Gonad Morphology, Histology, and Spermatogenesis in South Pacific Albacore Tuna *Thunnus alalunga* (Scombridae)

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The reproductive biology of tuna, and the albacore *Thunnus alalunga* in particular, is not well understood with respect to 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 gonad morphology, histology, and spermatogenesis and relate them to the reproductive biology of this species.

Materials and methods

Albacore specimens were collected onboard the U.S. NOAA RV *Townsend Cromwell* and the New Zealand RV *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, Laurs et al. 1987). The fish were caught using standard albacore troll-fishing methods (Dotson 1980). In addition, specimens were collected during commercial fishing operations conducted in 1987 by Japanese longline vessels. Locations of specimen collection are summarized in Table 1.

Soon after the fish were caught, fork lengths were measured to the nearest millimeter and the gonads and associated fat body were dissected from each fish. The right and left gonads were preserved separately in 10% neutral buffered formalin. 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 5 microns and stained with Harris' hematoxylin followed by eosin counter stain (Humason 1979, Gabe 1976).

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. 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.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

We observed asymmetrical differences in the size of both ovaries and testes and in the size of the fat body associated with 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

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

Gonad general morphology

As in most teleosts, the gonads in male and female albacore are paired, elongate organs, located in the dorsal portion of the body cavity. They

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Table 1
Summary of information on *Thunnus alalunga* specimens used in study.

Ship	Date	No. species	Fork length (cm) Range	Median	Location in South Pacific
RV *Townsend Cromwell*	1986 17–21 Feb.	33	50.6–84.4	71.5	Central lat. 38°–40°S long. 146°–152°W
RV *Townsend Cromwell*	1987 25 Jan–1 Feb.	33	50.6–97.5	63.8	Central lat. 35°–39°S long. 151°–157°W
RV *Kaharoa*	1986 15 Feb.–28 Mar.	13	50.0–76.0	70.0	Western lat. 33°–44°S long. 166°E–178°W
FV *Wakashio*	1987 21 June	9	63.0–98.0	88.0	Western lat. 37°S long. 179°E
FV *Zuiho*	1987 20–23 June	18	85.2–101.1	94.5	Western lat. 37°–38°S long. 179°E

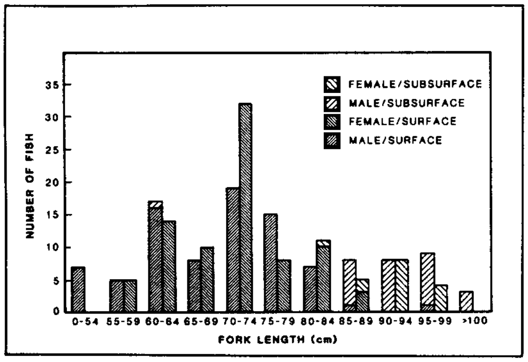

Figure 1
Length-frequency distributions for male and female South Pacific albacore tuna examined in this study. Surface troll-caught fish and subsurface longline-caught fish are differentiated.

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. 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. Ovaries in immature fish closely resemble 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 genetic-variability studies of North Pacific albacore, 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 shows a pair of ovaries and associated fat bodies, portion of the digestive tract, and ventral fin dissected from a 94-cm FL North Pacific albacore. The disparity in size between the right and left ovaries and associated fatty bodies 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 size differences between the two. Data summarized in Table 2 show that the right testis was larger than the left in 72% of male fish examined, the two testes were equal in size in 2%, and the left was larger than the right in 23%.

The results given in Figure 3 show that the dissimilarity in size increases with increasing fork length. The right testis is about 28–32% larger than the left in fish less than 80 cm FL, but increases to about 66–75% 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 cross-sectional area of the

