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TESTES MORPHOLOGY, HISTOLOGY AND SPERMATOGENESIS IN SOUTH PACIFIC ALBACORE TUNA

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INTRODUCTION

The reproductive biology of tuna, and the albacore (Thunnus alalunga) in particular, is not well understood with respect to the functional morphology of the gonads in relation to sexual maturity. In the course of an investigation of the genetic variability of albacore, differences in morphology were observed between the right and left gonad of male and female fish and the size of the fat body associated with the gonads. Histological examinations were made to determine the relationship between these morphological differences and the reproductive state of the gonads. In this paper we report findings made on testes morphology, histology and spermatogenesis.

MATERIALS AND METHODS

The albacore specimens were collected on board the U.S. NOAA R/V TOWNSEND CROMWELL and the New Zealand R/V KAHAROA during cooperative studies conducted in 1986 and 1987 to investigate the biology/ecology and fishery exploration of albacore tuna in the South Pacific Ocean (Laurs, 1986 and Laurs et al., 1987). The fish were caught on the research vessels using standard albacore troll fishing methods (Dotson 1980). In addition, specimens were collected during commercial fishing operations conducted in 1987 by Japanese longline vessels. The locations where specimens were collected are summarized in Table 1.

Soon after the fish were caught, the fork lengths were measured to the nearest millimeter and various tissues and samples, including the gonads and associated fat body were dissected from each fish. The right and left gonads were preserved separately in 10% buffered formalin.

When the gonads were returned to the laboratory, the formalin was changed and the gonads from each fish were further divided into a right and left rostral, medial, and caudal portions. Each segment was placed in a separate biopsy bag and all bags from each fish were stapled together. Great care was exercised to maintain proper identification for each subsample throughout the course of the study.

Histological preparations were initiated by washing the tissue in running water for 12 hours. An American Optical T/P tissue processor was used to dehydrate and embed the tissue in paraplast. The tissue was sectioned at five microns and stained with Harris' hematoxylin followed by eosin counter stain (Humason 1979 and Gabe 1978). The stained tissue sections were examined with an Olympus Universal Vanox light microscope, which was also outfitted with an Olympus C35A camera to photograph representative sections.

Each testis subsample histological preparation was classified according to: a) estimates of the relative abundances of spermatocytes, spermatids and sperm; b) sperm duct development; and c) sexual maturity. In addition, the cross sectional area of the medial section of each testis was determined using a Model 100 Image Analysis System[1] interfaced with a minicomputer. Electron micrographs were prepared of sperm, which had been washed from the sperm duct of selected testes with physiological saline and fixed in 3% gluteraldehyde in 0.1 M phosphate buffer.

Table 1. Summary of Information on Specimens Used in Study

Ship	Date	No. Spec.	Range FL(cm)	Median FL(cm)	Location
R/V TOWNSEND CROMWELL	1986 2/17-2/21	33	50.6-84.4	71.5	Central S. Pacific 38°-40°S 146°-152°W
R/V TOWNSEND CROMWELL	1987 1/25-2/1	33	50.6-97.5	63.8	Central S. Pacific 35°-39°S 151°-157°W
R/V KAHAROA	1986 2/15-3/28	13	50.0-76.0	70.0	Western S. Pacific 33°-44°S 166°E-178°W
F/V WAKASHIO	1987 6/21	9	63.0-98.0	88.0	Western S. Pacific 37°S 179°E
F/V ZUIHO	1987 6/20-6/23	18	85.2-101.1	94.5	Western S. Pacific 37°-38°S 179°E

[1] Developed by Analytical Imaging Concepts, Irvine, Ca.

RESULTS

We observed asymmetrical differences in the size of both the ovaries and testes and in the size of the fat body associated with the gonads from both sexes of fish. Histological examination showed that all stages of sexual maturity were represented in the specimens of testes, allowing us to describe spermatogenesis. No sexually mature ovaries were found, limiting the results for females to asymmetrical size differences.

Number and Size of Fish Examined

The gonads from 197 albacore were examined histologically during the study. The sex ratio was nearly 1:1, with 106 males and 91 females. The fish ranged in fork length from 50 to 101 cm. Over 90% of the females and over 80% of the males were less than 90 cm in fork length, the size where sexual maturity is believed to first occur in female albacore (Ueyanagi, 1955; Otsu and Uchida, 1959; and Otsu and Hansen, 1961). The length frequency distribution of the fish examined is given in Figure 1.

General Morphology of the Gonad

As in most teleosts, the gonads in the male and female albacore are paired, elongate organs, located in the dorsal portion of the body cavity. They are suspended by the mesentery which contains a fat body closely associated with the gonad between it and the dorsal body wall (Godsil and Byers, 1944). The fat body will be discussed in a later section. The testes are thin and ribbon-like in immature fish, and develop into somewhat flattened, whitish-yellow organs which are relatively solid as the fish advance in maturity. The ovaries in immature fish closely resemble the immature testes in appearance. They become progressively enlarged in length and girth and tend to be somewhat pinkish in color as the fish progresses in maturity.

We initially made casual observations when collecting gonad tissue samples for North Pacific albacore genetic variability studies, that the right gonads were most often larger than those on the left side. The present study of nearly 200 South Pacific albacore showed that while right and left gonads of both sexes were about the same length, the cross sectional area and volume of the right ovaries and testes were regularly larger than those on the left side. Figure 2 is a photograph showing a pair of ovaries, part of the digestive tract and the ventral fin dissected from a 94 cm North Pacific albacore. The disparity in size between the right and left ovaries and associated fatty tissue is typical of what we have observed in this study and in casual observations.

Size differences between right and left testes

Measurements of the cross sectional area (mm^2) of the medial sections of the right and left testes provide quantitative estimates of the differences in size between the two. Data summarized in Table 2 show that the right testis was larger than the left in 72% of the male fish examined, the two testis were equal in size in 2% and the left was larger than the right in 23% of the male fish investigated.

Table 2. Relative size of right and left testes, n = 106.

Relative Size of Testes	Percent Occurrence
Right Larger Than Left	72%
Right Equal To Left	2%
Right Smaller Than Left	23%
No Data	3%

The results given in Figure 3, show that the dissimilarity in size increases with increasing fork length. The right testis is between about 28% and 32% larger than the left one in fish less than 80 cm, but increases to between about 66% and 75% larger in fish over 80 cm. Data on displacement volumes measured on a sample of the right and left testes showed results similar to those made on the measurements of cross section. Examination of relationships between fork length and the cross sectional area of the right and left testes showed that the sizes of both gonads increase exponentially with increasing length of the fish, and that the area of the right testis does not increase at a faster rate than the left.

