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REPRODUCTIVE PATTERNS OF SOUTH PACIFIC ALBACORE *(Thunnus alalunga)* AS INDICATED BY GONOSOMATIC INDEX AND MEIOTIC ACTIVITY

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Reproductive patterns of South Pacific albacore, *Thunnus alalunga*, as indicated by gonosomatic index and meiotic activity

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ABSTRACT

In order to determine the spawning seasonality of albacore, *Thunnus alalunga*, in the South Pacific, ovaries and testes of albacore were collected from longline vessels operating in the waters of New Caledonia (21°-23° S, 164°-166° E) and Tonga (16°-29° S, 171°-177° W) over the period January 1990 to February 1992. Gonad pairs from 246 female and 444 male albacore were weighed and gonosomatic indices (GSI) were calculated. A subset of 167 ovary pairs were examined histologically to determine the extent of meiotic activity. The monthly variation in GSI values and mean oocyte diameters clearly showed that albacore are annual rather than semestral spawners, with spawning limited to the austral summer months from December to February. No advanced, mature or spawned ovaries were observed in the sample. Most albacore showed increased levels of activity once they had reached a fork length of 85 cm. However, the highest GSIs were seen in a small group of 70 to 80cm female and male albacore taken in Tongan waters in January and February 1992. Unfortunately, gonads from these fish were not collected for histological verification, so the evidence of early spawning must at present be treated with caution. Asymmetry in the weight of the left and right gonad pairs was apparent in the samples from the two collection sites, with most of the right ovaries and testes being larger than the left. However, an examination of oocyte diameter showed no significant difference in the development between left and right ovaries.

INTRODUCTION

One of the research areas that was recognized by the second South Pacific Albacore Research (SPAR) workshop as needing further study was the spawning seasonality of albacore, *Thunnus alalunga*, in the South Pacific. This work was recommended to help clarify the periodicity of length frequency modes observed in samples of the troll catch, and the specific suggestion that albacore may be semestral spawners. A small-scale sampling and histological project was organized by the Tuna and Billfish Assessment Programme (TBAP) of the South Pacific Commission (SPC) and the Southwest Fisheries Science Center (SWFSC) to provide a better understanding of albacore reproduction in the South Pacific.

Albacore are distributed throughout the Pacific in temperate and tropical waters. The North and South Pacific populations are considered separate because of extremely low catch rates in the equatorial region, non-overlapping spawning areas and seasons, and the absence of movement of tagged fish from the North Pacific to the South Pacific (Lewis 1990). In the South Pacific, albacore occur from the Equator to 50° S latitude and from the surface to depths of 300 meters (Yoneta and Saito 1973). South Pacific albacore reach sexual maturity in the size range of 85 to 90 cm fork length (Ueyanagi 1957; Otsu and Hansen 1962), at which time they are usually between 6 and 8 years old (Labelle et al. MS).

Two major fisheries currently target albacore in the South Pacific: the longline fishery concentrating on adult fish (80-110 cm) in tropical and subtropical waters (10°-30° S) throughout the year and the surface troll fishery targeting sub-adults (50-80 cm) in temperate waters (30°-40° S) in the austral summer (Lewis 1990; Rensink 1991). As adult albacore in various stages of reproductive development were needed, sampling was limited to the longline fishery.

MATERIALS AND METHODS

Gonad Collection

Albacore were sampled from two longline operations: Japanese-New Caledonia joint-venture longliners fishing in New Caledonia waters and unloading in Noumea, and onboard the Tongan-government longliner MV *Lofa* operating in Tongan waters (Figure 1). These sites were selected because the vessels fished throughout the year in the known spawning areas and offered ease of access to the albacore catch.

Sampling regimes were designed to cause minimum disturbance to the commercial operations while providing adequate samples and data. The two regimes attempted to collect the same basic data -- fork length, whole weight, gonads and gonad weights of females from all 10-cm length classes available (70-79 cm, 80-89 cm, 90-99 cm, 100-110 cm). In Noumea, ovaries were collected from all length classes; however, on *Lofa*, ovaries were only taken from the 80-90 cm class because of limited sampling time and space. This was balanced out to some degree by weighing the ovaries of albacore from the other length classes present in the Tongan fishery. Testes were only weighed on *Lofa*, and only from those males encountered while searching for female albacore. Sampling in Noumea was carried out by TBAP staff once every week from May 1990 to February 1992, while sampling on *Lofa* occurred every second set of the longline over the period January 1990 to February 1992. The latter work was undertaken by crew members of *Lofa* who had been trained by a TBAP staff member. No gonads were measured on *Lofa* in November and December of either year of sampling because of equipment malfunction in 1990 and no fishing effort in 1991.

