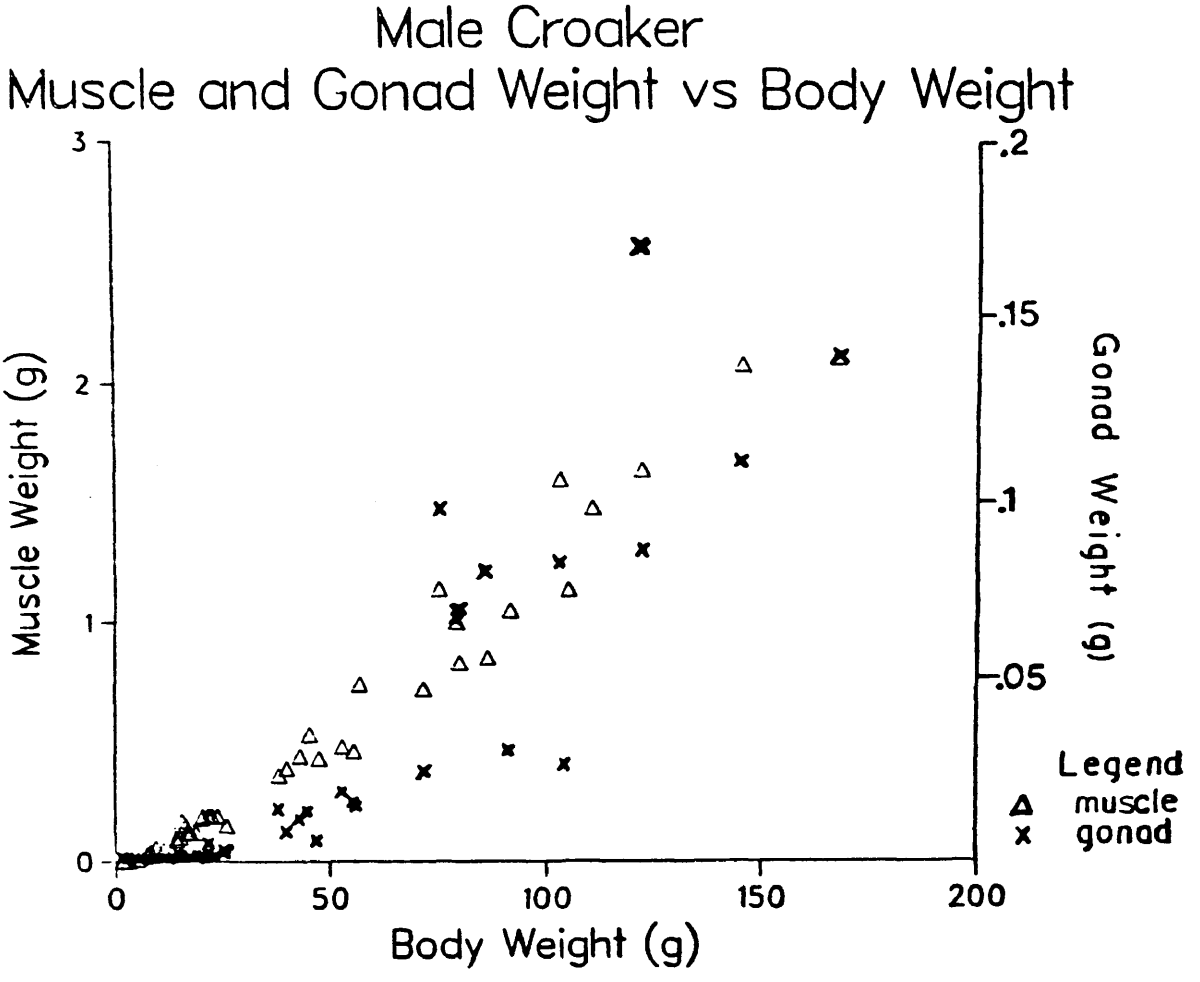

Male Croaker
Muscle and Gonad Weight vs Body Weight
Muscle Weight (g)
Gonad Weight (g)
Body Weight (g)
0
1
2
3
.05
.1
.15
.2
50
100
150
200
Legend
muscle
gonad

FIGURE 5. Regression of sonic muscle and gonad weight against body weight in female croaker.

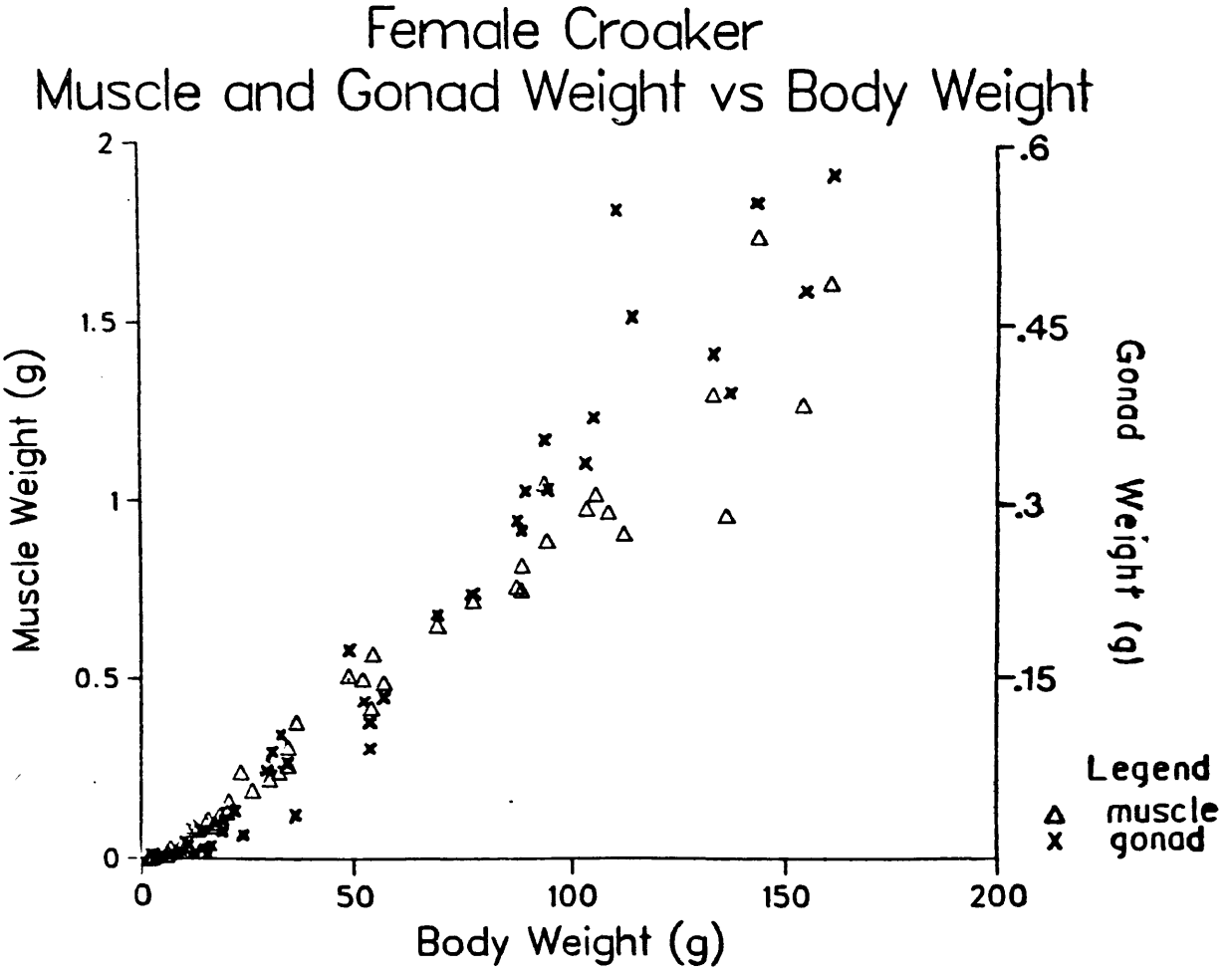

Female Croaker
Muscle and Gonad Weight vs Body Weight
Muscle Weight (g)
Gonad Weight (g)
Body Weight (g)
0
0.5
1
1.5
2
.15
.3
.45
.6
0
50
100
150
200
Legend
muscle
gonad

FIGURE 6. (A)Photomicrograph of cross section of immature testis in 109 mm S.L. male croaker; 525X. (B)Photomicrograph of cross section of developing testis in 182 mm S.L. male croaker showing active spermatogenesis (arrows show areas of spermatogenesis; 740X)

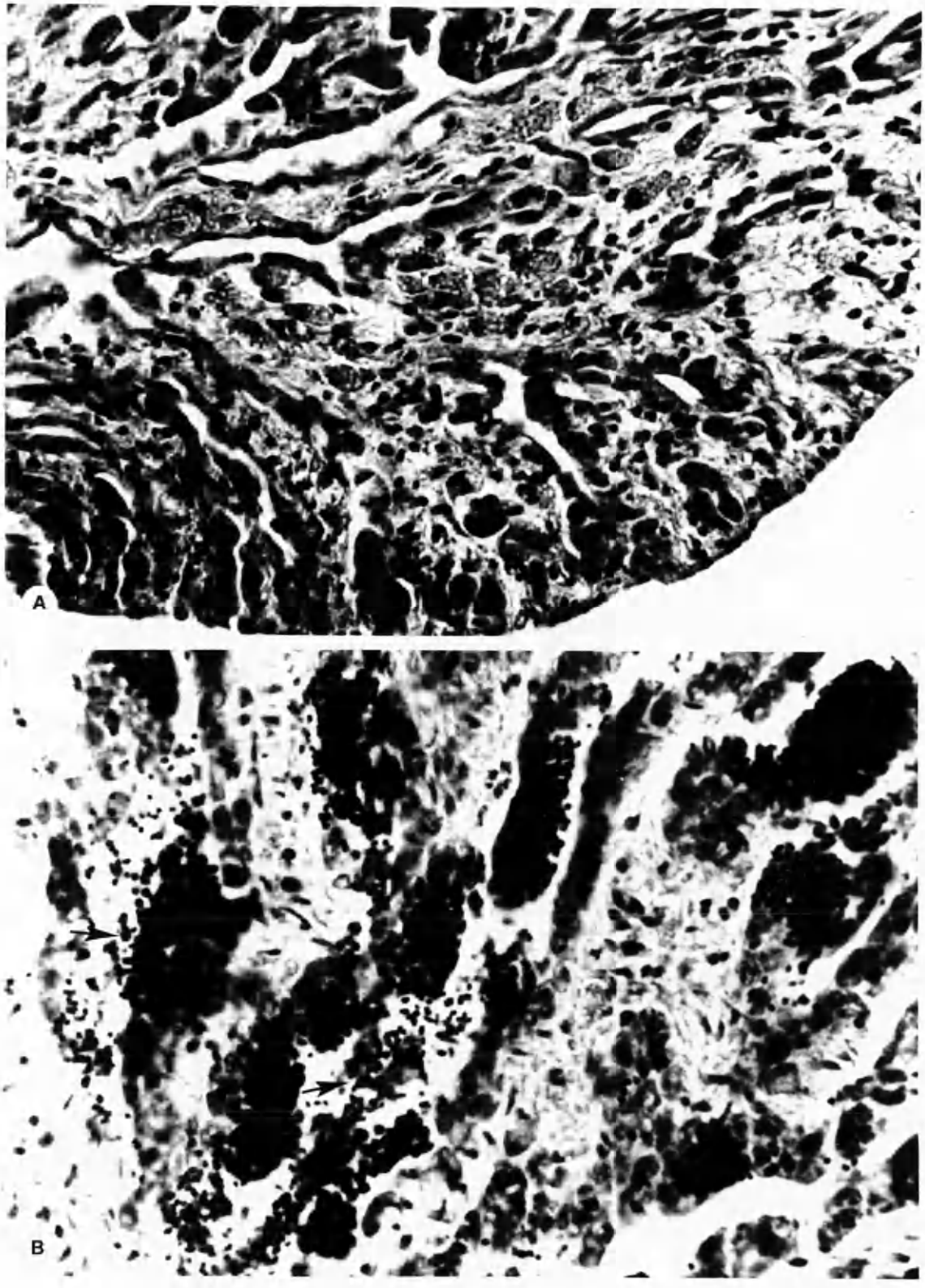

A
B

FIGURE 7. (A)Photomicrograph of cross section of immature ovary in 93 mm S.L. female croaker; 470X. (B)Photomicrograph of cross section of developing ovary in 188 mm S.L. female croaker showing early stage of gametogenesis (arrows show 2 ova in later stage of maturation; 470X).