In summary, the right testis is predominately larger than the left, however, they both appear to increase in size at similar rates as the fish increases in length.

Histology of Testes

The cells in the albacore testis have a lobular type arrangement, characteristic of most teleosts (Billard et al., 1982). There are numerous seminiferous lobules which are separated from each other by a thin layer of connective tissue. Each lobule contains abundant numbers of cysts of germ cells. Each cyst contains spermatogenic cells that are in the same stage of spermatogenesis. However, the cysts in the lobules may be in different phases of development. Upon maturation, the cells in each cyst are released into the lobule duct, which is continuous with the main sperm duct. The spermatogonia are limited to the peripheral cysts within a tubule. As spermatogenesis proceeds, the cysts extend toward the lumen of the tubule. Lobules containing the more advanced stages are situated toward the center of the testis.

We classified the germ cells into the traditional five phases of development: spermatogonia, primary spermatocytes, secondary spermatocytes, spermatids and spermatozoa.

The primary spermatogonia are the largest cells with diameters from 12 to 16 um. The cells are usually found singly near the periphery of the testis. They have a prominent nucleolus and are basophilic. The primary spermatogonia differentiate into secondary spermatogonia whose nuclei take on a deeper stain. They are found in cysts with varying numbers of individual cells. A cyst of these cells can be seen situated on the lobule wall in Figure 4A.

The primary spermatocytes develop from the spermatogonia by mitotic division. These cells are oval or spherical and are smaller than the spermatogonia. They have no visible nuclear membrane and the chromatin material occupies most of the cell. They have diameters ranging from 8 to 12 um. Figure 4B shows examples of primary spermatocytes.

The secondary spermatocytes are derived from the mitotic division of the primary spermatocytes. These are very small, spherical cells with diameters ranging from 4 to 7 um. Unlike the primary spermatocytes, the chromatin is found in a clumped condition, similar to the spermatids. The cells occur in groups and are strongly basophilic. Figure 4B shows secondary spermatocytes.

Mitotic division of the secondary spermatocytes produces the spermatids. Spermatids are strongly basophilic spherical cells with diameters ranging from 2 to 4 um. As they mature, they become smaller and the chromatin becomes uniformly condensed. Figure 4C shows that after detaching from the lobule wall, the spermatids remain in dense clusters.

The spermatozoa are the smallest of all the germ cell types in the testis, measuring 1 to 2 um in diameter, excluding the tail. An electron micrograph of an individual sperm is given in Figure 5. The sperm has a rounded nucleus and is morphologically subdivided into head, neck piece, short midpiece and tail; as in other teleosts, there is no acrosome.

Meiotic Activity

The relative abundances of sperm, spermatids and spermatocytes were taken as a measure meiotic activity. As previously discussed, the albacore testes were generally asymmetrical in size with the right testis more often larger than the left one. However, we found that the meiotic activity and sperm duct development showed the opposite relationship. The left testis was meiotically more active than the right in 61% of the males examined, the left and right testis had about equal activity in 26%, and the right was more active than in the left in 10%, see Table 3.

Table 3. Differences in meiotic activity between right and left testes, n = 106.

Meiotic Activity	Percent Occurrence
Left Less Than Right	10%
Left Equal to Right	26%
Left Greater Than Right	61%
No Data	3%

Examination of the data for each pair of testes showed that there was a 60% occurrence where the meiotic activity was greater in the left testis than the right and the right testis was larger than left. Other combinations of meiotic activity and relative size of the testes showed a 15% or less occurrence, see Figure 6.

Relative Abundance of Sperm, Spermatids and Spermatocytes

Absolute counts of the number of spermatogenic cells would be exceedingly difficult to make. Instead we estimated the relative abundance of spermatocytes, spermatids and sperm present using the categories none, few, some and many. The results show that for all sizes of fish, the relative abundance of sperm was higher in the left testis than the right testis. For example, there were nearly 2 times more "many" and 2 1/2 times fewer "none" categories observed for the left than the right testis. In both the left and right testes of fish in all sizes, the relative abundance of sperm was highest in the caudal portion and decreased towards the rostral end, see Figure 7.

The findings for the spermatids and spermatocytes are similar, but the differences between testes are not as pronounced as those for sperm. For all sizes of fish, the relative abundance of both the spermatids and the spermatocytes was higher in the left than the right testis. There were about 20% and 30% more "many" and 40% and 50% fewer "none" categories for the spermatids and spermatocytes, respectively, observed for the left than for the right testis. The relative abundance of each group of germ cell was highest in the caudal portion and decreased towards the rostral portion in both the left and right testes in all sizes of fish.

Sperm Duct Development

During testicular morphogenesis, teleost sperm ducts are formed by somatic cells derived from the somatic wall (Nagahama 1983). The main duct is present in immature testes (Figure 8A) in which no sperm are found. In mature albacore, we observed that the sperm duct is located near the center of the testis (Figure 8B) and that a branching system of tubules radiate toward and end blindly at the testicular periphery. These observations differ from those reported for many other teleosts, where the main duct is located along the dorsal surface of the testis and may not be present in immature stages of the testis Grier et al., 1980).

As the production of sperm increases, morphological changes occur in the main sperm duct. In the immature testis the main sperm duct is thin walled and highly convoluted (Figure 8A). In the mature testis when the main duct is filled with sperm, it has much thicker walls, and is less convoluted and more rounded. (Figure 8B). The production of sperm is also associated with increased vascularization of the testis, first in the caudal portion and followed by the medial and rostral portions.

Ratios of observations characterizing immature and mature stages of sperm duct development - thin:thick, convoluted:round, and large:small - showed a higher proportion of mature sperm ducts in the left testis than the right. The results also reveal that the sperm duct development is greatest in the caudal, intermediate in the medial and least in the rostral portions in both the right and left testis. As would be expected, there was a trend for sperm duct development to increase with increasing fork length of fish.

Sexual Maturity

The fish were classified into five levels of sexual maturity based on the relative abundance of sperm observed in the testes. The classification levels and criteria include: 1) no sperm present in any portion of either testis, 2) immature, few sperm observed in one or more portions of either or both testes, 3) intermediate, few or some sperm in more than one portion of both testes, but not the sperm duct, 4) mature, many sperm observed in most portions of both testes and the sperm duct, and 5) fully mature, many sperm observed in all portions of both testes and the sperm duct.