Albacore were measured to the nearest centimeter of fork length, and where possible, whole weights were also obtained. Gonads were removed from the gut cavity, each gonad of a pair being separated into left and right gonads, depending on the gonads dorsal position in the cavity, and weighed fresh to the nearest gram in New Caledonia and to the nearest 5 grams on *Lofa*. The weight of the gonads included the weight of the associated fatbody. Ovaries destined for histological examination were preserved in 10 percent formalin in their separated state. The samples from Tonga were sent by air to the South Pacific Commission, Noumea, at the end of each 2-3 month Lofa cruise. Samples were subsequently dispatched to the Southwest Fisheries Science Center after sufficient quantities had accumulated.

A total of 1,105 albacore were examined and measured (300 females, 799 males, 6 indeterminate); of this number, 246 ovary pairs and 444 pars of testes were weighed and 150 pairs of ovaries collected for histological examination. A summary of these numbers by collection site is provided in Table 1.

Histological Examination

Albacore have asynchronous gonads, in that they contain oocytes and sperm in various stages of development at any given time during their spawning season (Ratty et al. 1990; West 1990). Fish that are categorized as having asynchronous gonads are considered to have multiple spawnings over an extended period (deVlamming 1982). The gonads are paired structures located in the posterior dorsal region of the body cavity. They are suspended from the dorsal wall by mesentery tissues. Often, a fatbody is found in association with the gonad. It is found on the exterior edge of the gonad running the entire length of the gonad. The size of the fatbody varies significantly depending upon season, sex, and size of fish; for instance, it is usually absent in mature females during spawning season. The physical descriptions of the testes and ovaries are as follows: Testes are thin, elongated organs translucent in immature male albacore and whitish in color in mature albacore. Immature albacore ovaries are similar to immature testes making it difficult to sex them macroscopically, these were labeled indeterminate. As female albacore mature, their ovaries become larger and rounded yellow organs that are readily distinguished from the male testes.

A detailed examination of the ovaries from 150 albacore in various stages of development was conducted using histology, microscopic, and macroscopic examinations. The ovaries were processed in the laboratory using the following procedures: The ovary was removed from the formalin, patted dry, and weighed to the nearest tenth of a gram. The associated fatbody was then removed, and the gonad weighed without the fatbody. Ovaries were initially staged by their appearance. An ovary's macroscopically staged appearence was verified by slicing the ovary lengthwise to expose the lumen which was examined for the presence of residual hyaline oocytes which are indicative of mature or recently spawned fish. Two samples were taken from the ovary, one for histological examination and the second sample for microscopic examination. As we were interested in the mean diameter of the most advanced group of oocytes within the ovary, a site from the middle region of the ovary was selected because Otsu and Uchida (1959) found the mean diameter of oocytes sampled from the middle cross section of the ovary to be greater than the mean oocyte diameter of those sampled from either the posterior or anterior region of the ovary.

The first sample taken was a cross section from the middle region of the ovary, it was then embedded in paraffin, sectioned at 7 microns, and stained with Harris' hematoxylin followed by Eosin counter-stain. The sections were later examined with

a compound microscope to determine their development state using such characters as the presence of yolk, lipid vesicles, hydrated oocytes, and postovulatory follicles. The developmental stages were classified as early developing, developing, late developing, advanced, mature, and spawned. The characteristics of ovaries and ova within these stages are described in Table 2. The second sample taken was a thin section of ovarian tissue from the outer edge of the ovary to the lumen. This sample was placed in 33 percent glycerol for 10 to 20 minutes before the largest oocytes were separated from the ovarian connective tissue (Hunter et al. 1986). The separated oocytes were then measured to determine the average size of the largest mode of oocytes in each ovary; this was done to the nearest micron by measuring the diameter of the 20 largest oocytes in the subsample using a dissecting microscope.

Gonosomatic Index

Gonosomatic indices (GSI) were calculated for New Caledonia females and Tonga females and males using the following standard formula:

$$GSI = 10^4 W * L^{-3}$$

where W = total gonad weight in grams and L = fork length in centimeters.

RESULTS

Length Frequency Distributions of Sampled Albacore

The length frequency distributions of the examined albacore are shown in Figure 2. Although the sample sizes are not particularly large, it appears that male and female albacore from both sampling sites exhibit differences in size structure. In both the New Caledonia and Tonga samples, few females over 100 cm in length were encountered, whereas both male samples exhibit a pronounced mode centered on 100-102 cm. Dimorphic size differences between male and female albacore randomly sampled from landings had previously been seen by Otsu and Sumida (1968). And in yellowfin tuna, sexually dimorphic growth has been age verified and males were found to comprise the largest fork length mode (Wild 1986). Therefore, this apparent dimorphism is unlikely to be an artifact of sampling and warrants further research, particularly with respect to any ageing and mortality studies undertaken.