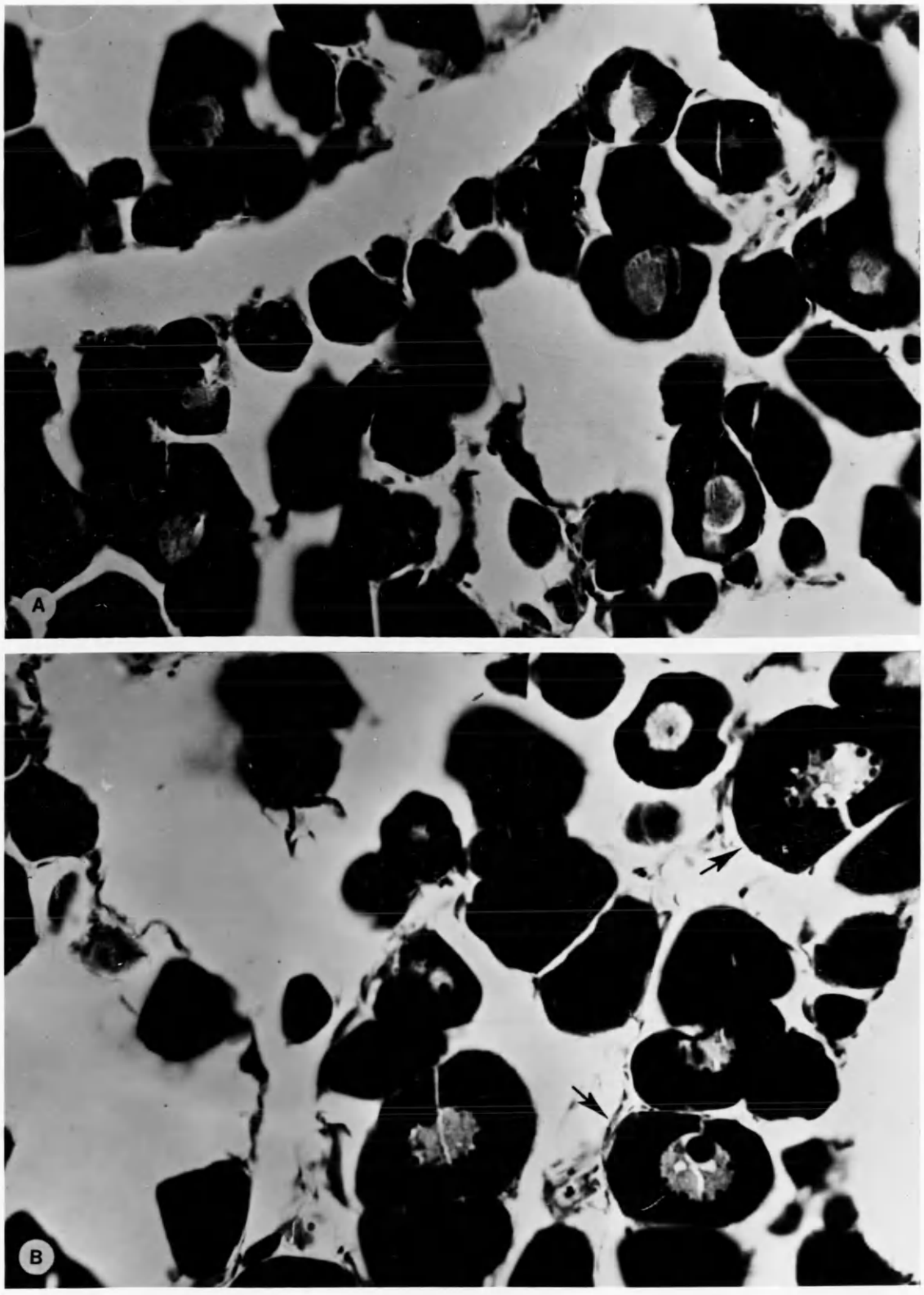
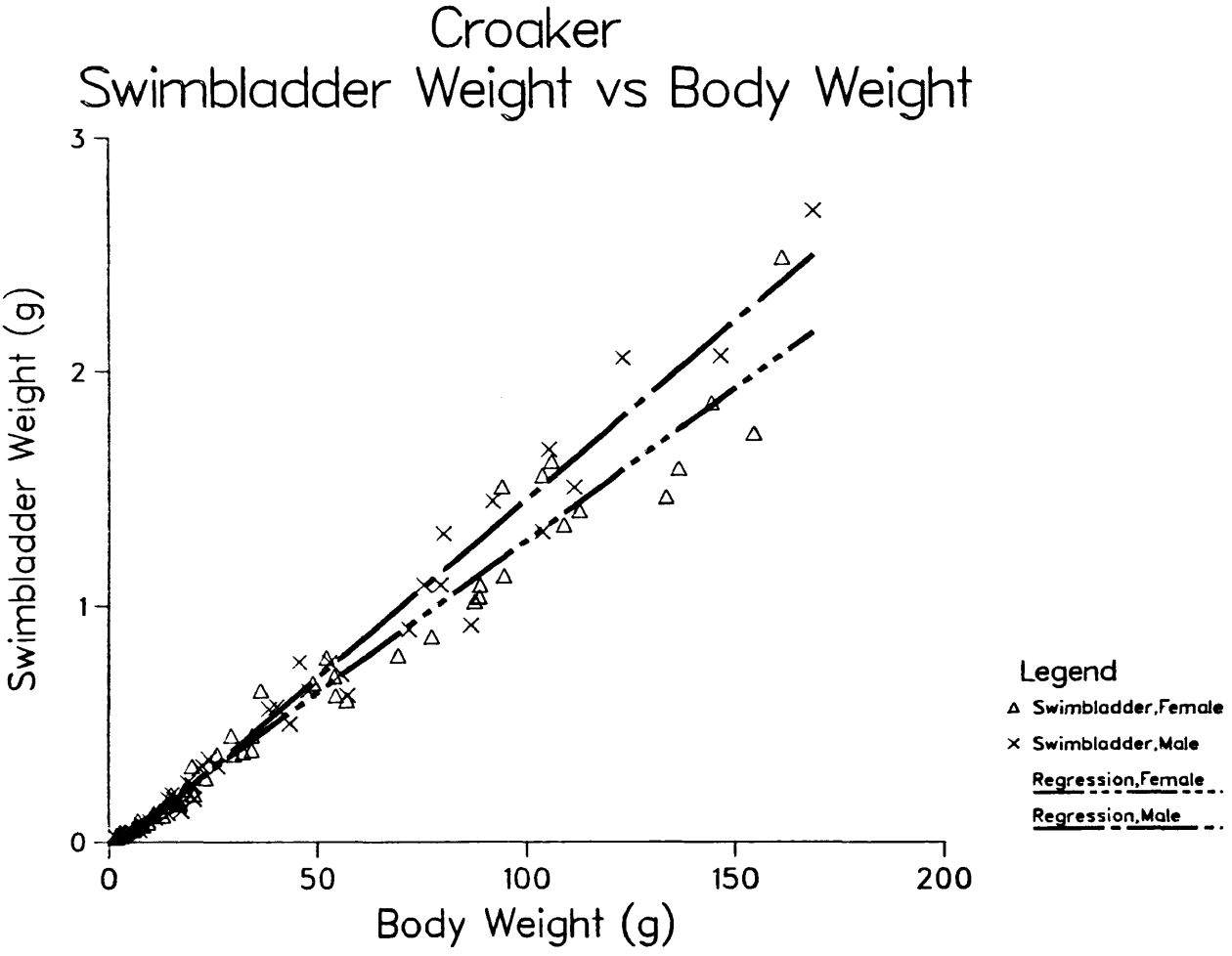

A
B

FIGURE 8. Regression of swimbladder weight against body weight for male and female croaker.


Croaker
Swimbladder Weight vs Body Weight
Swimbladder Weight (g)
Body Weight (g)
0
1
2
3
0
50
100
150
200
Legend
Swimbladder,Female
Swimbladder,Male
Regression,Female
Regression,Male

Spot

Twenty-seven male and thirty-one female spot were collected between the months of April and August, 1984. Numbers of individuals were low due to difficulties in catching males; several trawl catches consisted only of females. Eight males (ranging from 90 - 117 mm S.L.) possessed no visible sonic muscle tissue. In addition, sonic muscle was not observed in ten male specimens, all below 100 mm S.L., examined in a previous pilot study. The smallest individual collected with sonic muscle was 106 mm S.L. with a muscle weight of 2.9 mg. Ten fish between 108 and 118 mm S.L. were in early stages of sonic muscle development, with muscle weights of 6.5 mg to 7.6 mg (Appendix B). Weight of the sonic muscle increased linearly with body weight from this initial point (Fig. 9; Table 1). Equation of best fit line for spot was: Muscle weight = -0.0722 + 0.0023(Body weight). The largest fish examined was caught in July and was 165 mm S.L. with a swimbladder muscle weight of 210.0 mg. Lengths and widths of muscle tissue are presented in Appendix B. Spot sonic muscle was consistently thinner and lighter in weight than in croaker or weakfish.

The initiation of sonic muscle growth and of increased growth of the gonads occured when spot were approximately 30.9 g (Fig. 11.) and there was a significant correlation between gonad growth and growth of the sonic muscle (R^2= 0.702). As gonads developed, sonic muscle growth was initiated. From this point on, growth of the sonic muscle coincided with development of the gonads. Gonadal tissue from one of the largest males (158 mm S.L.) was examined and found to be immature:

undifferentiated spermatagonia were present, but spermatogenesis was not yet occuring (Fig. 12). No mature male spot were captured.

Swimbladder weight increased as a linear function of body weight for males and females (Fig. 13; Table 1), and there was no statistical difference between the regressions for each sex ($F=2.7333$; df= 1,51; $p=0.1044$). Equation of best fit line for females was: Swimbladder weight = 0.0516 + 0.0036(Body weight); and for males was: Swimbladder weight = 0.0079 + 0.0047(Body weight).

FIGURE 9. Regression of sonic muscle weight against body weight in spot.