Information on sexual maturity in relation to fork length size categories is given in Figure 9 and Table 4. Slightly over 50% of the fish between 50 cm and 70 cm were immature, including 28% (derived from Figure 9) that had no sperm present in any portion of either testis. Over 40% were in the intermediate level and 7% were judged sexual mature, but none was fully mature. Fish in size groups larger than 70 cm had a lower proportion of immature individuals than did fish less than 70 cm, ranging from 18% to 40% (Table 4), including only 3% to 10% that had no sperm present in any portion of either testis (derived from Figure 9). The proportion of fish in the intermediate level of maturity ranged between 20% to 46% for fish in the size groups larger than 70 cm. The percentages of fish in the mature plus fully mature categories were nearly the same for size groups 71-80 cm and 81-90 cm, 36% and 40%, respectively, but only 21% for the size group over 90 cm. The 71-80 cm size group had the highest proportion of fully sexually mature individuals, 23%, while only about 5% of the fish larger than 90 cm were fully sexually mature (derived from Figure 9).

The lower proportion of mature and fully mature individuals in the size group of fish larger than 90 cm appears to be related to geographic region where the fish were caught and/or the type of fishing gear type used to catch the fish. Figure 10 gives a comparison of maturity levels between fish caught in the mid-ocean region of the central South Pacific by surface trolling and fish caught in coastal waters off New Zealand by subsurface longline. It is evident in Figure 10 that a higher proportion of immature and lower proportion of mature plus fully mature individuals were caught in the coastal waters than in the mid-ocean region. This is so, even though the longline-caught fish were much larger, averaging 92.3 cm, than the troll-caught fish, averaging 69.2 cm. Figure 1 shows that virtually all of the fish in the greater than 90 cm size category were caught in the coastal waters by subsurface longline.

Table 4. Sexual Maturity of Fish by Fork Length Category

Sexual Maturity Stage	Fork Length (cm) <70	71-80	81-90	>90
No Sperm Present and Immature	51%	18%	40%	37%
Intermediate	42%	46%	20%	42%
Mature and Fully Mature	7%	36%	40%	21%

Fat Body

A lobulated mass of fat-like tissue was usually observed in the mesentery attached to the testes and ovaries. In some cases it was extremely large and well developed, but in others it was quite rudimentary. It was generally white to creamy in color and always formed in segmental lobes. The extent of the fat body was usually coincident with that of the gonad, but sometimes it extended a variable distance anteriorly beyond the gonad. The mass of the fat body was generally correlated with the size of the gonad. We observed that the right testis or ovary of the albacore, which is generally larger than the left one, usually had a larger fat body (see Figure 2). In addition, we observed that the fat body was proportionately larger in the immature fish that were not meiotically active compared to fish with gonads that were actively producing sperm.

DISCUSSION

According to literature pertaining to the general structure and function of teleost gonads, the development of the gonads is usually similar on both sides of the fish. However, asymmetry in gonad size has been observed sometimes in some species, usually at or near the time of breeding (Turner, 1919; Robertson, 1957; Sanwal and Khana, 1972; Dalela et al., 1976; and others).

Asymmetry in gonad size appears to be common for albacore, at least in the pre-spawning stages. We observed asymmetry in 95 % of the fish examined, with the right being larger than the left in 72 % of the cases. The disparity in size increased with increasing fork length. The right testis averaged about 30 % larger than the left in fish less than 80 cm and averaged more than 70 % larger in fish greater than 80 cm. We do not have data collected during active spawning to ascertain if this relationship exists at that time.

Otsu and Uchida (1959) reported that the right ovary was usually slightly larger than the left in albacore specimens from the central North Pacific, but they did not quantify the difference. Ueyanagi (1955) noted that the right and left albacore ovaries from a mature female caught in the Indian Ocean differed in weight by 100 gms. However, he did not indicate the weights of the ovaries or which ovary was larger. Partlo (1955) conducted histological studies on 44 albacore from the eastern North Pacific, but did not publish information on the sizes of the gonads nor made mention of asymmetry. The gonads of other tunas are more-or-less symmetrical in size and usually do not have a conspicuous fat body (Kurt Schaefer, pers. comm.).

The finding that the meiotic activity is higher in the smaller of a pair of testes is puzzling, and we have no ready explanation for it. It may be that this relationship holds true only for pre-spawning individuals and possibly during other periods when albacore are not actively spawning. We are unable to determine whether this condition continues through the spawning cycle because our samples were collected over an insufficient period and not in the primary geographic region where South Pacific albacore are believed to spawn (Otsu and Hansen, 1961). A remote possibility is that the smaller testes is kept in an advanced reproductive state for "opportunistic" spawning and that the larger testis matures only when the fish is in the more prevalent location of spawning. If this is so, the species could extend its reproductive potential with presumably relatively low expenditures of energy. It is also possible that sperm are not shed by precocious fish, but are reabsorbed. Progressive reabsorption of sperm by Sertoli cells has been observed in rainbow trout (van den Hark et al., 1978).

Our results show that some males less than 70 cm may be sexually mature and that the proportion of sexually mature individuals increases with increasing fork length, up to 90 cm. There is a decrease in the percentage of sexually mature males in the size category above 90 cm which may be related to the method of capture and/or the habitat type where they were collected. All of the fish larger than 90 cm, except one, were caught during subsurface longline fishing operations within about 75 miles of the coast of the New Zealand north island. Whereas, nearly all other fish were caught by surface trolling in mid-ocean waters. Oceanographic observations made concurrently with albacore troll fishing operations indicate that albacore in the mid-ocean region of the South Pacific are associated with Subtropical Convergence Waters (Laurs, 1986 and Laurs, et al., 1987).

Female albacore have been reported to attain sexual maturity and first spawn at about 90 cm (Ueyanagi, 1955; Otsu and Uchida, 1959). However, the size at maturity for males has not been well established. Otsu and Hansen (1961) found that some male albacore are probably mature when they attain a length of about 90 cm. Based on the general appearance of testes and oozing of milt, Ueyanagi (1957) postulated the smallest mature male to be 97 cm in a sample of albacore collected in the western North Pacific. Brock (1943) reported that "...Milt could be squeezed from the testes of some of the more mature males, but no females were found in which eggs could be discerned by the unaided eye..." Brock examined fish caught off the Oregon coast that ranged in fork length between 53 and 90 cm, but did not specify the size of fish that contained milt.

Partlo (1955), in the only published histological study that includes albacore testes as well as ovaries, concluded that both males and females in age-groups he assigned as V and VI, were in a condition approaching spawning. Partlo calculated that the mean fork length for males and females in age-group V is approximately 70 cm, and for age group VI is about 85 cm for males and 79 cm for females. Partlo also reported observing small numbers of fully mature sperm restricted to the tubules of the posterior portion of testes in age group IV, which he reported as having a mean length of 62 cm. Partlo examined on a total of 44 testes and ovaries, but unfortunately did not specify the sex or number of individuals in each of the age-groups.
this study were caught.