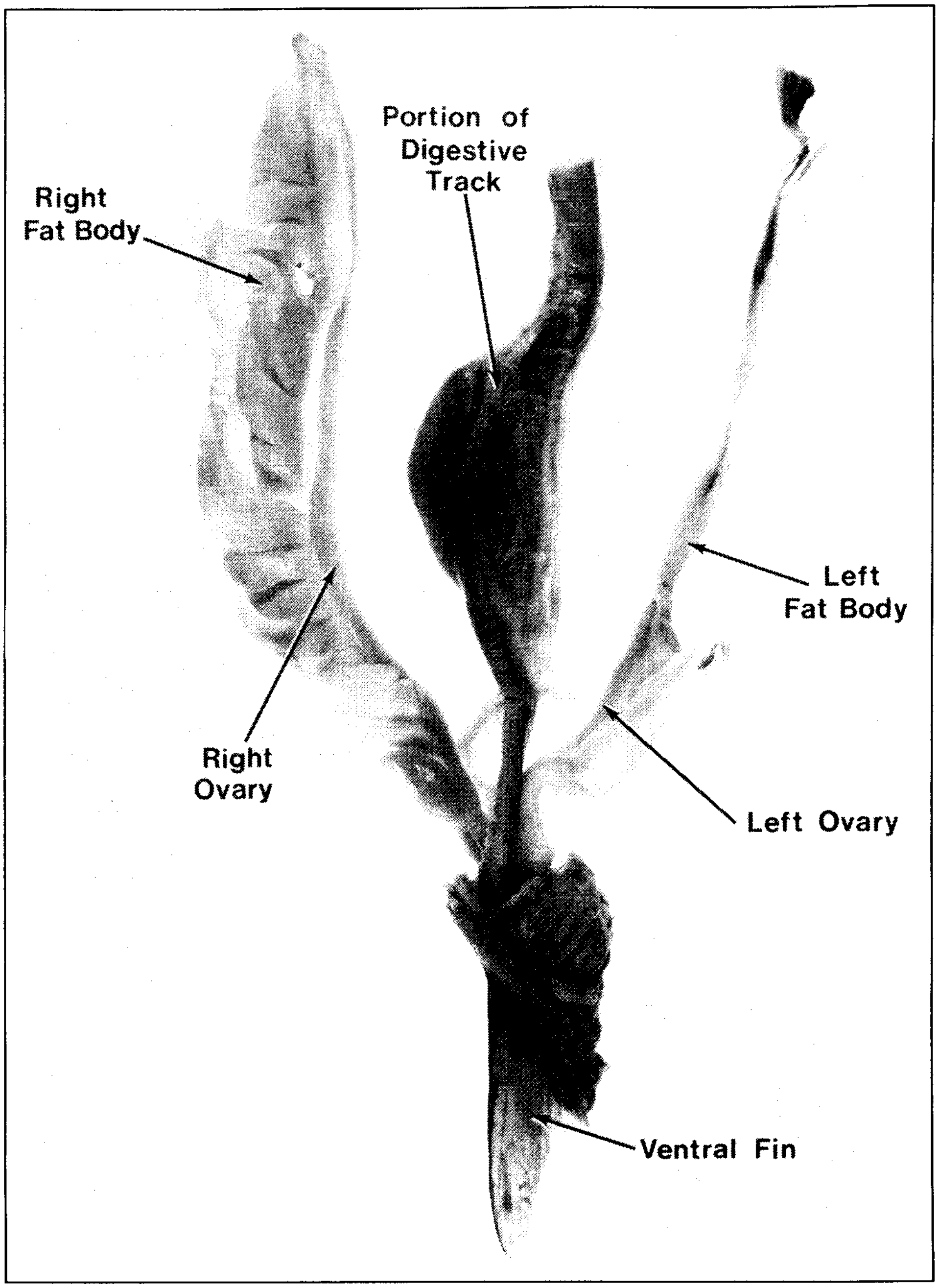

Figure 2
Pair of ovaries and associated fat bodies, portion of digestive system, and ventral fin from a 94-cm FL albacore tuna caught in the North Pacific.

Table 2
Relative size of right and left testes, *Thunnus alalunga* ($n = 106$).

Relative size of testes	Percent occurrence
Right larger than left	72
Right equal to left	2
Right smaller than left	23
No data	3

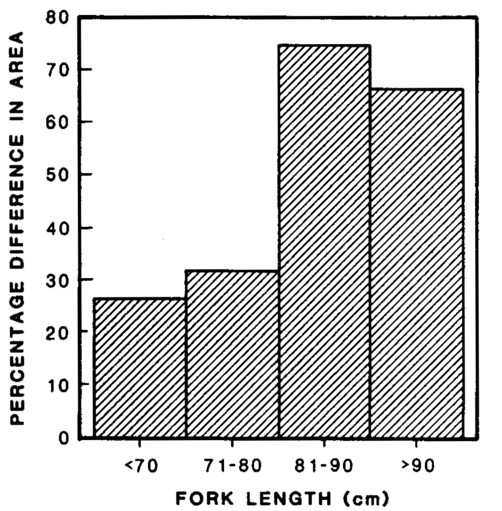

Figure 3
Percentage difference in cross-sectional area of the medial sections of right and left testes of South Pacific albacore, by fork-length.