Gonosomatic Index

The relation between GSI and fork length of sampled female albacore is presented in Figure 3. The ovary weight also includes the weight of the fatbody that was found to compose an average of 4.4 percent of the ovary with a maximum of 31.6 percent and a minimum of 0.0 percent. Therefore, the weight of the fatbody having being included in the gonad weight will be a source of error in the calculation of the GSI. Assuming that a GSI of 2.00 corresponds to the minimum level for tuna approaching spawning condition (Koido and Suzuki 1989), it appears that female albacore from New Caledonia are capable of spawning once they reach a minimum length of about 85 cm (Figure 3a). This length and a GSI of 2.00 corresponds to a total ovary weight of 130 g. While a similar minimum length is apparent in the Tonga females (Figure 3b), this sample is confused by the appearance of a small number of 70-80 cm fish with relatively high GSIs (3.20-7.40). All of these small

females were collected on *Lofa* in January and February of 1992. Although the vessel fished in the same area in the same months of 1991, no similar-sized albacore were caught. Similarly, no small fish were sampled in New Caledonia during the summer months of 1991 or 1992. As there is no reason to believe that the data are inaccurate, this information provides the first indication that 70-80 cm female albacore are possibly capable of spawning. However, we are not prepared to say with the present data that this seemingly precocious activity is actually spawning, solely based upon high GSI values.

The largest GSI values measured for female albacore were 4.85 for a 93cm fish captured in New Caledonia in February with a ovary weight of 390 g and 7.40 for a 74cm fish captured in Tonga in February 1992 with a gonad weight of 300 g. The ovaries from the New Caledonia albacore were collected and sent to SWFSC for histological examination, where they were classified as late developing. Unfortunately, because of the sampling regime on Lofa, neither the ovaries of the 74cm albacore nor any of the other 70 to 80cm females in the Tonga sample were collected.

The monthly variations in GSI of the female samples shown in Figures 4 and 5 clearly show that peak reproductive development occurs in the austral summer months of November to February. The first indication of maturation is observed in October, when two albacore from the 14 sampled were found to have GSIs greater than 2.00 (2.52, 2.81). The mean, however, remains below 2.00 and there is no significant difference in maturity level between this month and the preceding three months. The first significant increase occurs in November when the GSI's increase to 2.97 and the GSI peaks in February with a mean of 4.15. In March the mean declines to 1.54 although a small number of females still exhibit some spawning activity, then drops to a resting level of close to 1.00 for the autumn and winter months (April - 0.89, May - 0.89, June - 0.66, July - 0.98, August - 1.04, September - 0.90). It is interesting to note that in the early months of the spawning season, only albacore 90cm and longer appear to be in spawning condition, although this conclusion is tempered somewhat by the small sample sizes, and only in January and February do the fish below 90cm appear to enter spawning condition. This suggests that larger albacore may have a longer spawning season and bears further investigation.

Only 11 of the 444 male albacore examined from *Lofa* sample had GSIs exceeding 2.00 (Figures 6 and 7); the majority of those above this level measured 70 to 80 cm in length and were captured at the same time as the precocious females mentioned above. The largest GSI value obtained for males was 4.08 for a 70cm fish with a testes weight of 140 g, that was caught in February 1992. Outside the 70-80 cm group, the largest GSI was 2.35, which corresponded to a 88cm fish with testes weighing 160 g. This particular fish was also caught in February 1992. In terms of monthly variation, the males follow a similar but much less pronounced pattern than the females, with the greatest development occurring in January and February, followed by a decline in March and a long resting period from April to October (Figure 8). Although a small burst of activity is seen in September, it does not appear to be related to a specific size range of fish, time of month, area or latitude. Females caught at the same time from the same area were in resting state.

Meiotic Development

No advanced, mature or spawned-stage ovaries were found in the New Caledonia or the Tonga samples that were examined histologically. Mean diameters of the most advanced groups of oocytes were tracked at monthly intervals to look for seasonal trends that would indicate spawning condition (Figure 9). During the austral winter

months, the samples contained immature oocytes, with the largest mode centered on 0.1 mm. Oocyte diameters rapidly increased between September and December and progressed from immature to late-developing. The late-developing stage was maintained through the summer months until a decline occurred in March. By April, oocyte diameters had returned to the resting state of 0.1 mm for all samples.

The relationship between oocyte diameter and GSI is shown in Figure 10. A positive correlation between the most advanced group of oocytes and GSI exists, as indicated by a r^2 of 0.79. However, GSI values in isolation may not present an accurate picture of gonadal activity, as seen by the overlapping GSI values for a given reproductive stage in Figure 11 (deVlamming 1982). Nevertheless, the close similarity in the distributions of monthly variation in GSIs and oocyte diameters (Figures 5 and 9, respectively) suggests that either method can be used to effectively determine spawning season for the samples as a group. But as indicated in Figure 11, GSI may not be used to determine the spawning potential of an individual fish.

Gonad Asymmetry

The difference in size between the right and left gonads sampled are summarized in Table 3. The right gonad was found to be heavier than the left in 80.0 percent of the females examined and in 98.6 percent of the males. In terms of collection site, this difference in females was less pronounced in New Caledonia (55.8%) than in Tonga (95.1%). Oocyte diameter and developmental stage were examined to see if these differences in weight were consistent with reproductive state. No significant difference was seen in the oocyte diameters from the left and right ovaries (paired t-test, P = 5.199, $\alpha = 0.05$), and only one of the 150 ovary pairs examined exhibited differences in maturity stage, with the left and smaller ovary being classified as developing and the right and larger as late developing. It should be noted that all ovaries collected from New Caledonia, and Tonga ovaries with differences in weight of up to 60 g, were included in this examination.