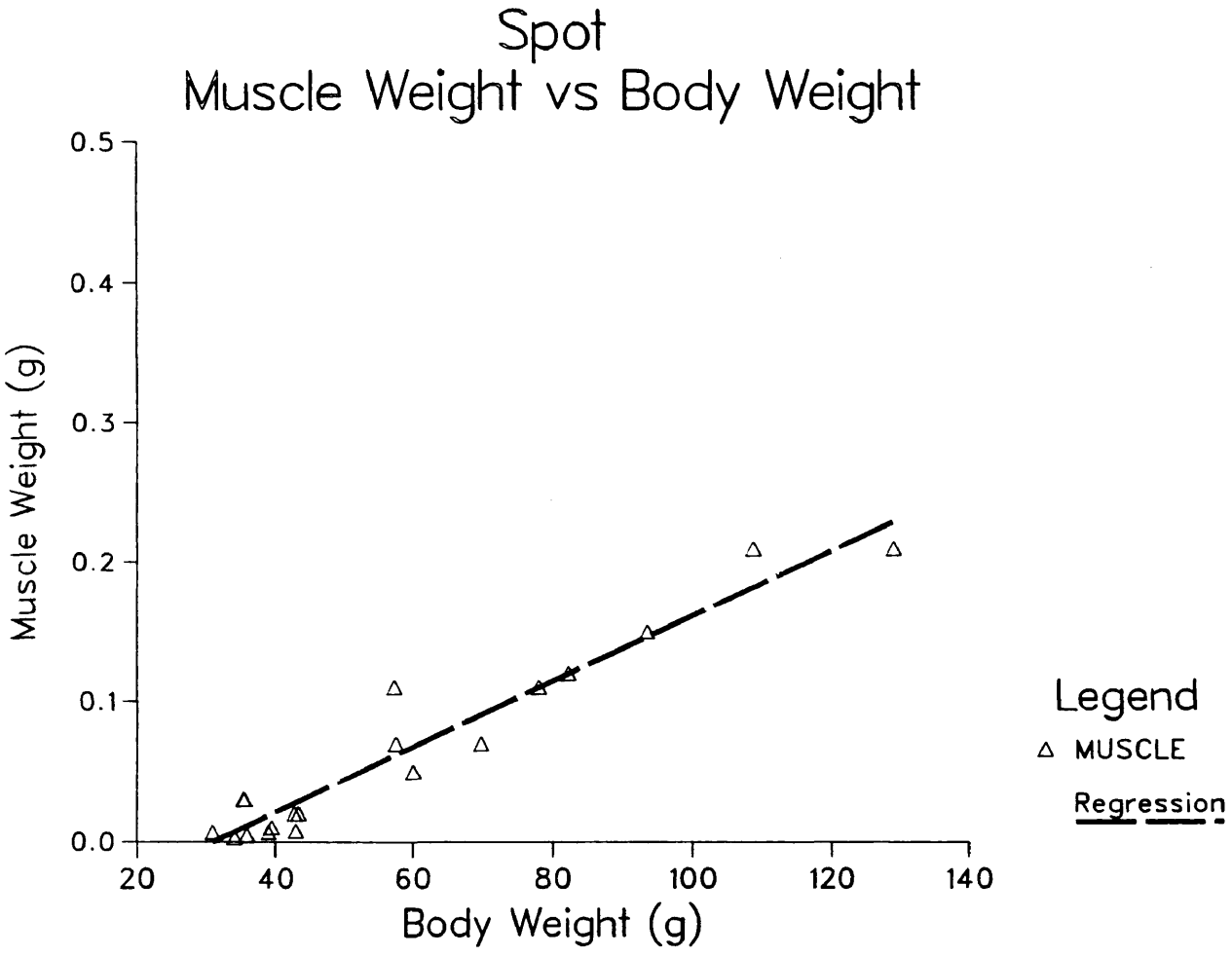

Spot
Muscle Weight vs Body Weight
Muscle Weight (g)
0.5
0.4
0.3
0.2
0.1
0.0
20
40
60
80
100
120
140
Body Weight (g)
Legend
MUSCLE
Regression

FIGURE 10. Regression of body weight against standard length in spot.

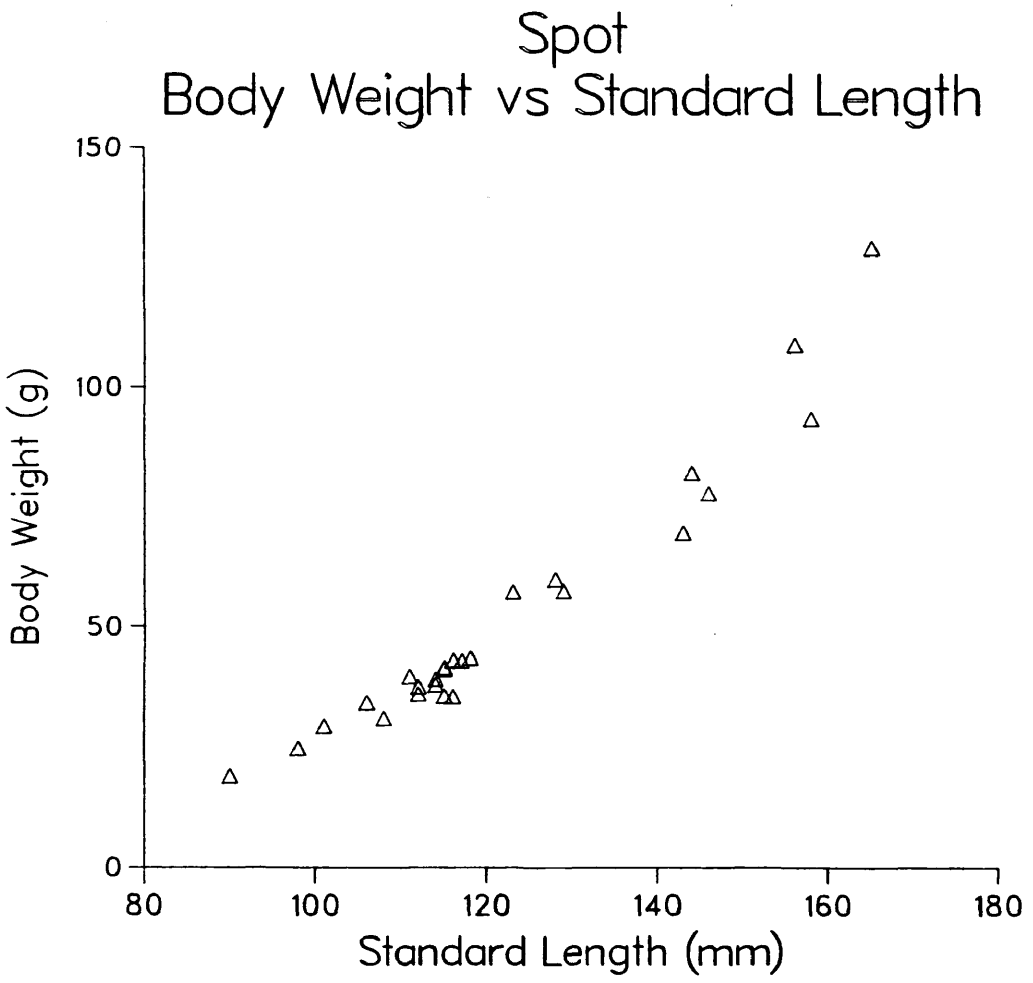

Spot
Body Weight vs Standard Length
Body Weight (g)
150
100
50
0
80
100
120
140
160
180
Standard Length (mm)

FIGURE 11 Regression of sonic muscle weight and gonad weight against body weight in spot.

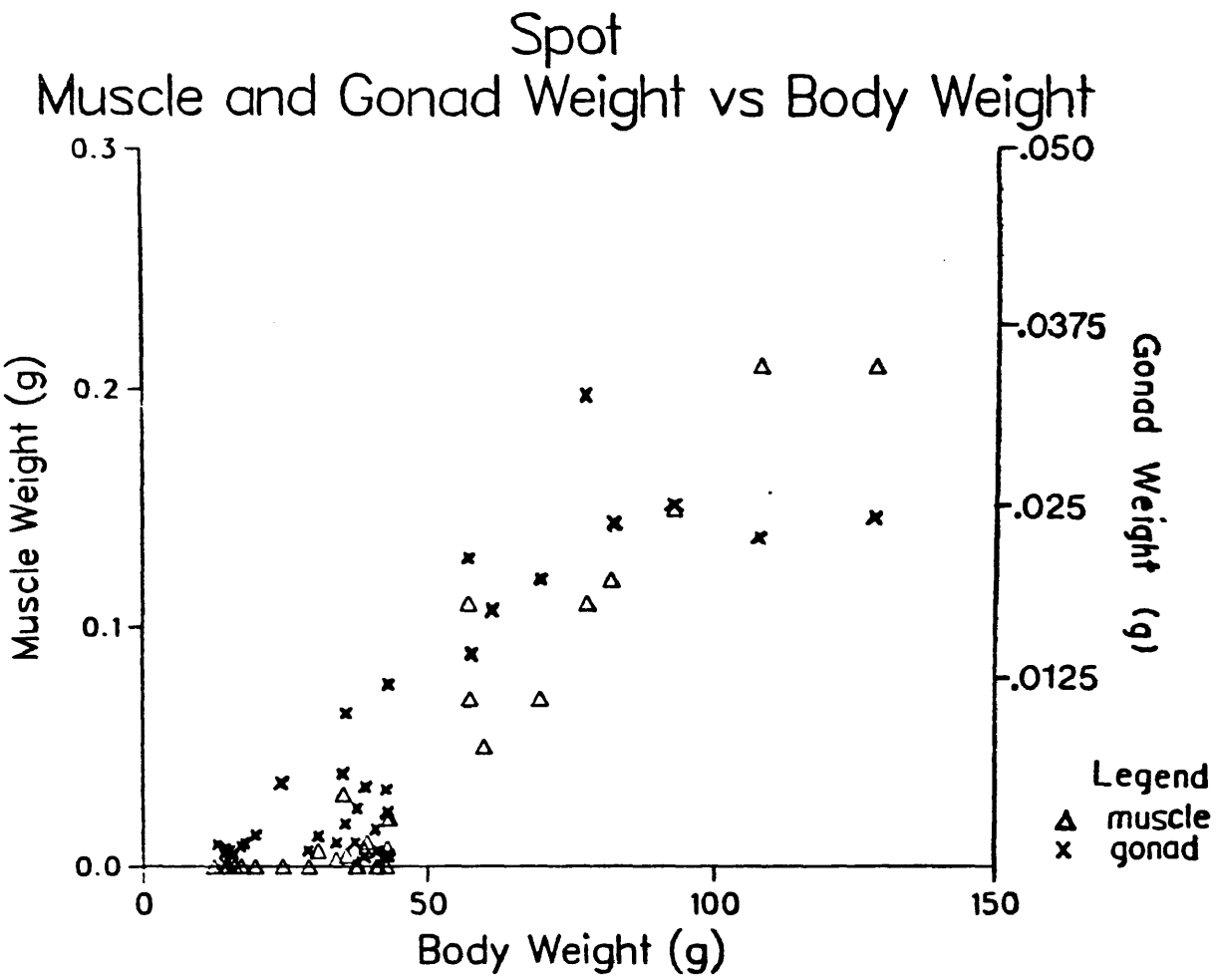

Spot
Muscle and Gonad Weight vs Body Weight
Muscle Weight (g)
0.3
0.2
0.1
0.0
.050
.0375
.025
.0125
Gonad Weight (g)
0
50
100
150
Body Weight (g)
Legend
muscle
gonad

FIGURE 12. Photomicrograph of longitudinal section of immature testis in 158 mm S.L. male spot; 470X.