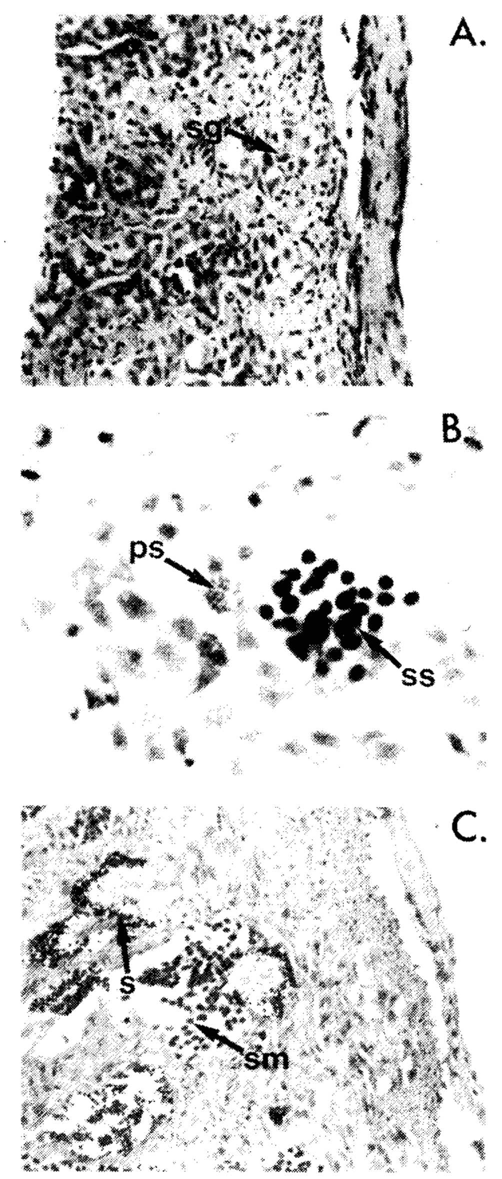

Figure 4
Spermatogenic cells observed in testes of South Pacific albacore. (A) Spermatogonia (sg) situated on lobule wall (×400); (B) primary spermatocyte (ps) cells and secondary spermatocyte (ss) cells (×600); (C) spermatids (sm) and spermatozoa (s) (×400).

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 albacore testis has a lobular-type cellular arrangement, characteristic of most teleosts (Billard et al. 1982). We classified the germ cells into the following phases of development: spermatogonia, primary spermatocytes, secondary spermatocytes, spermatids, and spermatozoa.

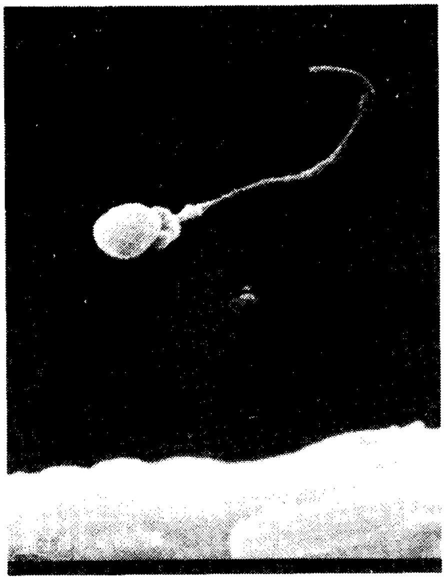

Figure 5
Electron micrograph of South Pacific albacore spermatozoa (scale indicates 1 μm).

The primary spermatogonia are the largest cells with diameters of 12–16 μm. They have a prominent nucleolus, are basophilic, and are found in cysts with varying numbers of individual cells. The cysts are usually found singly near the periphery of the testis; a cyst situated on the lobule wall is shown in Figure 4A.

Primary spermatocytes are oval or spherical with diameters of 8–12 μm. They have no visible nuclear membrane and the chromatin material occupies most of the cell. Figure 4B shows examples of primary spermatocytes. Secondary spermatocytes are very small, spherical cells with diameters of 4–7 μm. Unlike 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.