DISCUSSION

The information presented here indicates that South Pacific albacore are annual rather than semestral spawners, with spawning being limited to the austral summer months between December and February. This supports the findings of Otsu and Hansen (1962), the initial work on albacore reproduction in the South Pacific. The larval survey work of Nishikawa et al (1985) and Ueyanagi (1969) is also supported, although the former authors suggest that spawning peaks in spring and early summer (October-December) rather than in mid to late summer, as found here. However, few larval surveys were undertaken from January to March in the spawning area (see Figure 37, Nishikawa et al. 1985). Leis et al. (1991) found high concentrations of albacore larvae near the islands of French Polynesia (14°-17° S) in January and February. There appear to be few published works on albacore reproduction in other oceans in the southern hemisphere; one such work (Kikawa and Ferraro 1966, from Stequert and Marsac 1986) mentions austral summer spawning in the southern Indian Ocean.

The spawning area of South Pacific albacore has been hypothesized by various authors to lie between 10°-20° S (Otsu and Hansen 1962, Nishikawa et al. 1985) and centered on 20° S (Ishii and Inoue 1956; Ueyanagi 1969). In the present study, most of the maturing albacore (i.e. with GSIs above 2.00) were taken from between 20° and 22° S, which suggests that the spawning area extends to the south of 20° S. No

developed fish were found to the south of 23° S. As mentioned, attempts to sample from other fisheries that operate further to the north proved unsuccessful.

The New Caledonia data and much of the Tonga data support the view the female albacore reach maturity at a minimum length of around 85 cm (Otsu and Hansen 1962). The presence of albacore from the January and February 1992 Tonga samples having lengths between 70 and 80 cm and relatively high GSIs, is the first evidence that female albacore maybe capable of spawning at much smaller sizes than had previously been documented. The presence of similar-sized, active males in the same area and time suggests that either the activity was real or there had been a problem with the weighing equipment. As problems with the scale did not appear to be the case, we can only assume that the data are indicative of spawning activity but this assumption must be treated them with caution until ovaries are available for examination. With respect to males, there is good evidence that maturity can be attained in this size range. Ratty et al (1990), in examining testes from albacore caught in the summer troll fishery in the temperate South Pacific, found that there were more mature males in the 71 to 80 cm range than in larger or smaller size ranges of albacore. These authors also noted that 55 to 95 cm long females from the fishery showed "few signs of sexual maturation," although they did not quantify this statement.

The absence of advanced and fully ripe ovaries in the sample is reflected in other studies of albacore reproduction in the Pacific that have relied on longline fisheries as the main source of samples (Otsu and Hansen 1962; Otsu and Uchida 1959). As these authors have noted, this indicates that albacore in or close to spawning condition are generally unavailable to the fishery, either because they stop feeding and will not take hooks or because they move outside the range of the gear, be it in a spatial or temporal plane. With regard to the latter, both the New Caledonia longliners and *Lofa* set and hauled their gear during daylight hours; it is possible that albacore, like other tunas, spawn at night (Hunter et al. 1986). Added to this is the possibility that albacore pass rapidly through the mature and spawned stages of the cycle, as Hunter et al. (1986) found with skipjack and as McPherson found with yellowfin (1991). Thus, there remains a number of key areas in the reproduction of South Pacific albacore, such as spawning frequency and batch fecundity, that require further investigation and ultimately will depend on our obtaining ripe ovaries. Setting longlines so that they fish during the night may prove effective. Even though albacore are usually considered as diurnal predators, they can contribute significantly to the catches of night-time longline operations (Michael et al. 1989). If longline operation prove ineffective, Nets may prove effective if hook response is a deciding factor, but as albacore generally are not purse seined because of their particular schooling behavior, although small quantities of typically juvenile fish are taken as by-catch in some areas, albeit rarely (New Zealand - Habib et al. 1982, Fiji - Farman 1984). It is interesting to note the presence of spent albacore (73-113 cm FL) in the eastern tropical Atlantic purse seine catch (Bard and Kothias 1986), although the sex involved or descriptions of reproductive states are not included.

Gonad asymmetry has been recorded in several fish species (Ovchinnikov 1971; Sanwal and Khana 1972) and was previously documented in albacore by Otsu and Uchida (1959) and Ueyanagi (1955). The latter authors both noted that one side of the ovary was usually heavier than the other. Otsu and Uchida (1959) compared oocyte diameters from different areas of one pair of ovaries and found that differences existed between anterior and posterior regions of a single ovary but not between sides. In contrast, Ratty et al. (1990) found that the smaller left testis of males from the temperate troll fishery were consistently more active than the larger right testis.

The present study found no significant difference in oocyte diameter between the left and right ovaries in each pair. However, as no ovaries undergoing hydration or containing postovulatory follicles were examined, it can not be stated that each ovary continues to develop at the same rate.