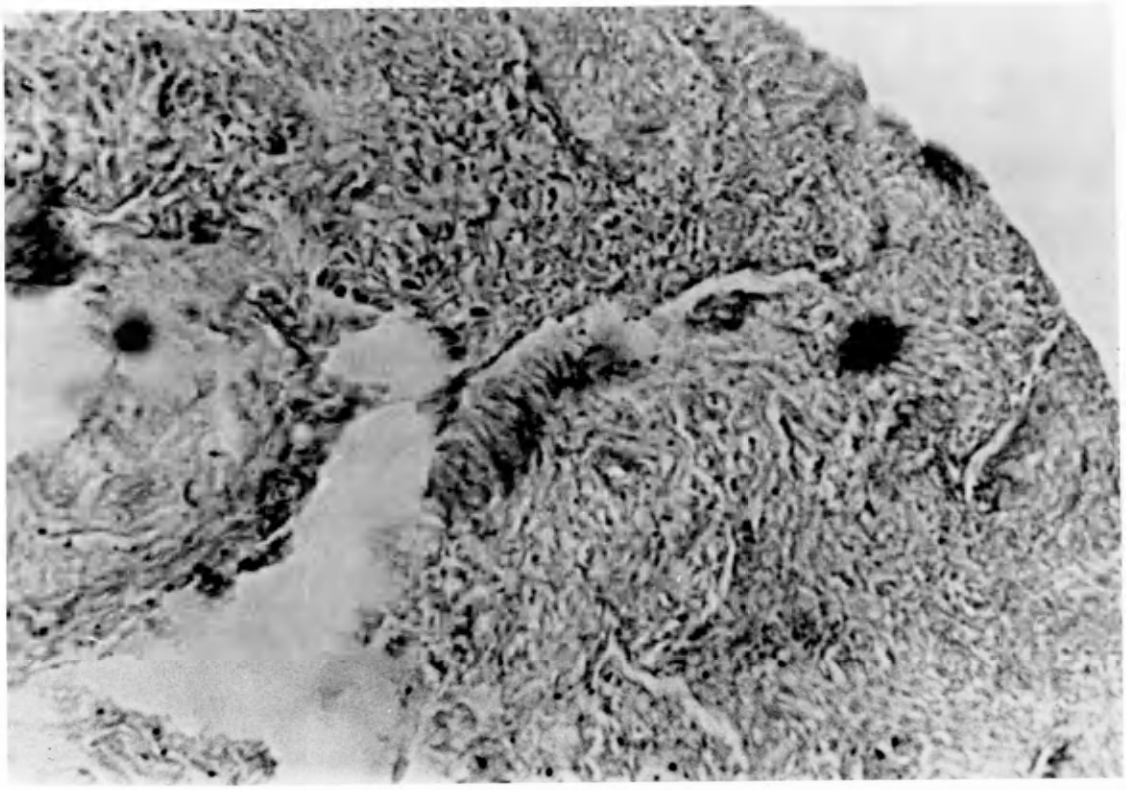
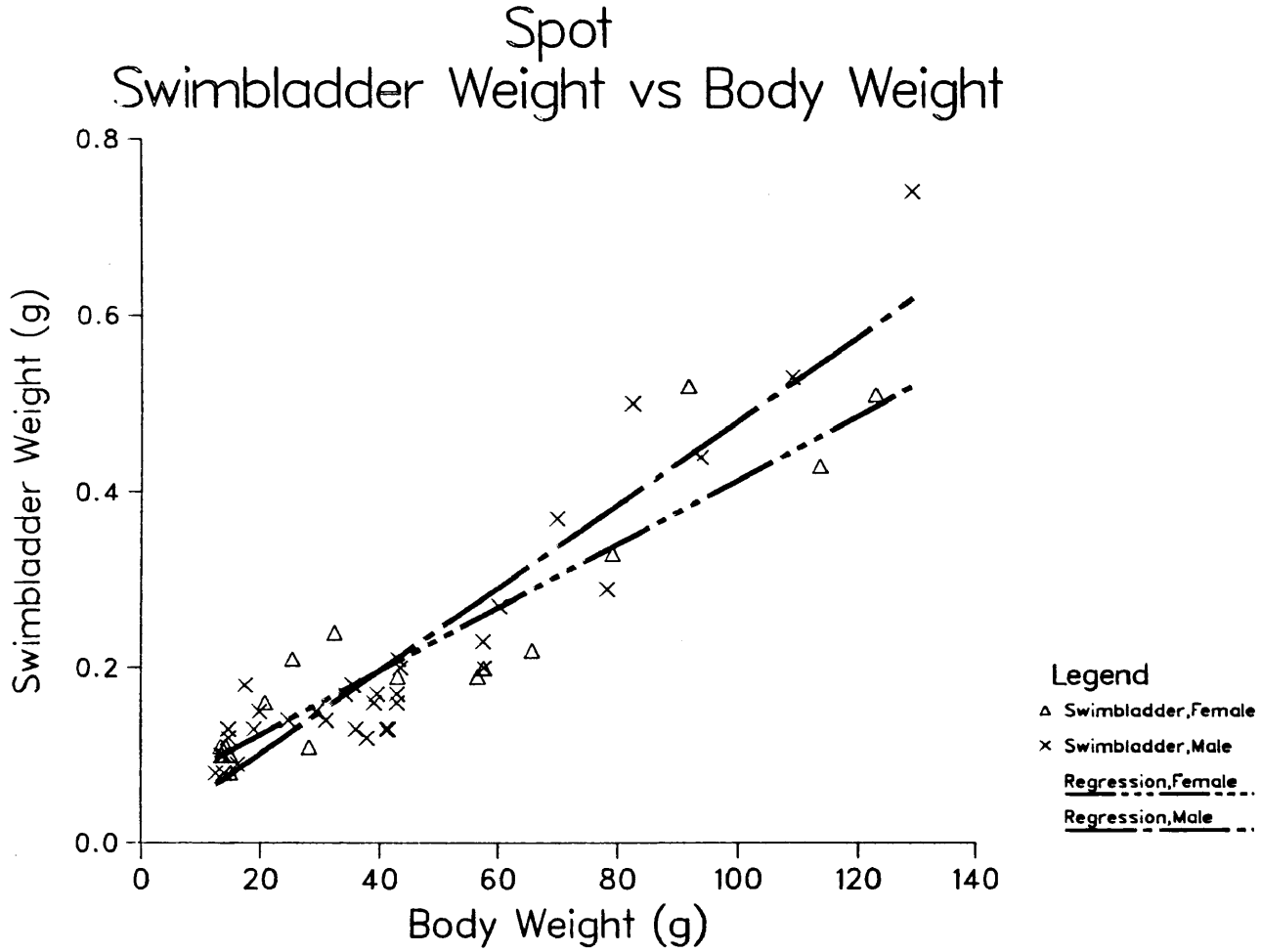


FIGURE 13. Regression of swimbladder weight against body weight for male and female spot.


Spot
Swimbladder Weight vs Body Weight
Swimbladder Weight (g)
0.0
0.2
0.4
0.6
0.8
0
20
40
60
80
100
120
140
Body Weight (g)
Legend
Swimbladder,Female
Swimbladder,Male
Regression,Female
Regression,Male

Weakfish

Twenty-three male and sixteen female weakfish were collected between the months of June and August, 1984. Numbers of male specimens were again low due to their absence in areas surveyed. No sonic muscle was observed in two males of 126 and 129 mm S.L. The smallest individual with sonic muscle was 119 mm S.L. with a sonic muscle weight of 7.7 mg (Appendix C). Sonic muscle weight increased linearly with body weight from this initial point (Fig. 14; Table 1). Equation of best fit line for weakfish was: Muscle weight = -0.5245 + 0.0162(Body weight). The largest male examined, 182 mm S.L., had a sonic muscle weight of 870.0 mg, though a slightly smaller individual at 179 mm S.L. possessed a sonic muscle of 1630.0 mg. Lengths and widths of muscle tissue are presented in Appendix C.

As in croaker and spot, the initiation of sonic muscle development and the acceleration of gonad growth began at approximately the same weight (Fig. 16) and there was a significant correlation between gonad growth and sonic muscle growth (R^2= 0.909). Muscle tissue was first observed at 29.6 g in weakfish. At this same weight, growth of the gonads began to increase steadily. From this point on gonad development remained synchronous with muscle development. Gonadal tissue were examined in two of the males. In the smallest individual caught (119 mm S.L.), histological sections with primary and secondary spermatocytes present demonstrated that spermatogenesis was just beginning (Fig. 17-1;17-2). Muscle development occured at approximately the same time as the onset of spermatogenesis (Table 2).

A larger male of 148 mm S.L. showed active spermatogenesis with spermatazoa present (Fig. 18).

Swimbladder weight increased as a function of body weight for males and females (Fig. 19; Table 1), and there was no statistical difference between the regressions for each sex ($F=0.0096$; $df=1,37$; $p=0.9221$). Equation of best fit line for females was: Swimbladder weight = -0.1874 + 0.0255(Body weight); and for males was: Swimbladder weight = -0.1619 + 0.0251(Body weight).

FIGURE 14. Regression of sonic muscle weight against body weight in weakfish.

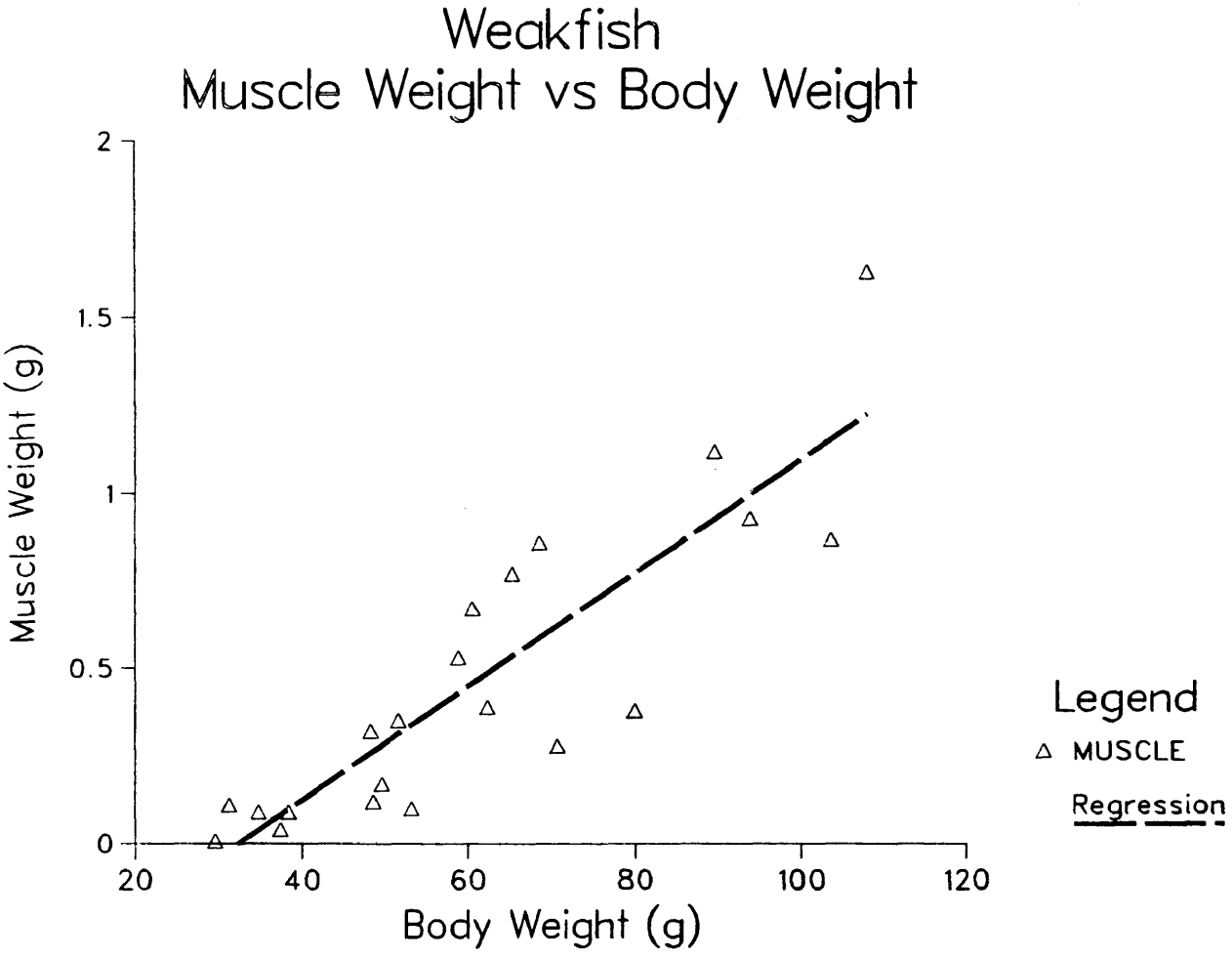

Weakfish
Muscle Weight vs Body Weight
Muscle Weight (g)
2
1.5
1
0.5
0
20
40
60
80
100
120
Body Weight (g)
Legend
MUSCLE
Regression

FIGURE 15. Regression of body weight against standard length in weakfish.