Spermatids are strongly basophilic spherical cells with diameters of 2–4 μm. 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 have a rounded nucleus and are morphologically subdivided into head, neck piece, short midpiece, and tail; as in other teleosts, there is no acrosome. They measure 1–2 μm in diameter, excluding the tail. An electron micrograph of an individual sperm is shown in Figure 5.

Table 3
Differences in meiotic activity between right and left testes, *Thunnus alalunga* ($n = 106$).

Meiotic activity	Percent occurrence
Left < right	10
Left = right	26
Left > right	61
No data	3

Meiotic activity

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

Examination of data for each pair of testes showed a 60% occurrence of greater meiotic activity in the left testis relative to larger size of the right testis. Other combinations of meiotic activity and relative size of testes showed a 15% or less occurrence (see Fig. 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 relative abundances 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 2½ times fewer *none* categories of sperm observed for the left than the right testis. In both the left and right testes of fish in all sizes, relative abundance of sperm was highest in the caudal portion and decreased towards the rostral end (Figure 7).

The findings are similar for spermatids and spermatocytes, but the differences between testes are not as pronounced as those for sperm. For all sizes of fish, relative abundances of both spermatids and spermatocytes were higher in the left than the right testis. For the left testis, there were about 20% and 30% more *many* and 40% and 50% fewer *none*, categories observed for spermatids and spermatocytes, respectively,

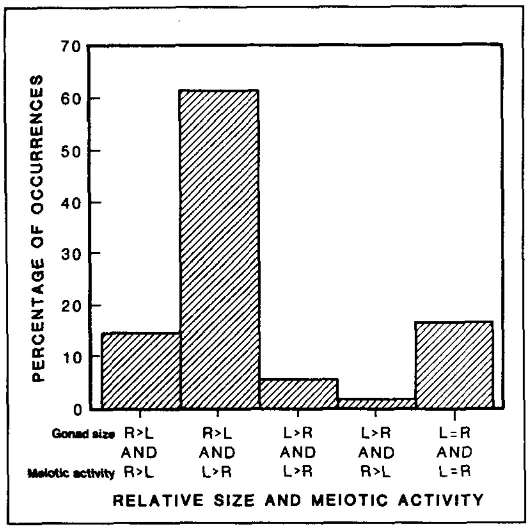

Figure 6
Percentage occurrence of relative level of meiotic activity and relative size of right (R) and left (L) gonads of South Pacific albacore. On the abscissa, upper expression refers to relative gonad size, and lower expression refers to relative level of meiotic activity.

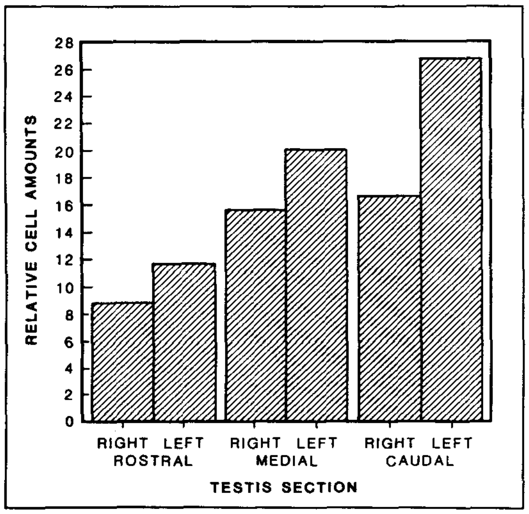

Figure 7
Relative abundance of sperm in rostral, medial, and caudal portions of the right and left testes of South Pacific albacore.