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Table 1. Summary of albacore gonads sampled and collected in the South Pacific, January 1990 - February 1992

Site	Sampling period	Area of capture	Sex	Number of albacore examined	Number of gonads weighed	Number of ovaries collected
New Caledonia	May 1990 - February 1992	21° - 23° S 164° - 166° E	Female Male Indeter.	108 239 6	104 105 0	105 0 0
Tonga	January 1990 - February 1992	16° - 29° S 171° - 177° W	Female Male	192 560	142 444	45 0

Table 2. Characteristics of developmental stages in albacore ovaries after Otsu and Uchida 1959 and Schaefer 1987.

	Maturity Stage	Gross Morphology; Ova Diameter	Microscopic Appearance of Ova
1	Early developing	Thin hollow tubes with fatty mesentary; Ova diameter 0 .01 mm to 0.18 mm	Transparent, ovoid to angular with a large nucleus found in all ovaries at all times
2	Developing	Yellow-tan tubes often with fatty mesentary; Ova diameter to 0.4 mm	Semi-transparent from yolk granules deposited near the nucleus
3	Late developing	Firm yellow-tan tubes with visible oocytes; Ova diameter to 0.8 mm	Opaque from heavy accumulation of yolk granules throughout the oocyte; small to medium oil droplets
4	Advanced	Firm, round yellow-tan tubes with heavy vascularization and reduced fat body; Ova diameter to 1.0 mm	Opaque from heavy accumulation of yolk granules medium sized oil droplets and migratory nucleus
5	Mature	Large, round tubes,reduced fat body Ova diameter greater than 0.8mm	Semi-transparent, ameboid form with a single large oil droplet
6	Spawned	Flaccid yellow-tan tubes with reduced fat body: hyaline oocytes present in lumen; Ova diameter to 0 .6 mm	Degenerating ova, thin walled and translucent

Table 3. Asymmetry in gonad weight of albacore sampled from New Caledoia and Tonga.

GONAD WEIGHTS	NEW CALEDONIA FEMALE	TONGA FEMALE	TONGA MALE
RIGHT > LEFT	55.80%	95.10%	98.60%
RIGHT = LEFT	17.30%	4.90%	1.10%
RIGHT < LEFT	26.90%	0.00%	0.20%
n	104	142	444
$\bar{X}$	9.5	19.3	12.9
st. d	41.6	13.7	12.8
range	-130, +160	0-100	-30, +105

Figure 1. The South Pacific Ocean, showing longline (cross-hatched) and troll (slash) fisheries for albacore and gonad collection sites (shaded).

Figure 2. Length frequency distributions of albacore sampled from Tonga and New Caledonia, January 1990 - February 1992: (a) Overall distribution, (b) male and female albacore from New Caledonia, and (c) male and female albacore from Tonga.

Figure 3. Gonosomatic indices of female albacore from (a) New Caledonia and (b) Tonga (GSI = 2.0 minimum value showing development).

Figure 4. Monthly variation in the gonosomatic indices of female albacore against fork length (GSI = 2.0 minimum value showing development).

Figure 5. Mean monthly variation in the gonosomatic indices of female albacore sampled from New Caledonia and Tonga from 1990 to 1992. (+/- 2 standard errors; *N* = 246 (GSI = 2.00 minimum value showing development).

Figure 6. Gonosomatic indices of male albacore from Tonga, January 1990 to February 1992. (GSI = 2.00 minimum value showing development).

Figure 7. Monthly variation in the gonosomatic indices of male albacore against fork length. (GSI = 2.00 minimum value showing development).

Figure 8. Mean monthly variation in gonosomatic indices of male albacore sampled from Tonga from 1990 to 1992. (+/- 2 standard errors; *N* = 444)

Figure 9. Monthly variation in ova diameter of albacore sampled from New Caledonia and Tonga (+/- 2 standard errors; *N* = 97)

Figure 10. Relationship between the mean diameters of the most advance group of oocytes and the gonosomatic index of albacore sampled from New Caledonia and Tonga

Figure 11. Relationship between the gonosomatic index and developmental stage of albacore ovaries sampled from New Caledonia and Tonga, 1990 to 1992 (*N* = 149).