Godsil and Byers (1944) reported that the fat body was present in albacore collected throughout the North Pacific, except in three specimens from the area around the Hawaiian Islands, and that it always reached its greatest development on the right side of the fish. However, they made no mention of asymmetry in the size of the gon s.

There appears to be a functic al relationship between meiotic activity and the amount of fat i the mesentery. We presume the fat body provides a source of energy for spermatogenesis, although we have no information from the present study on the timing of sperm release from the albacore testis. Godsil and Byers (1944) also speculated tha the fat body acts as an energy reserve for female albacore that is expended during the spawning season. They based their supposition on the absence of the fat body in the three female albacore examined from the Hawaiian area, which based on inspection of the ovaries had recently spawned. Schaefer (1986) noted that spawning in the black skipjack, Euthynnus lineatus, is probably regulated by the available energy in fat storage. When the fat stores fall below a minimum level, ovarian atresia probably occurs over a short period of time.

CONCLU IONS

We provide quantitative evid ce that a substantial portion of male albacore caught in mid-o an areas of the South Pacific Subtropical Convergence Zone b ween about 35°- 40°S, may be sexually mature when they attain a size of 71-80 cm. Also, the proportion of mature fish increas s with increasing length. Males caught by subsurface longline fi ing in coastal waters off New Zealand also showed development i sexual maturity, but in lower proportions and not as accelerated as males caught by surface trolling in the mid-ocean region. Female fish caught in both regions, which ranged between 55 cm and 95 cm FL, showed little sign of advancement in sexual maturity. South Pacific albacore are believed to spawn generally in the region of the Southern Tropical Convergence waters between about 20°- 10°S (Knox, 1970). This region is about 1,000 to 1,500 miles south of the Subtropical Convergence Zone where the albacore investigated in

The adaptive significance is not clear as to the advantage for male albacore to be sexually mature at times, locations and ages when females are not in spawning condition. Sampling of both males and females over the ent e spawning cycle and in the locations where albacore are bel ved to spawn will be required to understand the reproductive iology of the South Pacific albacore population.

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FIGURE LEGENDS

Figure 1. Length frequency distributions for male and female albacore examined in study. Surface troll caught fish and sub-surface longline caught fish differentiated.

Figure 2. Photograph showing pairs of ovaries and fat bodies and ventral fin from 94 cm albacore.

Figure 3. Percentage difference in cross sectional area of the medial sections of right and left testes, by fork length categories.

Figure 4. Spermatogenic cells observed in albacore testes, x600. A. Spermatogonia (SG) situated on lobule wall. B. Primary spermatocyte (PS) cells and secondary spermatocyte (SS) cells. C. Spermatids (SM) and spermatozoa (S).

Figure 5. Electron micrograph of albacore spermatozoa, scale indicates 1 micron.

Figure 6. Percentage occurrence of relative level of meiotic activity and relative size of right and left gonads. First expression in each category refers to relative size of gonad and second to the relative level of meiotic activity, e.g. R>L and R>L refers to occurrences where the right testis was larger than the left and meiotic activity was greater in the right testis than the left.

Figure 7. The relative abundance of sperm in the rostral, medial and caudal portions of the right and left testes.

Figure 8A. Sperm duct of a mature albacore filled with sperm, and B. Empty sperm duct of an immature albacore, x100.

Figure 9. Comparison of maturity levels for fork length categories of male albacore.

Figure 11. Comparison of maturity levels of male albacore caught in coastal waters by subsurface longline with those caught in mid-ocean region by surface trolling.