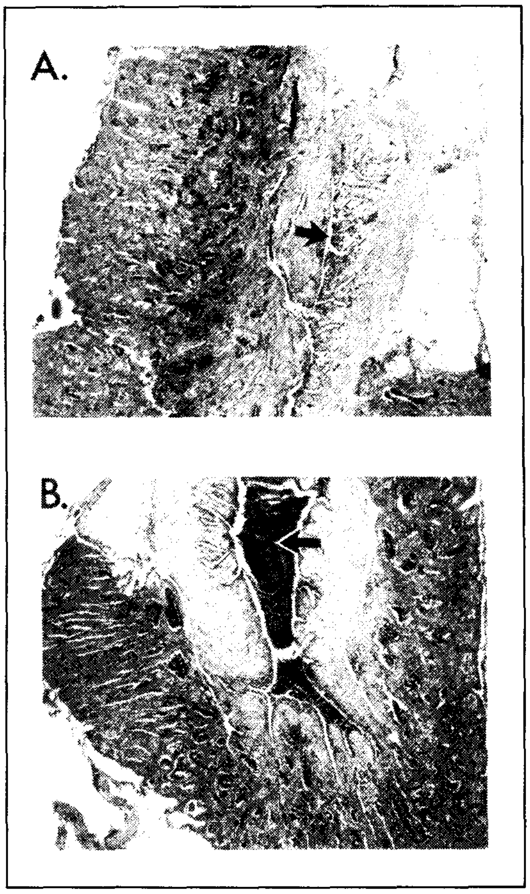

Figure 8
(A) Empty sperm duct of an immature South Pacific albacore; (B) sperm duct of a mature albacore filled with sperm, ×100.

than for the right testis. The relative abundance of each group of germ cells 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 albacore testes (Fig. 8A) in which no sperm are found. In mature albacore, we observed that the sperm duct is located near the center of the testis (Fig. 8B) and that a branching system of tubules radiates toward and end blindly at the testicular periphery. These obser-

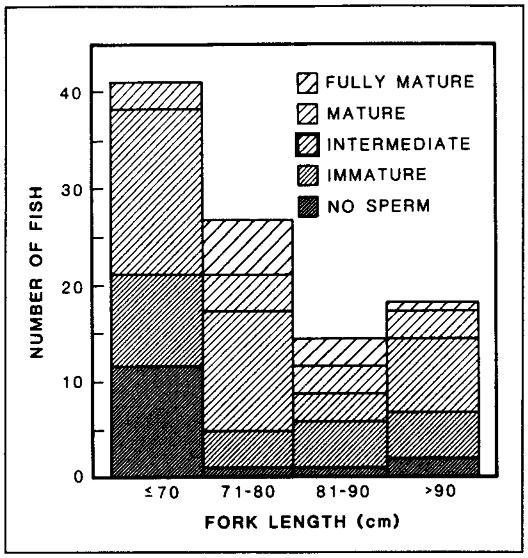

Figure 9
Comparison of sexual maturity levels of male South Pacific albacore by fork length.

Table 4
Percentage sexual maturity of fish by fork length.

Stage of sexual maturity	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

vations 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 (Fig. 8A). In the mature testis the main duct, when filled with sperm, has much thicker walls and is less convoluted and more rounded (Fig. 8B). The production of sperm is also associated with increased vascularization of the testis, first in the caudal portion followed by the medial and rostral portions.

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

Sexual maturity

Fish were classified into five levels of sexual maturity based on relative abundance of sperm observed in the testes: (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 more than 50% of fish 50–70 cm FL were immature, including 28% (derived from Figure 9) with no sperm present in any portion of either testis. Over 40% were in the intermediate level and 7% were judged sexually mature, but none was fully mature. Fish in size groups larger than 70 cm FL had a lower proportion of immature individuals than did fish less than 70 cm, ranging from 18% to 40% (Table 4), including only 3–10% with 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% and 46% for fish in size groups larger than 70 cm FL. The percentages of fish in the mature and fully mature categories were nearly the same for size groups 71–80 cm and 81–90 cm FL, 36% and 40%, respectively, but only 21% for the size group over 90 cm. The 71–80 cm FL size group had the highest proportion of fully sexually mature individuals, 23%, while only about 5% of 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 larger than 90 cm FL appears to be related to geographic region and/or type of fishing gear. Figure 10 compares maturity levels between fish caught in the midocean region of the central South Pacific by surface trolling and those caught in coastal waters off New Zealand by subsurface longline. It is evident in Figure 10 that a higher proportion of immature and a lower proportion of mature and fully mature individuals were caught in coastal waters than in the midocean region, even though the longline-caught fish were much larger, averaging 92.3

cm FL, than troll-caught fish, averaging 69.2 cm. Figure 1 shows that virtually all of the fish in the size category greater than 90 cm were caught in coastal waters by subsurface longline.

Fat body

A lobulated mass of fat-like tissue was usually observed in the mesentery attached to testes and ovaries. In some cases it was extremely large and well developed, but quite rudimentary in others. 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 size of the gonad. We observed that the right testis or ovary of the albacore, which is generally larger than the left, usually had a larger fat body (see Figure 2). In addition, we observed that the fat body was proportionately larger in immature fish that were meiotically inactive than in fish with gonads actively producing sperm.