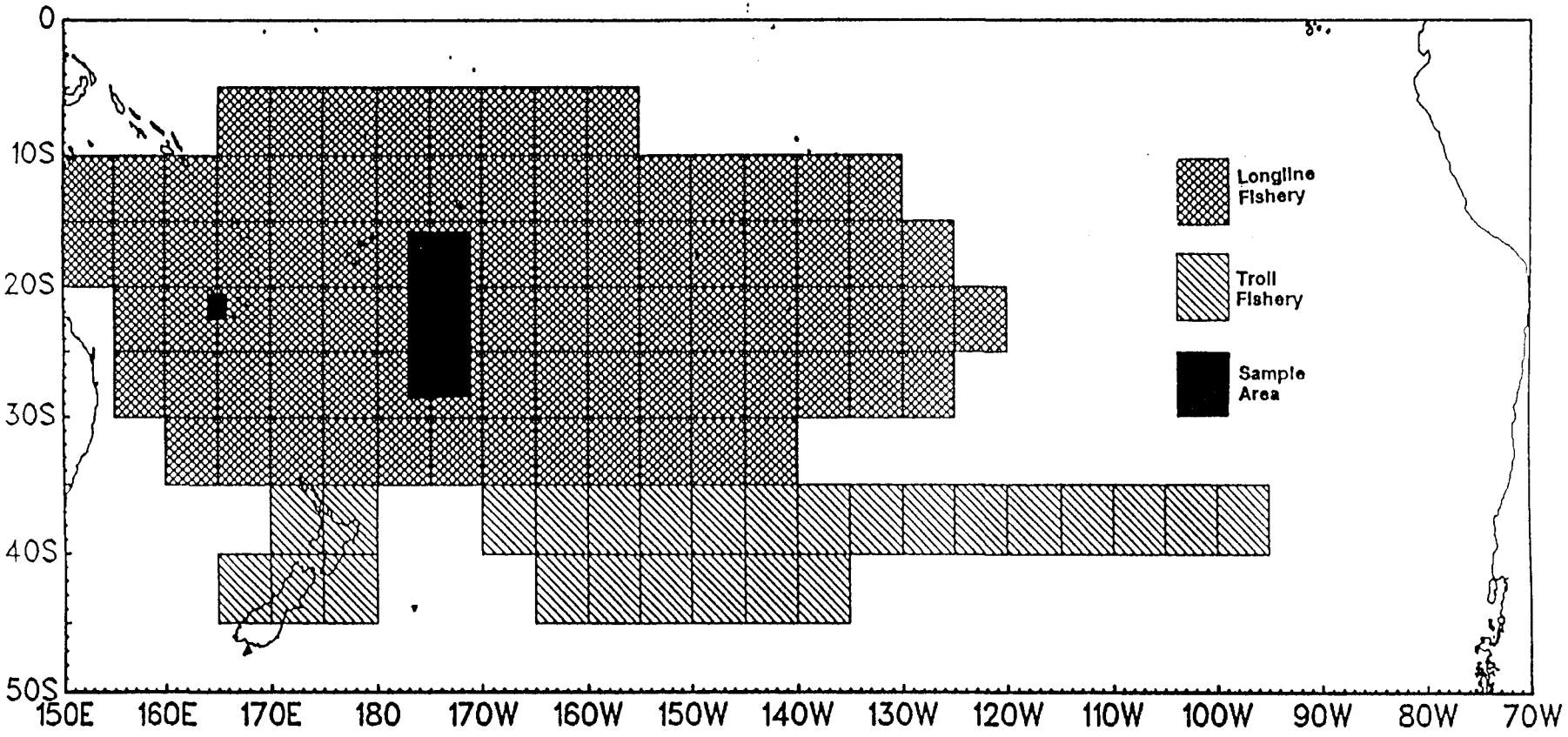

Figure 1. Major albacore fisheries in the South Pacific and gonad collection sites.