Male and Female Albacore Fork Length Frequencies

Surface Troll Caught Fish and Subsurface Longline Fish Differentiated

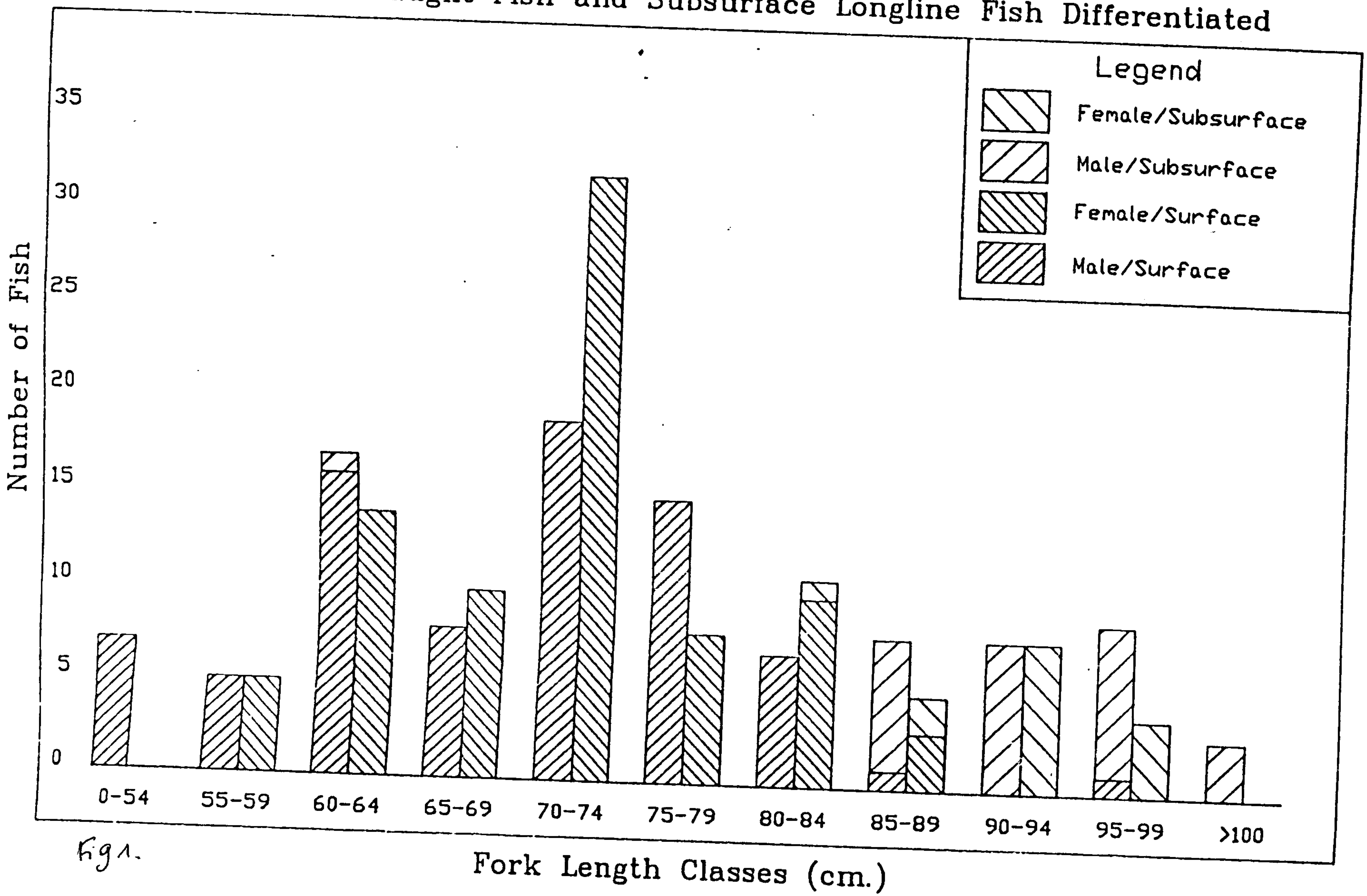
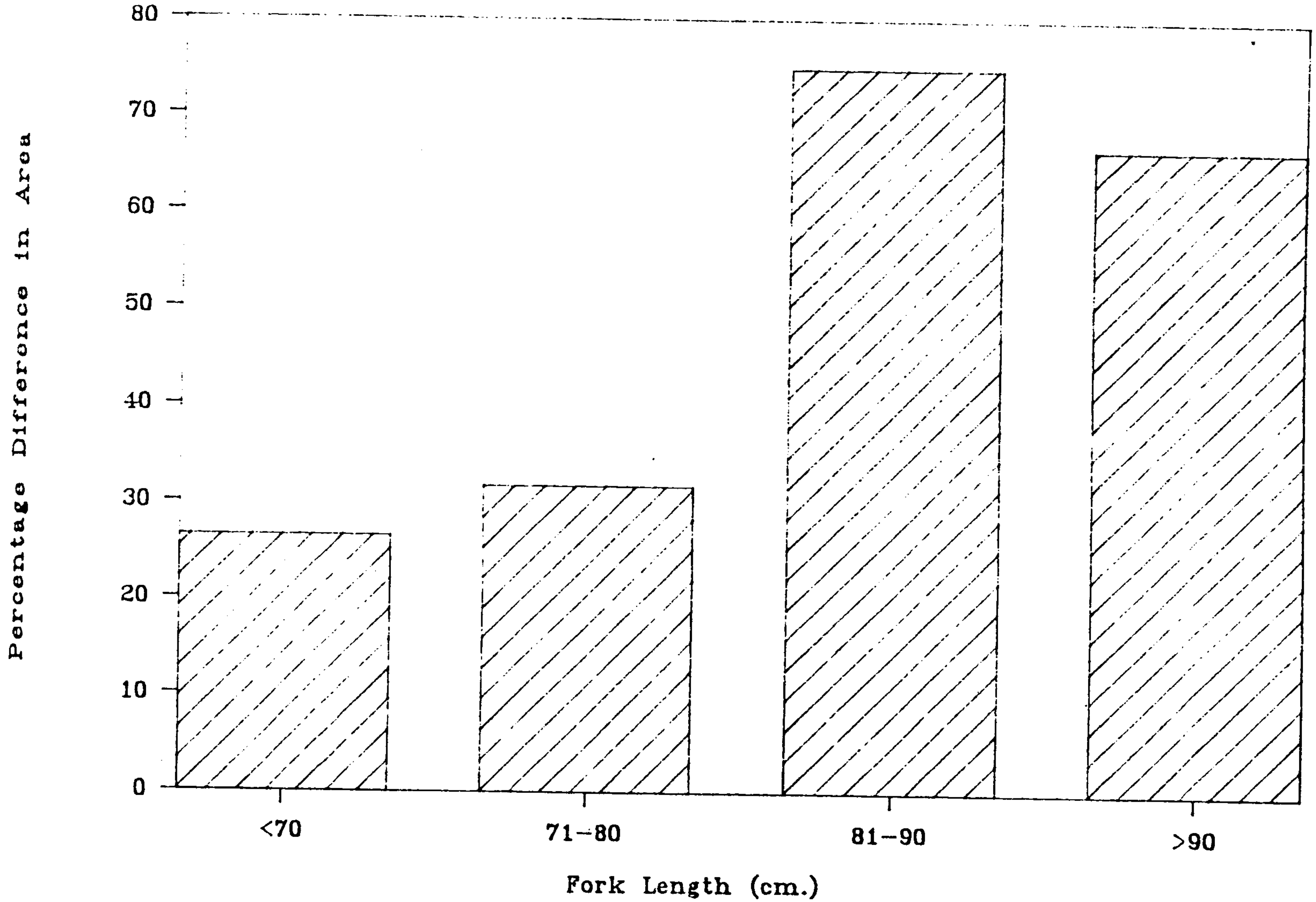


Fig 1.

FIG 1

fig 3.



80
70
60
50
40
30
20
10
0
Percentage Difference in Area
<70
71-80
81-90
>90
Fork Length (cm.)