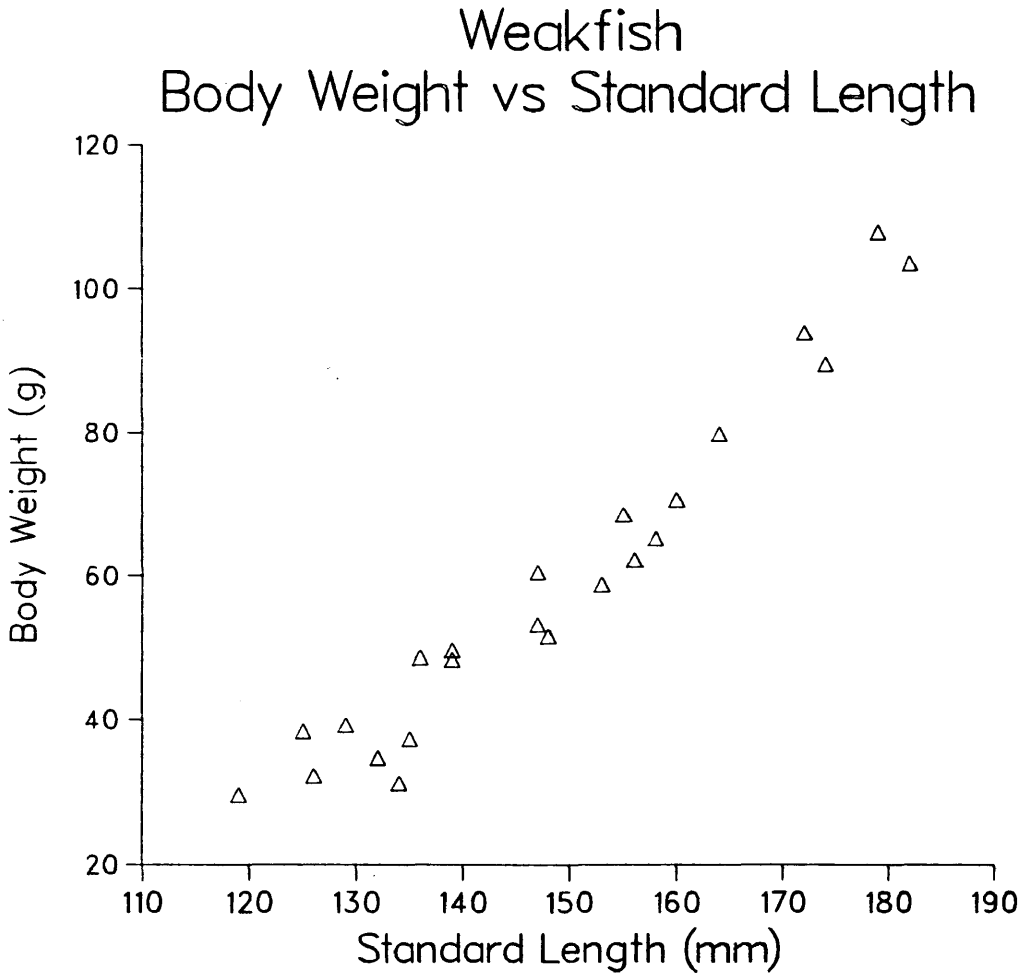

Weakfish
Body Weight vs Standard Length
Body Weight (g)
120
100
80
60
40
20
110
120
130
140
150
160
170
180
190
Standard Length (mm)

FIGURE 16. Regression of sonic muscle weight and gonad weight against body weight in weakfish.

Weakfish
Muscle and Gonad Weight vs Body Weight

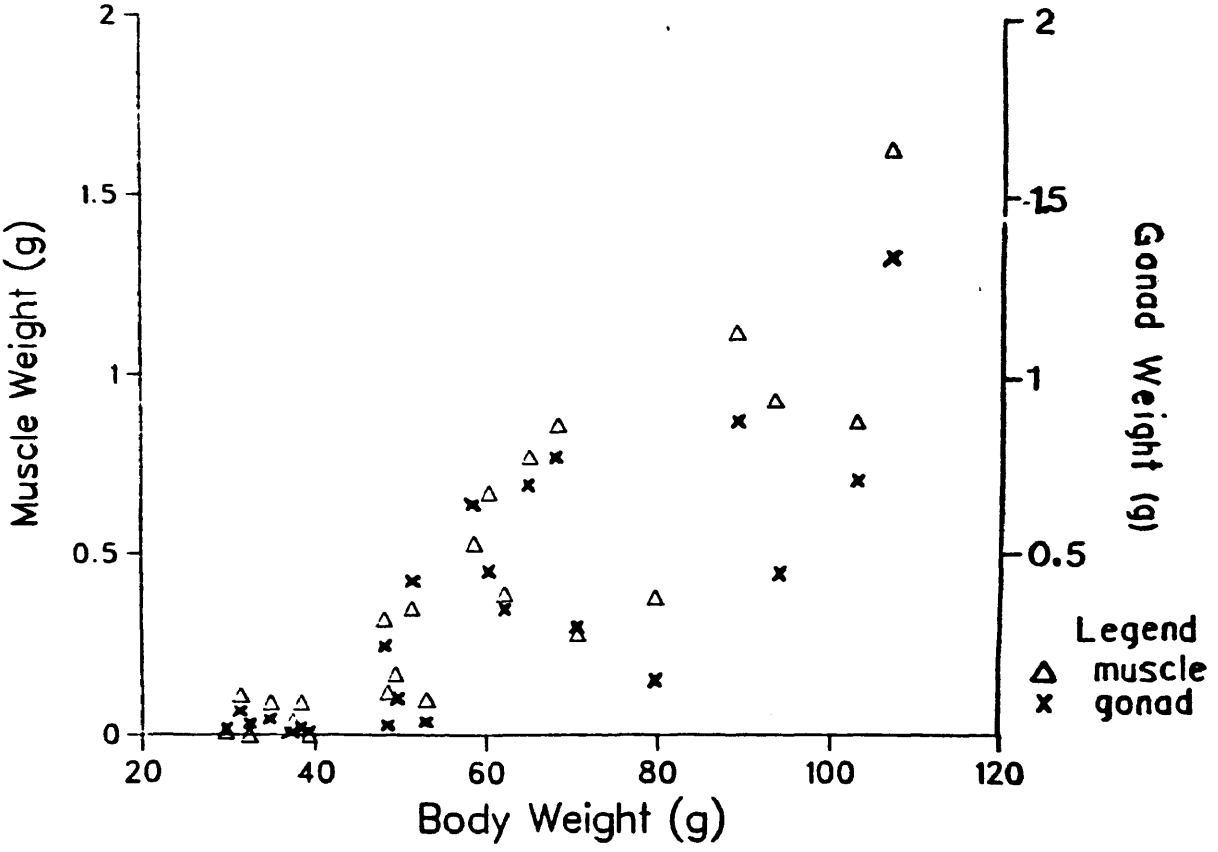


FIGURE 17. (A)Photomicrograph of cross section of developing testis in 119 mm S.L. male weakfish; 945X. (B)Photomicrograph of cross section of developing testis in same specimen showing area undergoing early stage of spermatogenesis; 1285X).

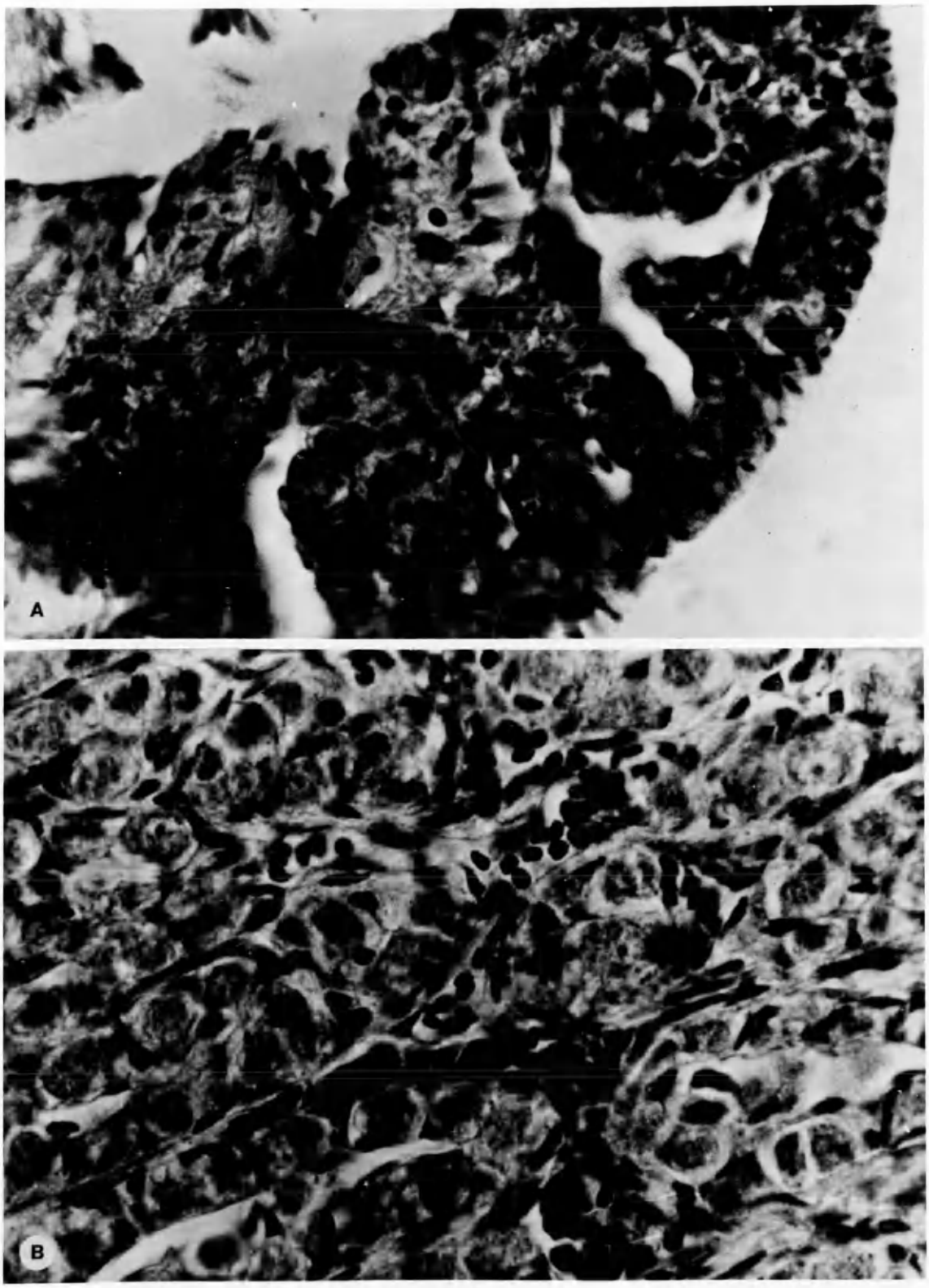

A
B

FIGURE 18. Photomicrograph of cross section of developing testis in 148 mm S.L. male weakfish undergoing active spermatogenesis. Arrows show several stages of spermatazoa are present (magnification = 768X).