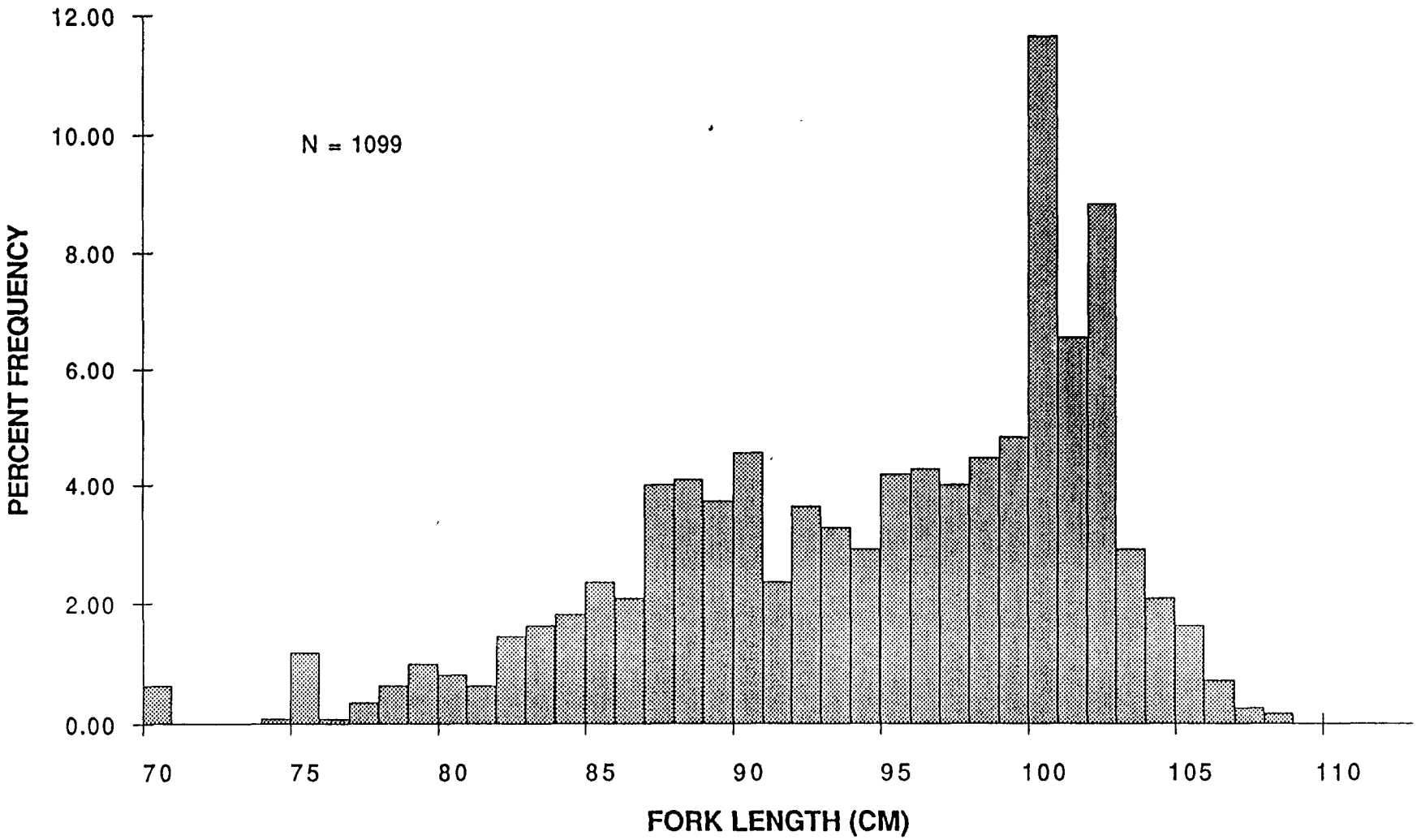

Figure 2a. Length frequency distribution of albacore sampled from Tonga and New Caledonia, January 1990 to February 1992