FIG 3

FIG. 4

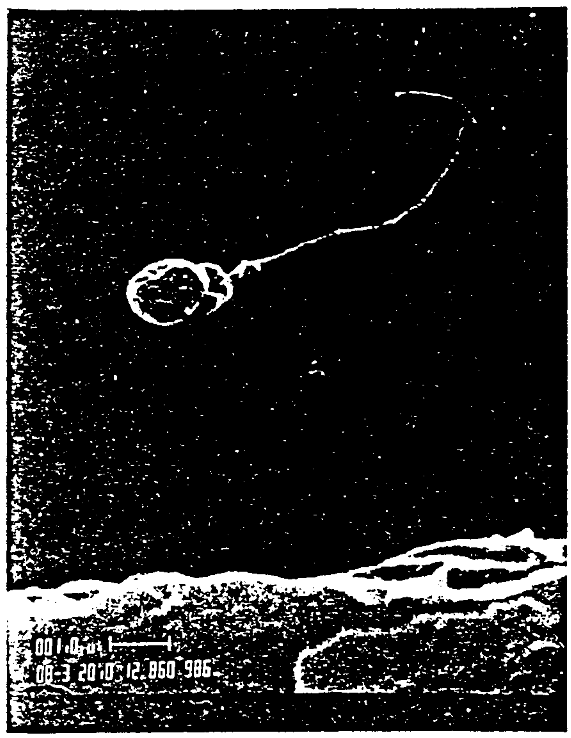
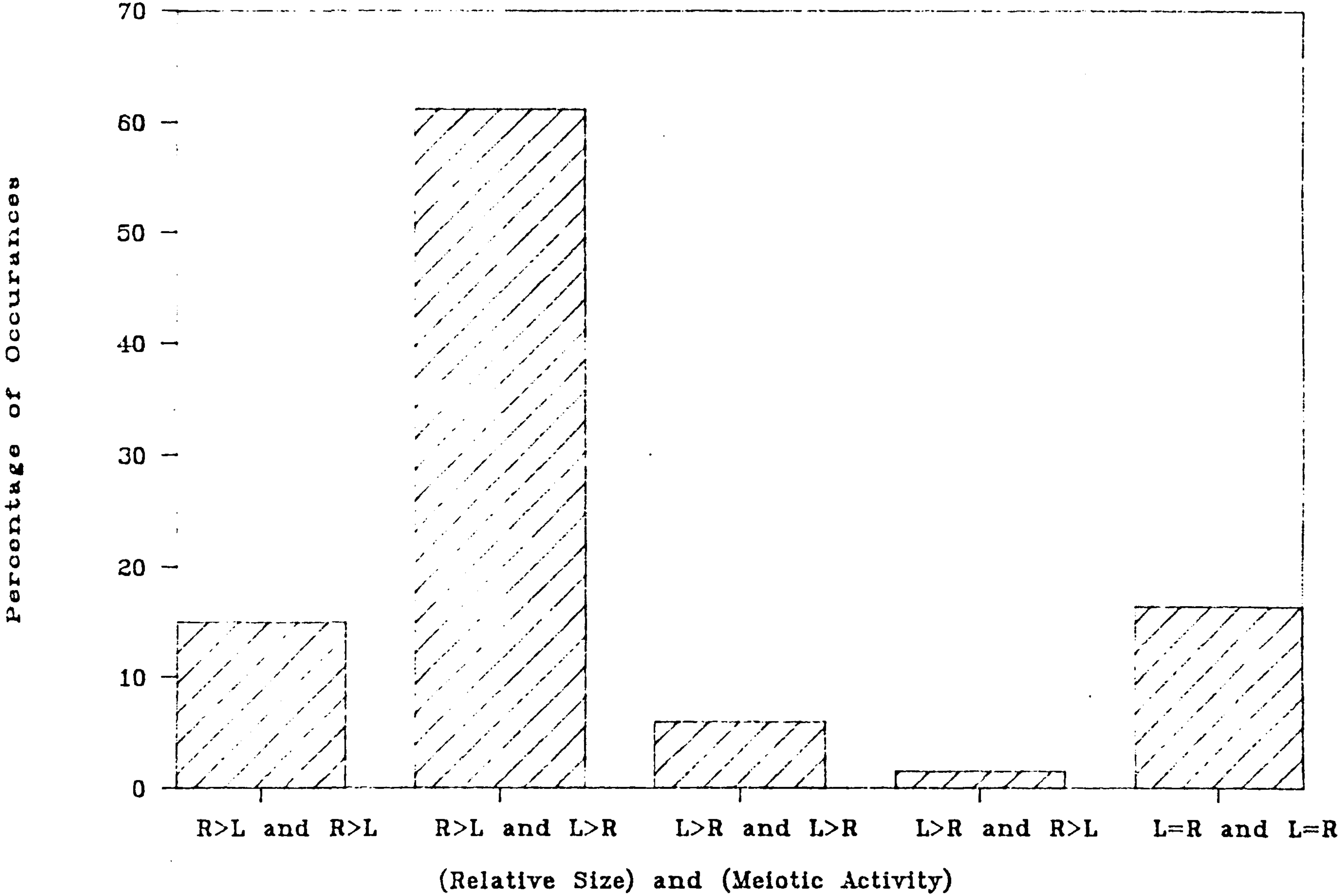


Fig5

Fig 6



70
60
50
40
30
20
10
0
Percentage of Occurances
R>L and R>L
R>L and L>R
L>R and L>R
L>R and R>L
L=R and L=R
(Relative Size) and (Meiotic Activity)