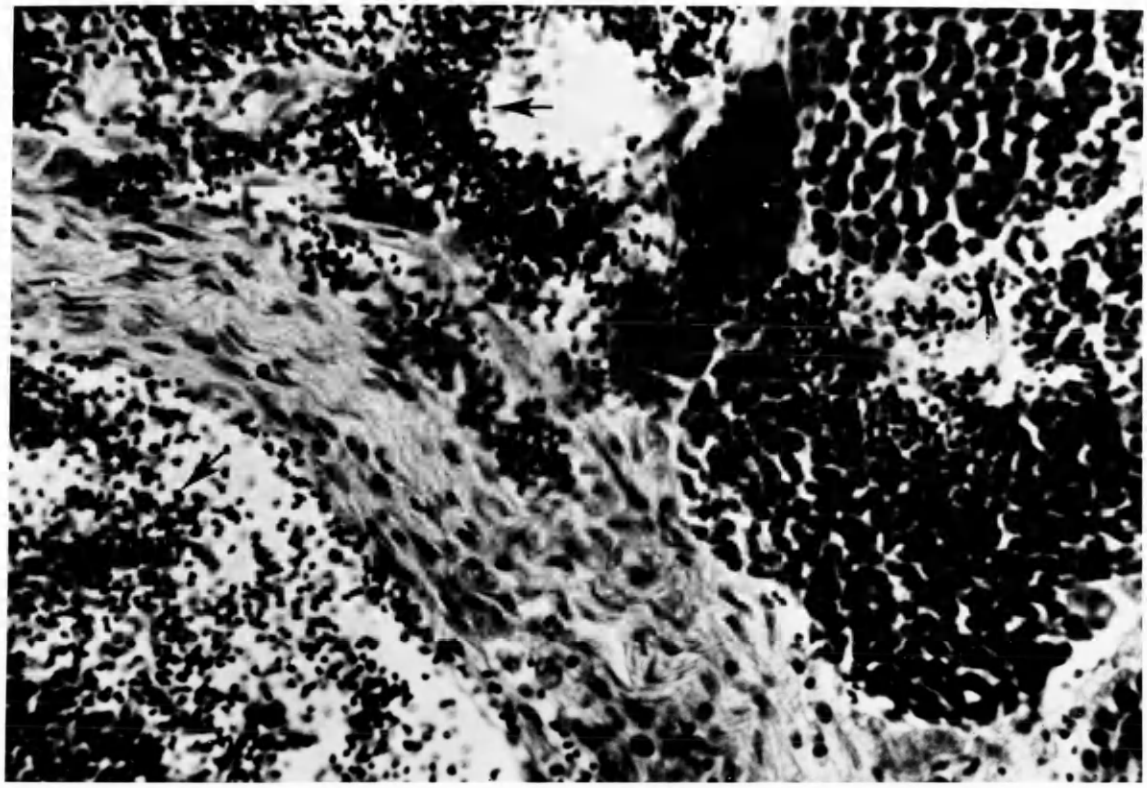
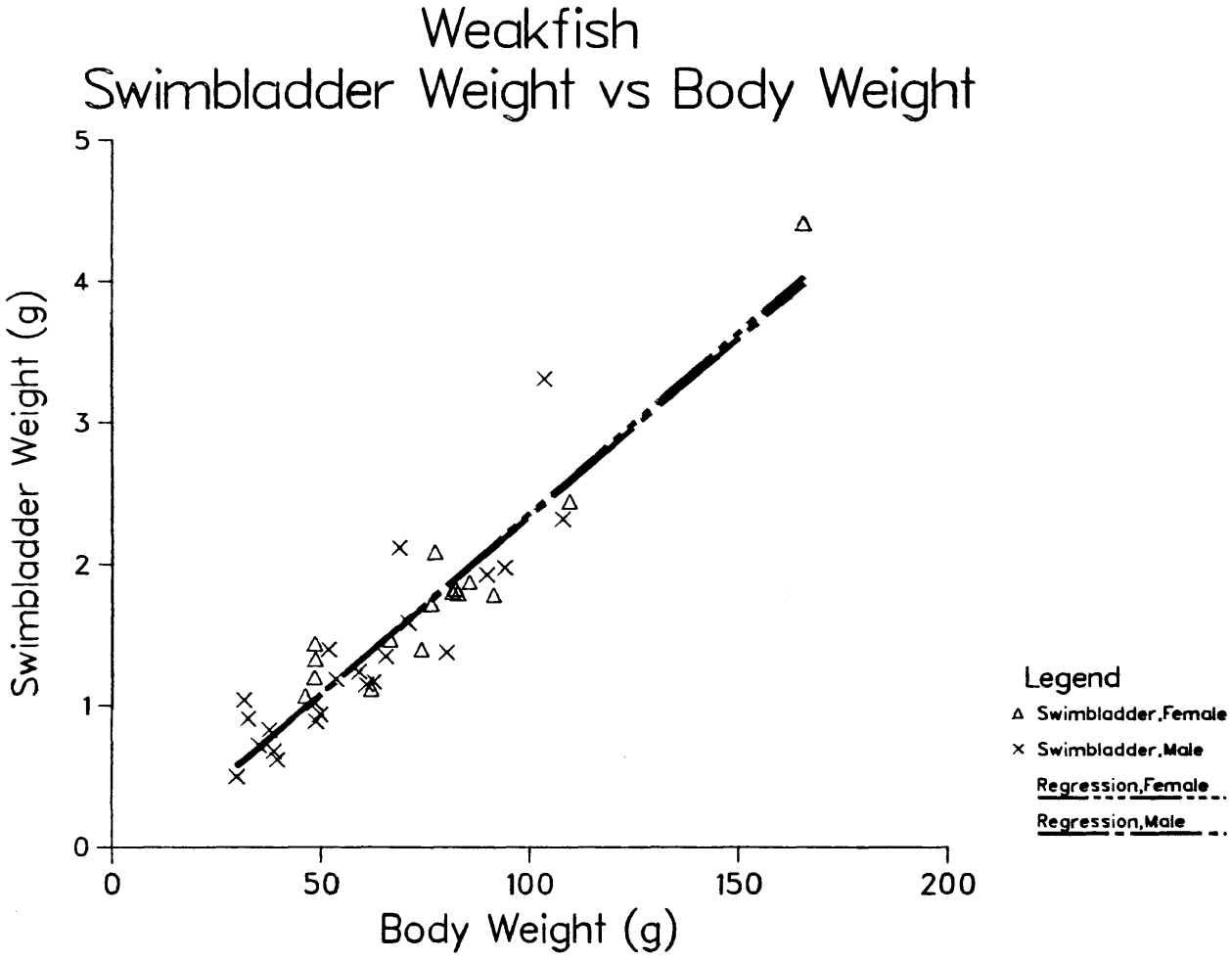


FIGURE 19. Regression of swimbladder weight against body weight for male and female weakfish.


Weakfish
Swimbladder Weight vs Body Weight
Swimbladder Weight (g)
Body Weight (g)
0
1
2
3
4
5
0
50
100
150
200
Legend
Swimbladder,Female
Swimbladder,Male
Regression,Female
Regression,Male

Discussion

Development of the sonic muscle in sciaenids can occur either through normal somatic growth or as a secondary sex character under the direct control of steroids. Of the two possible pathways, development under steroidal control seems the most likely. Fine and Pennypacker (in preparation) have shown that steroids cause an increase in the weight of the swimbladder and sonic muscles in toadfish. Males and females show significant treatment effects. Though toadfish sonic muscles form embryologically and are fully attached by the time the larvae are free swimming (Tracy, 1959, 1961), the tissues are responsive to steroids suggesting that the dimorphic condition of adults is a result of male hormone levels. In the present study, the first appearance of the sonic muscle occured when the fish were from 4 to 5 months old in croaker, 6 to 7 months old in spot and 11 months old in weakfish, and at sizes ranging from 45 mm S.L. in croaker to over 100 mm S.L. in spot and weakfish. Initiation of sonic muscle growth, then, took place after several months of development which suggests hormonal interaction. Further, in all three species, muscle development was concurrent with accelerated growth of the gonads. Sonic muscle development was nonexistent at weights below the point where gonads began to increase. As the rate of gonad growth became greater, however, sonic muscle development was initiated. The implication is that the sonic muscle develops as a secondary sex character, apparently forming de novo and growing in synchrony with the gonads. Development

of the sonic muscle would begin as muscle precursers are stimulated through the release of steroids. Though development of the muscle in my study occured before full maturity (coincidentally in weakfish), differentiated areas of the gonad, such as the interstitial cells, have been implicated in steroidogenic activity (Oota and Yamamoto, 1966; Takahashi and Iwasaki, 1973; Satoh, 1974; Van Den Hurk, 1974; Nagahama et al., 1978; Van Den Hurk et al., 1982;) and may be responsible for initiation of sonic muscle growth and the sex differences noted. Growth of the muscle would proceed under the controlling effects of gonadal steroids.

Swimbladder weight also varied sexually in croaker with male swimbladders heavier than females. Because selection pressures for the evolution of the swimbladder involve sound production, hearing, and hydrostatic functions, it is difficult to attribute relative size to any one factor. However, differences between swimbladders in male and female croaker may reflect a compensation for the larger sonic muscles in the male, since there were no sexual differences in swimbladder size in spot or weakfish. The sexually dimorphic condition of the croaker sonic muscle, however, is undoubtedly related to sound production. One might predict that males call more frequently, more intensely and produce a lower dominant frequency sound than females.

Croaker

Spawning in Atlantic croaker occurs over a protracted period extending at least from September to late March with a distinct peak

around October (White and Chittenden, 1977). The spawning season may begin as early as August or July in some areas as Chao and Muscick (1977) observed young of the year first entering trawl and beach seine catches in August in the York River. Pearson (1941) found young of the year near the mouth of the Chesapeake Bay in late July ranging from 1.5 to 15 mm, indicating either the presence of early spawners or that the breeding season may extend later than March. Offshore spawning grounds are unknown though some spawning occurs around the mouth of the Chesapeake Bay (Pearson, 1929). Atlantic croaker spawn in the Mid Atlantic Bight from Cape May, N.J. to Cape Hatteras, N.C. with greatest concentrations in the middle and southern parts of this range (Norcross, 1983).

A variety of data exists concerning length and age at sexual maturity in croaker (Table 2). Wallace (1940) examined almost 1000 gonads from fish of various ages in Chesapeake Bay and found that only 45% of males reach maturity at the end of their second year and that no females at this age give signs of ripening. By the third year, all males and females are mature. The smallest mature male and female croaker are 240 mm in total length (T.L.) (2 years old) and 275 mm T.L. (3years old) respectively. Pearson (1929), in studying length distribution in Texas croaker, reported a total length of about 150 mm reached by the end of the first year, extending up to 220 mm T.L. by the end of the second year. In further observations, he notes the length distribution of 230 sexually mature individuals. Mature males range from 140 mm to 320 mm T.L. with mature females occuring over a

similar, though higher, range of 150 mm to 370 mm T.L. The modal length for the entire group of males and females is 220 mm T.L. which corresponds to fish at the end of their second year. Thus, the majority mature near the end of the second year though some reach maturity earlier. This data is not necessarily contradictory to Wallace's findings on croaker in Chesapeake Bay that the fish reach maturity at the end of their second or third year since Chabanand (1929) and Hildebrand and Cable (1930) suggested that individuals of the same species may mature at an earlier age in warmer climates (Wallace, 1940). White and Chittenden (1977) reached a similar conclusion observing that while croaker started to mature at 140 - 170 mm T.L. in the Gulf of Mexico, fish living north of Cape Hatteras reached maturity when greater than 200 mm T.L. as they approached age 2.

Croaker sonic muscle first appeared at about 45mm S.L., which corresponds to approximately 4 to 5 months of age in both males and females (Welsh and Breeder, 1923; Hildebrand and Cable, 1930; Parker, 1971). Because of the extended spawning season it is difficult to give a specific age. Devlopment of the sonic muscle, though, began long before the gonads approached maturity. But muscle development proceeded together with the initiation of increased growth of the gonads. This may be more important since gonad tissue is capable of steroid production before sexual maturity, which could initiate muscle development. The sonic muscle of individual male and female croaker taken below 60 g were roughly equal with respect to size and weight of

the muscle tissue. Above 60 g male sonic muscle increased in weight at a faster rate than female muscle. This difference was more pronounced as croaker increased in size so that muscle tissue of males became visibly thicker in size and larger in length and width. Sexual differences in sonic muscle at these larger body weights may be related to level of sexual maturity, assuming differences in steroid production between mature males and females.

Spot

Spawning in Atlantic spot may occur from October to March with December and January generally accepted as the spawning months (Dawson, 1958). This appears consistent with other reports. Chao and Musick (1977) observed that yearling or older spot leave the estuary after September and do not return until spring of the next year. Hildebrand and Schroeder (1928) reported offshore migration of maturing fish from September to October. Offshore data show ripe or nearly ripe fish taken during October, December, and February, with spent fish occuring in catches in February (Dawson, 1958). Spawning is believed to occur in deep water some distance offshore.

Studies on spot have revealed the size and age over which sexual maturity is reached (Table 2). Hildebrand and Cable (1930) observed no spot less than 8 in. (203 mm T.L.) with developing or nearly mature roe. At Alligator Harbor, Florida, Townshend (1956) examined the gonads of 56 spot and found the earliest development occuring at a standard length of 149 mm. He estimated that spot did not spawn until

their second winter or the beginning of the third year. Hildebrand and Schroeder (1928) found developing roe in 214 mm T.L. fish and stated that no fish less than 8 1/2 in. (215 mm) in total length contained gonads mature enough to spawn that year. Pearson (1929) found ripening adults ranging from 170 - 210 mm T.L. -- lengths attained in the second year. Noting that few Texas spot reach over two years in age, he postulated that most spawning took place at the end of the second year.