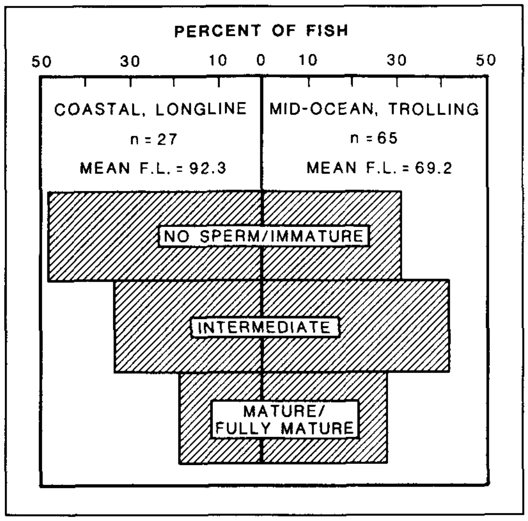

Figure 10
Comparison of sexual maturity levels of male albacore caught in coastal South Pacific waters by subsurface longline (left) with those caught in midocean South Pacific region by surface trolling (right).

Discussion

According to literature pertaining to the general structure and function of teleost gonads, the development of 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. 1977).

Asymmetry in gonad size appears to be common for albacore, at least in prespawning stages. We observed asymmetry in 95% of fish examined, with the right gonad 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 stage.

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 ovaries from a mature female albacore caught in the Indian Ocean differed in weight by 100 grams. However, he did not indicate weights or relative size of the ovaries. Partlo (1955) conducted histological studies on 44 albacore from the eastern North Pacific, but did not publish data on gonad size or mention asymmetry. The gonads of other tunas are more or less symmetrical in size and usually have no conspicuous fat body (Kurt Schaefer, Inter-Am. Trop. Tuna Comm., P.O. Box 271, La Jolla, CA 92038, pers. comm., 1 May 1989).

The finding that 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 prespawning individuals and possibly during other periods when albacore are not 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 testis 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 presumably extend its reproductive potential with 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 Hurk 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 FL which may be related to the method of capture and/or the type of habitat where collected. All 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 midocean waters. Oceanographic observations made concurrently with albacore troll-fishing operations indicate that albacore in the midocean region of the South Pacific are associated with Subtropical Convergence Waters (Laurs 1986, Laurs et al. 1987).

Female albacore have been reported to attain sexual maturity and first spawn at about 90 cm FL (Ueyanagi 1955, Otsu and Uchida 1959); however, 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 FL. Based on the general appearance of testes and oozing of milt, Ueyanagi (1957) postulated the smallest mature male to be 97 cm FL 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 (1943) 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 his age groups V and VI were in a condition approaching spawning. He 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. He also reported observing small numbers of fully mature sperm restricted to tubules of the posterior portion of testes in age-group IV, which he reported as having a mean fork length of 62 cm. Partlo (1955) examined a total of 44 testes and ovaries, but unfortunately did not specify the sex or number of individuals in each age group.

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, with its greatest development always on the right side of the fish. However, they made no mention of asymmetry in gonad size.

There appears to be a functional relationship between meiotic activity and the amount of fat in the mesentery. We presume the fat body provides an energy source 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 that 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 three recently spawned albacore from the Hawaiian Islands. Schaefer (1987) noted that spawning in the black skipjack, *Euthynnus lineatus*, is probably regulated by energy available in fat storage. When the fat stores fall below a minimum level, ovarian atresia probably occurs over a short period of time.

Conclusions

We provide quantitative evidence that a substantial portion of male albacore caught in midocean areas of the South Pacific Subtropical Convergence Zone about lat. 35°–40°S, may be sexually mature when they attain a fork length of 71–80 cm. Also, the proportion of mature fish increases with increasing length. A lower proportion of males caught by subsurface longline fishing in coastal waters off New Zealand showed development in sexual maturity, although not as accelerated as males caught by surface trolling in the midocean region. Female fish 55–95 cm FL caught in both regions showed few signs of sexual maturation. South Pacific albacore are believed to spawn generally in the region of the Southern Tropical Convergence waters about lat. 20°–10°S (Knox 1970). This region is about 1000–1500 miles north of the Subtropical Convergence Zone where the albacore investigated in this study were caught.

The adaptive significance of sexual maturity in male albacore at times, locations, and ages when females are not in spawning condition is not clear. Sampling of both males and females over the entire spawning cycle and in locations where albacore are believed to spawn will be required to understand the reproductive biology of the South Pacific albacore population.

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