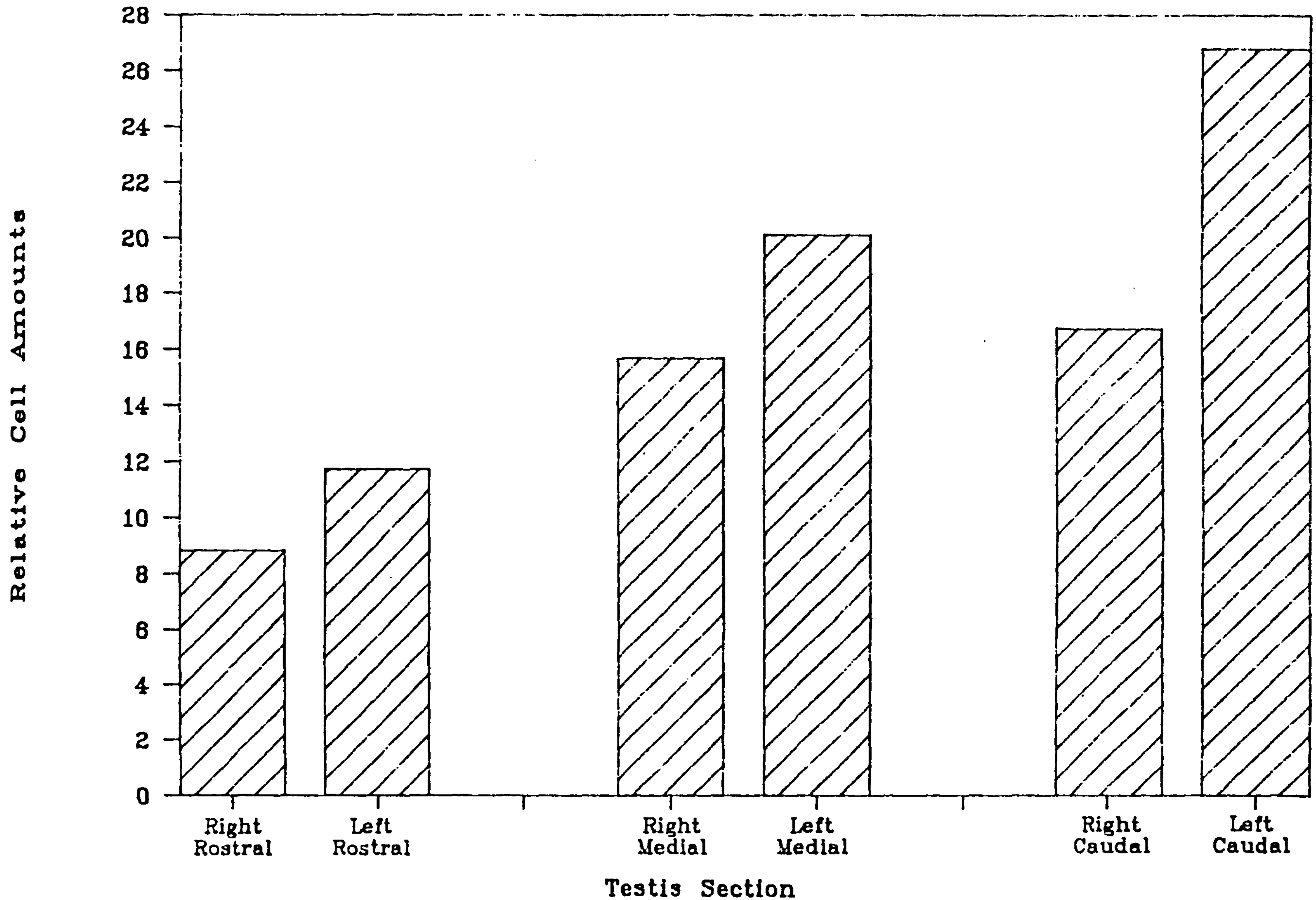
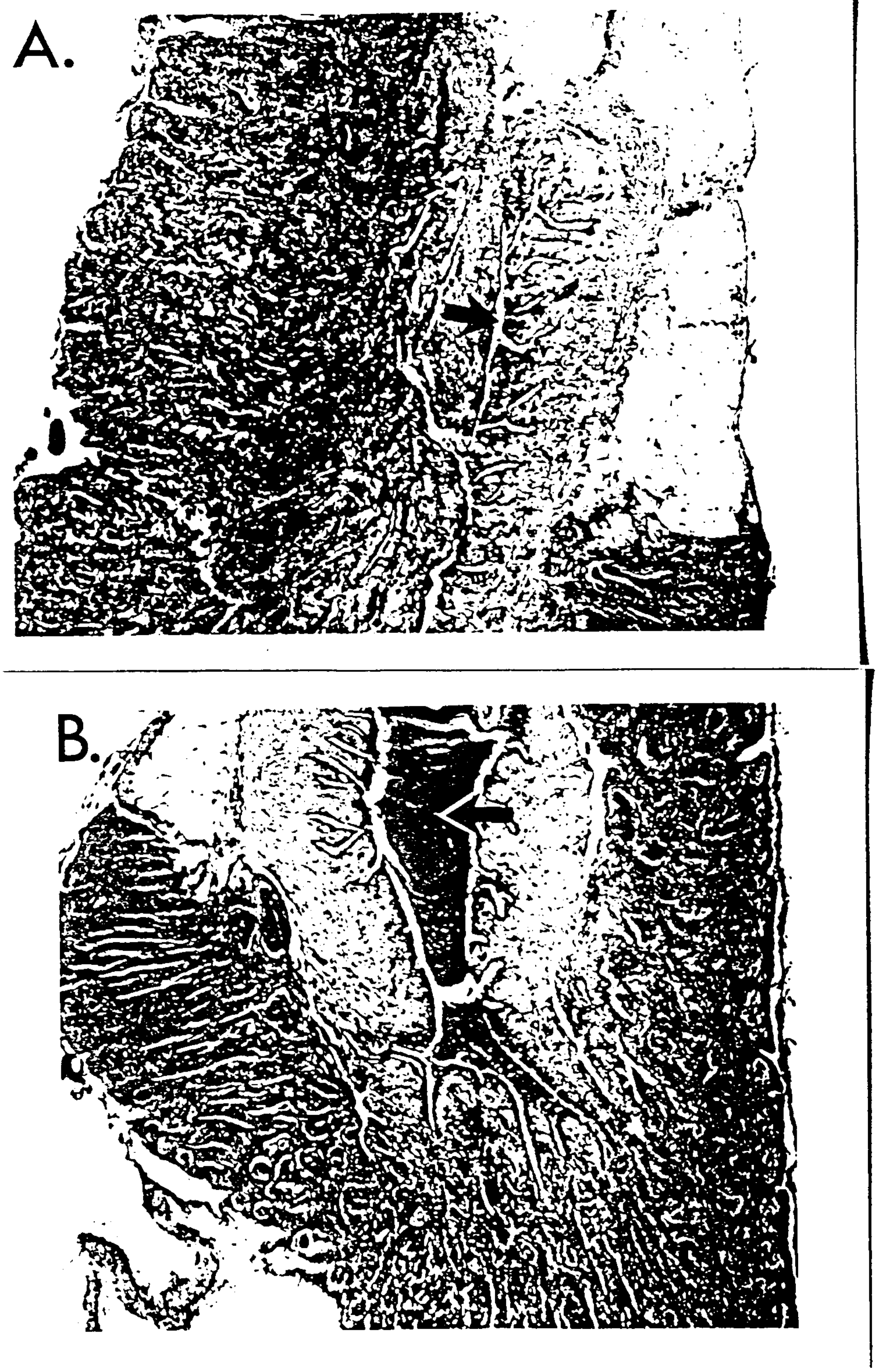
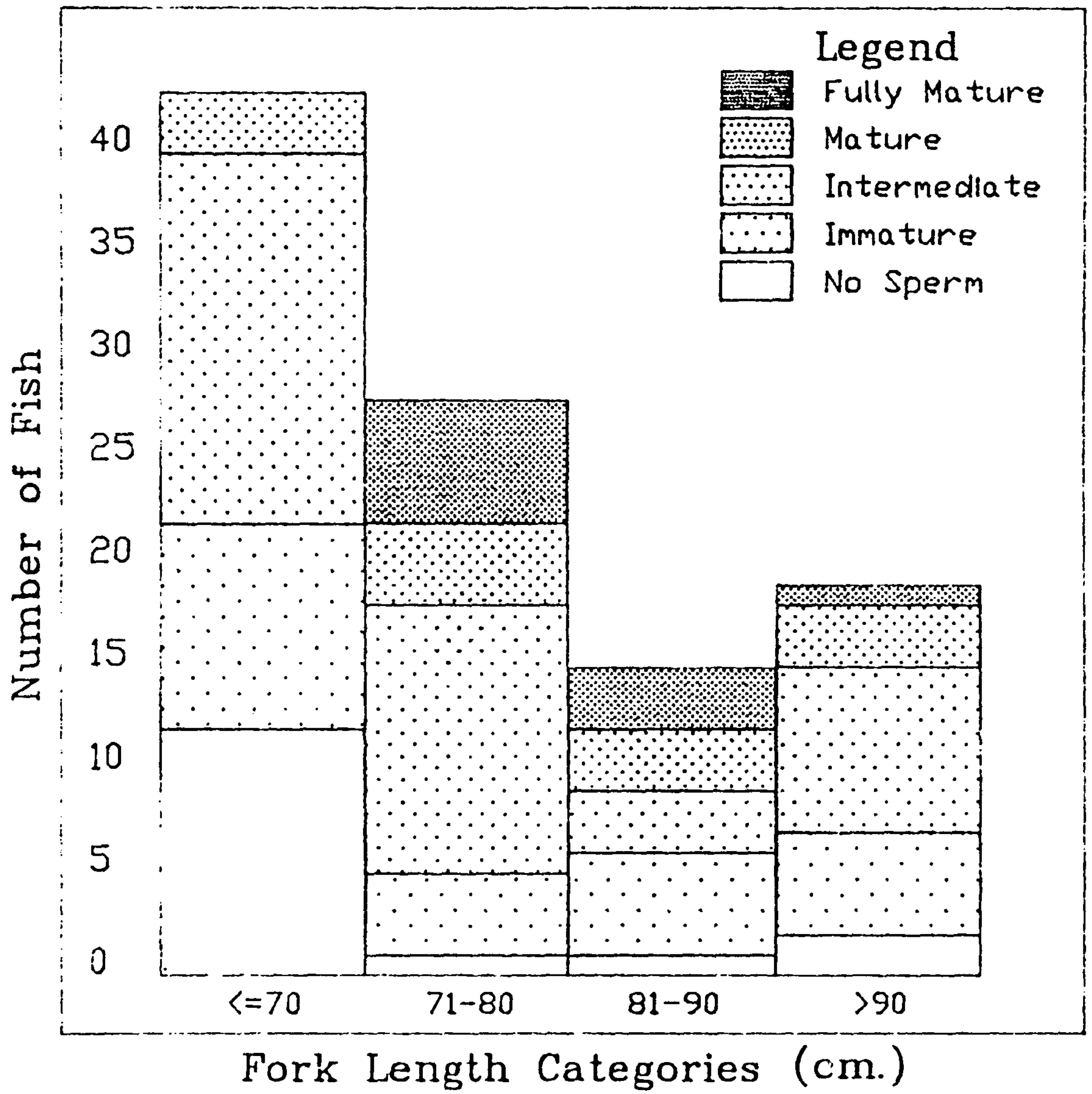