In each study of sexual maturity, lengths and age at maturity were much greater than the range over which the sonic muscle began to develop. Maturation of the gonads occurs at lengths ranging from 149 mm S.L. to 215mm T.L. and at ages of from two to three years. I observed the first appearance of sonic muscle in fish that were approximately 6 to 7 months old (Hildebrand and Cable, 1930; Pacheco, 1957; Parker, 1971). Hildebrand and Cable (1930) examined spot off the Beaufort, North Carolina coast and found an average length of 5.6 in. T.L. (139.3 mm) attained by the end of the first year. Further, in studying the size range of Texas spot, Pearson (1929) found an average length of 140 mm T.L. by the end of the first year. Even taking into account differences between standard and total length, one still finds that the size over which muscle tissue first appeared in western North Atlantic spot occured during the first year of growth. While maturation of the gonads has been shown in various studies to occur from two to three years of age, muscle development occured in fish of one year of age which were not yet fully mature. Though occuring before full maturation, sonic muscle development does proceed in synchrony with the

acceleration of gonad growth. Thus the initiation of muscle growth is directly related to development of the gonads.

Weakfish

The spawning season of weakfish is an extended one as in croaker and spot, occuring from late April through June as indicated by gonad condition (Merriner, 1976) and possibly extending to October (Welsh and Breeder, 1923). Females appear to spawn the major portion of eggs in May or June with a second, smaller spawning possibly occuring in late July or August (Merriner, 1976). Fertilized eggs are pelagic and larvae disperse to nursery grounds soon after hatching. Young of the year first entered trawl catches of the York River in July or August (Chao and Musick, 1977). Weakfish move offshore to spawn but are also found spawning in Pamlico Sound, North Carolina (Merriner, 1976). Thus, spawning may occur in sounds and bays as well as offshore -- these areas being at the edge of the spawning zone (Merriner, 1976).

The youngest weakfish collected in this study (approximately 119 mm) was approximately 11 months old assuming spawning occured in June (Merriner, 1976). In a summary of published data concerning C. regalis, Wilk (1978) listed a range of 130 - 315mm T.L. for growth of weakfish at the end of the first year. Based on Wilk's compiled data, my collection of weakfish were either approaching the end of their first year or were one year of age.

Merriner (1976), in a comprehensive study of weakfish off the coast of North Carolina, found sexually mature fish at one year of age

with some of the smaller individuals maturing at two years (Table 2). To determine maturity, the standard length range in which 50% of weakfish are classified as mature, ripe, or ripe running is considered the size at which sexual maturity is attained (Merriner, 1976). Using this criteria, male weakfish mature before females. In the Moorehead City area, males mature at 130 mm S.L and females at 145 mm S.L. Similarly, at Pamlico Sound, males mature first at 150 mm S.L. while females mature at 190 mm S.L. Though sexual maturity occurs in males on average around 130 - 150 mm S.L., there were specimens collected by Merriner which matured earlier. Fish at 105 mm S.L. and several at 115 mm S.L. are sexually mature.

One would expect weakfish to mature at a similar size range off the Virginia coast owing to a similar environment and seasonal component. Further, weakfish to the northward may move southward in winter for long distaces, and offshore, as some of the northward summering scup do (Bigelow and Schroeder, 1923). If this movement also occurs with respect to Chesapeake Bay weakfish, the population off the coast of North Carolina may be from the same population as those seen in the bay area during the summer months. In either case, Merriner's data is applicable to the data gathered during the present study. Merriner's 50% average size over which males are found to be sexually mature is greater than the size at which sonic muscle began to develop. However, maturity here is determined by the point at which 50% of the sample are fully mature. Thus, there are individuals who are immature, those who are only beginning the process of spermatogenesis, or have

yet to attain full maturity, as well as individuals who mature well before the average. In a closer examination of Merriner's data one finds an example of 105 mm and several at 115mm S.L. in which sexual maturity has already been reached. Thus, the smallest individual in the present study found to possess sonic muscle (119 mm S.L.) fell within the range over which spermatogenesis was taking place. In support of this, my data showed the initiation of muscle growth to be concurrent with increased growth of the gonads. As the rate of gonad development began to accelerate, then, the sonic muscle tissue began to appear.

Merriner (1976) observed an interesting phenomenon with weakfish which cannot be confirmed here due to a limited collection period. Drumming muscles begin enlarging in December for the next breeding season and recede in size after the breeding season. The changes in muscle size correlate with the ripe and spent condition of the gonads.

TABLE 1. Presentation of statistical data calculated for each species.

TABLE 1

SPECIES	REGRESSION	ANALYSIS OF COVARIANCE						ANALYSIS OF VARIANCE			
		R^2		SLOPE		D.F.	F-STAT	R^2	SLOPE	D.F.	F-STAT
		M	F	M	F						
Croaker	Muscle Wt/ Body Wt	0.9682	0.9610	0.01354	0.00958	1, 92	53.35841				
Croaker	Muscle Wt/ Body Wt (<60g)	0.9378	0.9639	0.01107	0.00994	1, 63	2.67624				
Croaker	Muscle Wt/ Body Wt (50-105g)	0.7208	0.8777	0.01527	0.00917	1, 24	9.83455				
Croaker	Bladder Wt/ Body Wt	0.9746	0.9637	0.01527	0.01299	1, 91	11.72854				
Spot	Muscle Wt/ Body Wt							0.92827	0.00234	1, 17	219.99353
Spot	Bladder Wt/ Body Wt	0.8765	0.8588	0.00474	0.00363	1, 51	2.73332				
Weakfish	Muscle Wt/ Body Wt							0.76397	0.01624	1, 19	61.49742
Weakfish	Bladder Wt/ Body Wt	0.7926	0.9081	0.02510	0.02555	1, 37	0.00969				

TABLE 2. Correlation of data on sexual maturity, muscle development, and spawning season.

TABLE 2

SPECIES	ONSET OF MUSCLE DEVELOPMENT SEX	SIZE	AGE CLASS	ONSET OF SEXUAL MATURITY SEX	SIZE	AGE CLASS	SPAWNING SEASON
CROAKER	MALE	45mm	0	MALE	140-320mm	I-II	SEPTEMBER TO LATE MARCH (White and Chittenden, 1977)
	FEMALE	45mm	0	FEMALE	150-370mm (Pearson,1929)	I-II	
				BOTH ABOVE	200mm (White and Chittenden,1977)	I	
SPOT	MALE	105mm	0	BOTH	170-210mm (Pearson,1929)	I	OCTOBER TO MARCH (Dawson,1958)
				BOTH ABOVE	215mm (Hildebrand and Schroeder,1928)	I	
WEAKFISH	MALE	119mm	0	MALE	105-200mm	0-I	LATE APRIL TO JUNE (Merriner,1976)
				FEMALE	140-195mm (Merriner,1976)	0-I	

Summary and Conclusion

Croaker

The croaker presents a unique case in sciaenid fishes in that both male and female possess the sonic muscle. Development began at the same length and age in both sexes and occured long before sexual maturity was reached. Croaker mature at ages of two years or more and at lengths exceeding 200 mm T.L. according to Wallace (1940). Gonads examined in my study support this. Individuals at 93 mm and 109 mm S.L. were immature. However, a male at 184 mm S.L. was sexually mature and a female at 187 mm S.L., though not fully mature, was developing primary oocytes. Croaker sonic muscle, on the other hand, began to develop around 45 mm S.L. -- well within the first year. Though sonic muscle did develop before full maturation of the gonads, initiation of muscle growth coincided with the increased growth of the gonads. Thus, as the rate of gonad development increased, sonic muscle growth began. Male sonic muscle, however, began to grow larger than that of the female at 50g (140 - 150 mm S.L.). This size difference in muscle, which is more highly exaggerated in larger individuals, may correlate with gonadal state of sexually mature individuals. This would indicate a connection (presumably hormonal) between the increased growth of the male muscle with increased development of the testes.

Spot

Although only male spot possess the swimbladder muscle, the muscle itself appeared before gonadal spermatogenesis. Sexual maturity begins to appear around lengths of 149 mm S.L. (Townshend, 1956) and 170 mm T.L. (Pearson, 1929) in southern locations, and over 200 mm T.L. in the Chesapeake Bay (Hildebrand and Schroeder, 1928). The largest male captured in the present study was 158 mm S.L. and was immature. Spot sonic muscle, however, first appeared in a specimen of 106 mm S.L., well before sexual maturity. Further, the muscle developed within the first year of age while sexual maturity in spot was not attained until the second or third year. Muscle development and the acceleration of gonad growth, however, did begin at the same time. As the rate of gonad growth increased, sonic muscle development was initiated. Development of both variables was concurrent from this point on.

Weakfish

The smallest male possessing sonic muscle was 119 mm S.L. which falls within the range of sexual maturity which Merriner (1976) found extended down to 105 mm S.L. in samples collected off the coast of North Carolina. Further, Merriner found most of the fish examined to be sexually mature by one year of age with some smaller individuals maturing at two years. The smallest specimen of the present study with developing sonic muscle,then, occured within the range of sexual development. As in croaker and spot, weakfish sonic muscle began as

gonad growth increased in rate. At the same point that gonad development accelerated, sonic muscle development was initiated. Muscle growth was concurrent with gonad growth from this point. Only further research combining data on hormonal levels with muscle development can provide the answers to the question of control over development of the sonic muscle.

In all three species, one would expect a sensitivity to androgen production during some stage of development because of the sexual differences between males and females with respect to the presence of the sonic muscle or its relative size. According to Foster et al. (1983), steroidogenic activities have been detected very early in the immature testis (Oota and Yamamoto, 1966; Takahashi and Iwasaki, 1973; Satoh, 1974; Van Den Hurk, 1974; Nagahama et al., 1978; Van Den Hurk et al., 1982;). Interstitial cells, which exist in the interstitium between gonadal lobules and which have been implicated in other species as possible sites of steroidogenic activity, were not examined. These areas may yet be shown to be similarly active in early hormonal production in those species (such as spot) where muscle tissue occurs before gonadal spermatogenesis. Further research in this area may determine whether this sensitivity of sonic muscle to androgen production occurs and, if so, whether it occurs as a result of increased androgen output during sexual maturation.

Appendix A - Croaker

SEX	STANDARD LGTH (mm)	BODY WT (g)	BLADDER WT (g)	GONAD WT (g)	MUSCLE WT (g)	MUSCLE LENGTH(mm) L R	MUSCLE WIDTH(mm) L R
F	044.0	001.70	0.02	0.0006	0.0000	---------	---------
F	045.0	001.90	0.02	0.0004	0.0013	---------	---------
F	047.0	002.10	0.02	0.0002	0.0029	---------	---------
F	050.0	002.60	0.04	0.0006	0.0033	---------	---------
F	052.0	002.80	0.03	0.0013	0.0062	---------	---------
F	057.0	003.80	0.04	0.0012	0.0091	---------	---------
F	057.0	003.90	0.04	0.0023	0.0100	---------	---------
F	064.0	005.90	0.05	0.0030	0.0100	09.0;09.0	05.0;05.0
F	068.0	006.20	0.06	0.0042	0.0200	07.0;07.0	05.0;05.0
F	070.0	006.90	0.09	0.0025	0.0300	10.0;09.0	06.0;06.0
F	071.0	008.10	0.07	0.0031	0.0200	---------	---------
F	074.0	009.35	0.08	0.0032	0.0400	11.0;10.0	06.0;06.0
F	080.0	010.50	0.11	0.0051	0.0400	09.5;09.5	07.0;07.0
F	081.0	010.80	0.12	0.0193	0.0800	14.0;13.0	07.0;07.0
F	084.0	013.00	0.11	0.0113	0.0800	13.0;13.0	07.0;07.0
F	085.0	012.30	0.13	0.0130	0.0900	13.0;13.0	08.0;08.0
F	089.0	017.00	0.16	0.0052	0.0900	15.0;14.0	08.0;08.0
F	090.0	015.60	0.17	0.0132	0.1100	16.0;15.0	08.0;08.0
F	091.0	017.10	0.16	0.0092	0.1000	13.0;13.0	09.0;09.0
F	092.0	018.30	0.22	0.0186	0.1200	14.0;14.0	09.0;09.0
F	093.0	015.00	0.20	0.0325	0.1000	15.0;15.0	08.0;07.5
F	099.0	020.44	0.20	0.0430	0.1600	18.0;18.0	11.0;10.0
F	101.0	020.00	0.32	0.0376	0.1300	19.0;19.0	09.0;09.0
F	108.0	025.94	0.37	0.0287	0.1900	20.0;20.0	11.0;11.0
F	109.0	023.29	0.27	0.0590	0.2400	21.0;20.0	10.0;10.0
F	115.0	029.38	0.45	0.0733	0.2600	21.0;22.0	12.0;12.0
F	118.0	034.29	0.39	0.0743	0.2600	23.0;22.0	13.0;13.0
F	118.0	036.40	0.64	0.0325	0.3800	22.5;23.0	10.0;10.0
F	119.0	029.96	0.37	0.0775	0.2200	23.0;21.0	12.0;12.0
F	120.0	032.20	0.38	0.1082	0.2400	23.0;22.0	11.0;12.0
F	123.0	034.40	0.45	0.0742	0.3100	27.0;29.0	10.5;11.0
F	134.0	054.00	0.70	0.0809	0.4200	29.0;29.0	11.0;11.0
F	135.0	052.05	0.78	0.1342	0.5000	26.0;26.0	14.0;14.0
F	136.0	048.87	0.67	0.1631	0.5100	26.0;26.0	13.0;13.0
F	139.0	056.90	0.60	0.1355	0.4900	22.0;23.0	12.0;12.0
F	144.0	054.30	0.62	0.1121	0.5700	27.0;27.0	13.0;14.0
F	146.0	069.20	0.79	0.1946	0.6500	28.0;29.0	14.0;14.0
F	153.0	077.20	0.87	0.2230	0.7200	30.0;30.0	14.0;14.0
F	159.0	088.60	1.04	0.3110	0.7500	32.0;30.0	13.0;13.0
F	159.0	109.00	1.35	0.5518	0.9700	29.0;30.0	15.0;16.0
F	162.0	087.50	1.02	0.2739	0.7600	29.0;29.0	13.0;13.0
F	162.0	088.80	1.09	0.2560	0.8200	32.0;32.0	16.0;17.0