Relative Cell Amounts
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Right Rostral
Left Rostral
Right Medial
Left Medial
Right Caudal
Left Caudal
Testis Section

FIG. 7

FIG. 8





Legend
Fully Mature
Mature
Intermediate
Immature
No Sperm
Number of Fish
0
5
10
15
20
25
30
35
40
<=70
71-80
81-90
>90
Fork Length Categories (cm.)

FIG. 9

Comparison of Maturity Levels Between Fish Caught in Coastal Waters by Subsurface Longline and in the Mid-Ocean Region by Surface Trolling

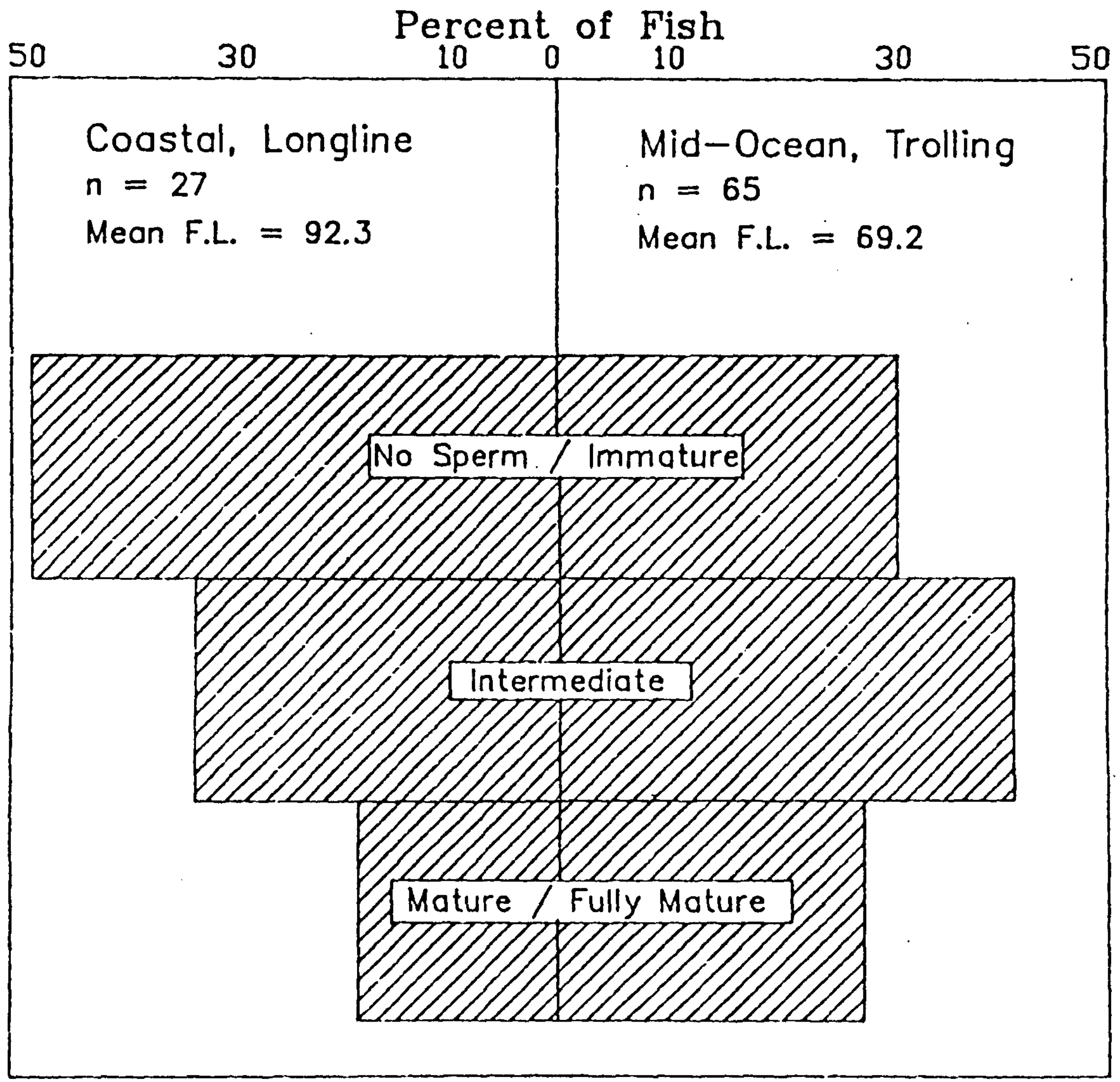


FIG 10