Appendix A (cont'd)

SEX	STANDARD LGTH (mm)	BODY WT (g)	BLADDER WT (g)	GONAD WT (g)	MUSCLE WT (g)	MUSCLE LENGTH(mm) L R	MUSCLE WIDTH(mm) L R
F	162.0	094.60	1.13	0.3078	0.8900	33.0;33.0	16.5;17.0
F	165.0	103.90	1.56	0.3305	0.9800	32.0;31.0	15.0;15.0
F	172.0	106.10	1.62	0.3771	1.0200	34.0;35.5	17.0;17.0
F	176.0	094.10	1.51	0.3609	1.0500	35.0;38.0	18.0;18.0
F	178.0	112.70	1.41	0.4554	0.9100	35.0;35.0	17.0;17.0
F	183.0	154.70	1.74	0.4779	1.2700	36.0;35.0	17.5;18.0
F	185.0	136.70	1.59	0.3847	0.9600	34.0;33.0	18.0;17.0
F	187.0	133.70	1.47	0.4202	1.3000	41.0;40.0	15.0;15.0
F	188.0	144.50	1.87	0.5571	1.7400	38.0;38.0	16.0;16.0
F	190.0	161.20	2.49	0.5721	1.6100	39.0;40.0	17.0;17.0
M	043.0	001.70	0.02	0.0001	0.0000	---------	---------
M	045.0	001.80	0.02	0.0001	0.0004	---------	---------
M	054.0	003.00	0.03	0.0006	0.0027	---------	---------
M	062.0	005.10	0.05	0.0002	0.0100	06.0;06.0	03.0;04.0
M	068.0	007.20	0.05	0.0003	0.0300	09.0;09.0	05.0;05.0
M	070.0	007.70	0.07	0.0009	0.0300	09.0;08.0	05.0;05.0
M	072.0	008.10	0.07	0.0009	0.0400	11.0;11.0	06.0;06.0
M	077.0	009.40	0.09	0.0007	0.0600	09.0;09.0	06.0;06.0
M	078.0	011.10	0.10	0.0011	0.0500	09.0;10.0	07.0;07.0
M	085.0	014.10	0.12	0.0030	0.1000	14.0;14.0	08.0;08.0
M	088.0	014.22	0.18	0.0014	0.0900	17.0;17.0	08.0;08.0
M	091.0	015.10	0.20	0.0026	0.1000	16.0;16.0	09.0;09.0
M	091.0	016.40	0.17	0.0022	0.1500	17.0;15.0	08.0;08.0
M	093.0	017.40	0.13	0.0023	0.1200	17.0;15.0	08.0;09.0
M	094.0	016.70	0.15	0.0023	0.1200	14.0;14.0	09.0;09.0
M	096.0	018.88	0.25	0.0017	0.1200	19.0;20.0	11.5;11.0
M	096.0	020.35	0.18	0.0024	0.1900	15.0;17.0	10.0;10.0
M	097.0	020.10	0.24	0.0026	0.1800	---------	---------
M	099.0	015.60	0.18	0.0085	0.1700	19.0;18.0	09.0;09.0
M	102.0	023.79	0.35	0.0068	0.1900	23.0;22.0	11.0;11.0
M	103.0	022.47	0.32	0.0035	0.1900	22.0;21.0	12.0;11.5
M	104.0	021.66	0.31	0.0007	0.1900	20.0;20.0	12.0;12.0
M	109.0	025.98	0.32	0.0031	0.1500	19.0;19.0	12.0;12.0
M	121.0	040.12	0.57	0.0093	0.3900	27.0;28.0	12.0;12.0
M	124.0	038.30	0.56	0.0194	0.3600	27.0;27.0	12.5;12.0
M	133.0	057.00	0.62	0.0136	0.7400	25.0;26.0	15.0;15.0
M	134.0	045.41	0.76	0.0123	0.5300	29.0;27.5	14.0;14.0
M	134.0	055.49	0.71	0.0145	0.4600	28.0;28.0	14.0;14.0
M	136.0	043.30	0.50	0.0100	0.4400	29.0;30.0	12.0;12.0
M	136.0	047.60	0.64	0.0068	0.4300	28.0;28.0	14.0;15.0
M	139.0	052.77	0.76	0.0187	0.4800	27.5;27.0	14.0;14.0
M	149.0	071.70	0.90	0.0230	0.7200	32.0;30.0	15.0;16.0
M	155.0	075.30	1.09	0.0963	1.1400	33.0;34.0	15.0;14.0

Appendix A (cont'd)

SEX	STANDARD LGTH (mm)	BODY WT (g)	BLADDER WT (g)	GONAD WT (g)	MUSCLE WT (g)	MUSCLE LENGTH(mm) L R	MUSCLE WIDTH(mm) L R
M	155.0	079.30	1.09	0.0643	1.0000	33.0;35.0	16.0;16.0
M	161.0	091.80	1.45	0.0282	1.0500	34.0;33.0	18.0;17.5
M	164.0	086.50	0.92	0.0767	0.8500	37.0;36.0	17.0;16.0
M	166.0	105.40	1.67	0.0264	1.1400	33.0;32.0	18.0;18.0
M	168.0	079.90	1.31	0.0659	0.8300	36.0;36.0	16.5;16.5
M	170.0	103.80	1.32	0.0803	1.6000	38.0;38.0	14.0;14.0
M	182.0	146.60	2.07	0.1025	2.0800	42.0;42.0	15.0;15.0
M	183.0	111.40	1.51	0.1741	1.4800	44.0;44.0	16.0;16.0
M	184.0	168.50	2.69	0.1378	2.1100	44.0;42.0	16.0;15.0
M	188.0	123.00	2.06	0.0836	1.6400	42.0;42.0	17.0;17.0

Appendix B - Spot

SEX	STANDARD LGTH (mm)	BODY WT (g)	BLADDER WT (g)	GONAD WT (g)	MUSCLE WT (g)	MUSCLE LENGTH(mm) L R	MUSCLE WIDTH(mm) L R
M	090.0	018.88	0.13	0.0100	0.0000	---------	---------
M	098.0	024.59	0.14	0.0063	0.0000	---------	---------
M	101.0	029.20	0.15	0.0032	0.0000	---------	---------
M	106.0	034.10	0.17	0.0021	0.0029	---------	---------
M	108.0	030.90	0.14	0.0027	0.0065	---------	---------
M	111.0	039.50	0.17	0.0056	0.0100	---------	---------
M	112.0	035.90	0.13	0.0040	0.0046	---------	---------
M	112.0	037.40	----	0.0024	0.0000	---------	---------
M	114.0	037.80	0.12	0.0042	0.0000	---------	---------
M	114.0	039.00	0.16	0.0013	0.0067	---------	---------
M	115.0	035.50	0.18	0.0062	0.0300	---------	---------
M	115.0	041.00	0.13	0.0038	0.0000	---------	---------
M	115.0	041.40	0.13	0.0017	0.0000	---------	---------
M	116.0	035.40	0.18	0.0103	0.0300	---------	---------
M	116.0	042.80	0.17	0.0058	0.0200	---------	---------
M	116.0	043.00	0.21	0.0043	0.0076	---------	---------
M	117.0	042.80	0.16	0.0015	0.0000	---------	---------
M	118.0	043.40	0.20	0.0121	0.0200	---------	---------
M	123.0	057.30	0.23	0.0204	0.1100	21.0;21.0	07.0;07.0
M	128.0	060.00	0.27	0.0173	0.0500	20.0;18.0	06.0;05.0
M	129.0	057.50	0.20	0.0143	0.0700	29.0;27.0	08.0;07.0
M	143.0	069.70	0.37	0.0187	0.0700	22.0;22.0	06.0;06.0
M	144.0	082.20	0.50	0.0229	0.1200	21.0;20.0	04.0;05.0
M	146.0	078.00	0.29	0.0323	0.1100	21.0;20.0	06.0;06.0
M	156.0	108.80	0.53	0.0218	0.2100	27.0;28.0	09.0;09.0
M	158.0	093.50	0.44	0.0244	0.1500	29.0;29.0	07.0;07.0
M	165.0	129.10	0.74	0.0239	0.2100	32.0;32.0	08.0;08.0

Appendix C - Weakfish

SEX	STANDARD LGTH (mm)	BODY WT (g)	BLADDER WT (g)	GONAD WT (g)	MUSCLE WT (g)	MUSCLE LENGTH(mm) L R	MUSCLE WIDTH(mm) L R
M	119.0	029.60	0.50	0.0093	0.0077	---------	---------
M	125.0	038.40	0.68	0.0230	0.0900	29.0;28.0	08.0;08.0
M	126.0	032.28	0.91	0.0339	0.0000	---------	---------
M	129.0	039.30	0.62	0.0174	0.0000	---------	---------
M	132.0	034.80	0.72	0.0447	0.0900	27.0;27.0	10.0;10.0
M	134.0	031.30	1.04	0.0721	0.1100	28.0;21.0	10.0;09.0
M	135.0	037.40	0.83	0.0102	0.0400	---------	---------
M	136.0	048.60	0.89	0.0227	0.1200	33.0;32.0	08.0;08.0
M	139.0	048.30	1.02	0.2022	0.3200	37.0;33.0	09.0;09.0
M	139.0	049.60	0.94	0.0940	0.1700	28.0;29.0	10.0;10.0
M	147.0	053.18	1.19	0.0339	0.1000	---------	---------
M	147.0	060.50	1.15	0.4658	0.6700	40.0;40.0	15.0;15.0
M	148.0	051.60	1.40	0.4460	0.3500	35.0;35.0	11.0;11.0
M	153.0	058.80	1.24	0.6488	0.5300	40.0;35.0	12.0;12.0
M	155.0	068.60	2.12	0.7333	0.8600	42.0;42.0	15.0;15.0
M	156.0	062.30	1.17	0.3221	0.3900	45.0;43.0	13.0;13.0
M	158.0	065.30	1.35	0.6736	0.7700	42.0;42.0	13.0;13.0
M	160.0	070.70	1.59	0.2576	0.2800	33.0;33.0	15.0;15.0
M	164.0	079.90	1.38	0.1372	0.3800	42.0;36.0	12.0;12.0
M	172.0	093.90	1.98	0.4184	0.9300	50.0;50.0	18.0;18.0
M	174.0	089.60	1.93	0.8542	1.1200	47.0;46.0	18.0;18.0
M	179.0	107.90	2.33	1.3494	1.6300	51.0;51.0	19.0;19.0
M	182.0	103.57	3.31	0.6974	0.8700	47.0;47.0	15.0;15.0

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