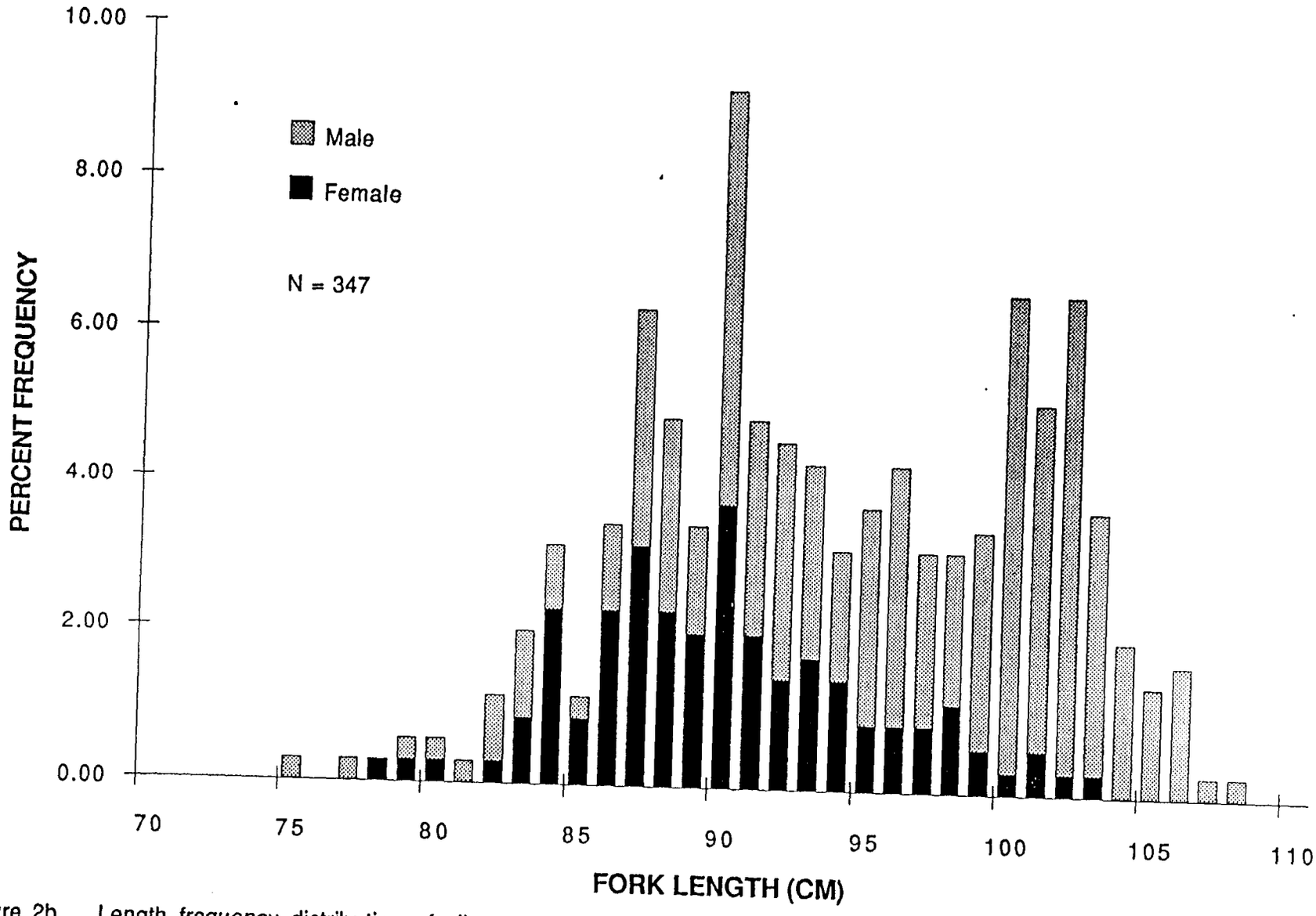

Figure 2b. Length frequency distribution of albacore sampled from New Caledonia, May 1990 to February 1992.

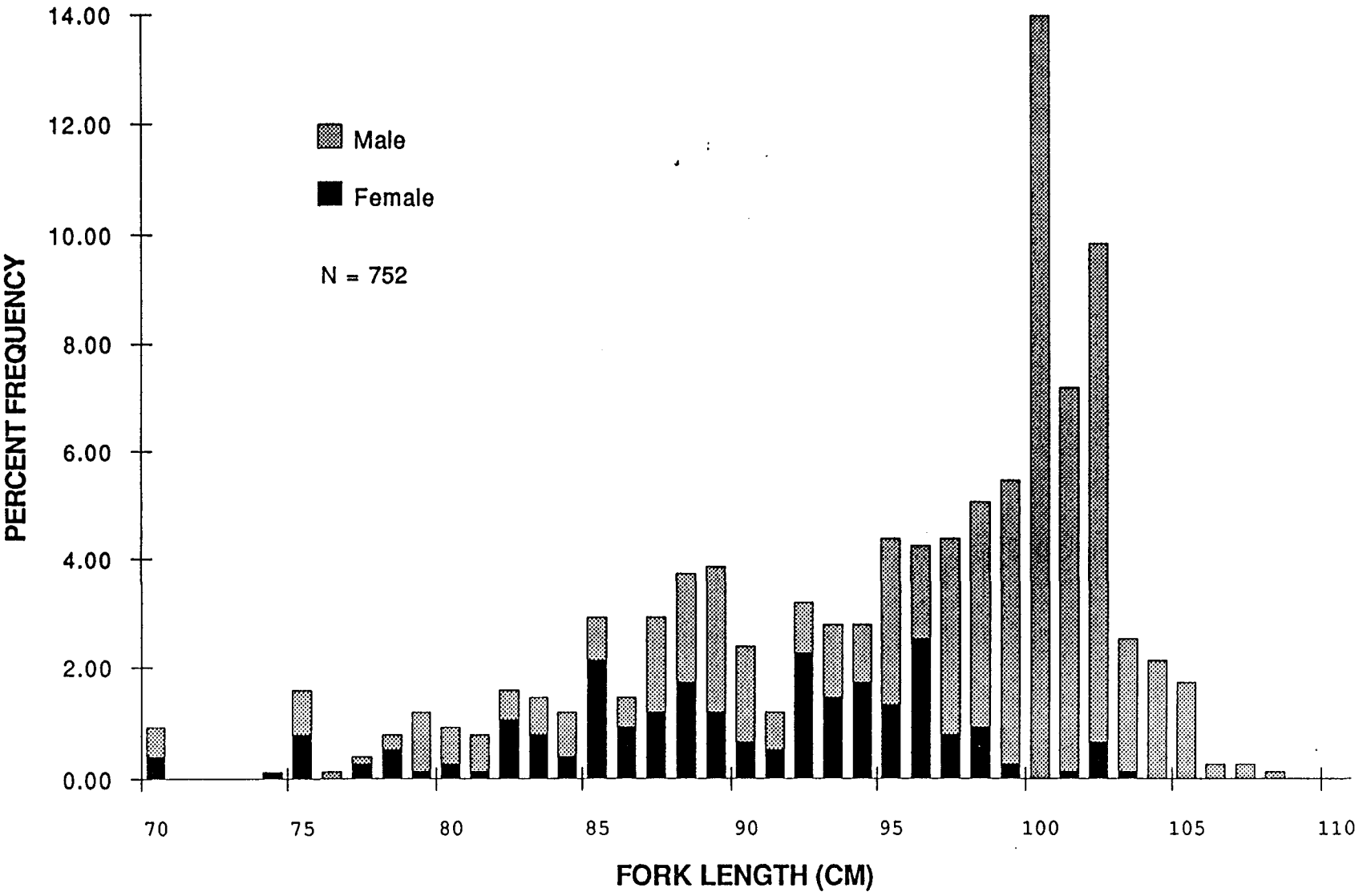

Figure 2c. Length frequency distribution of albacore sampled from Tonga, January 1990 to February 1992.

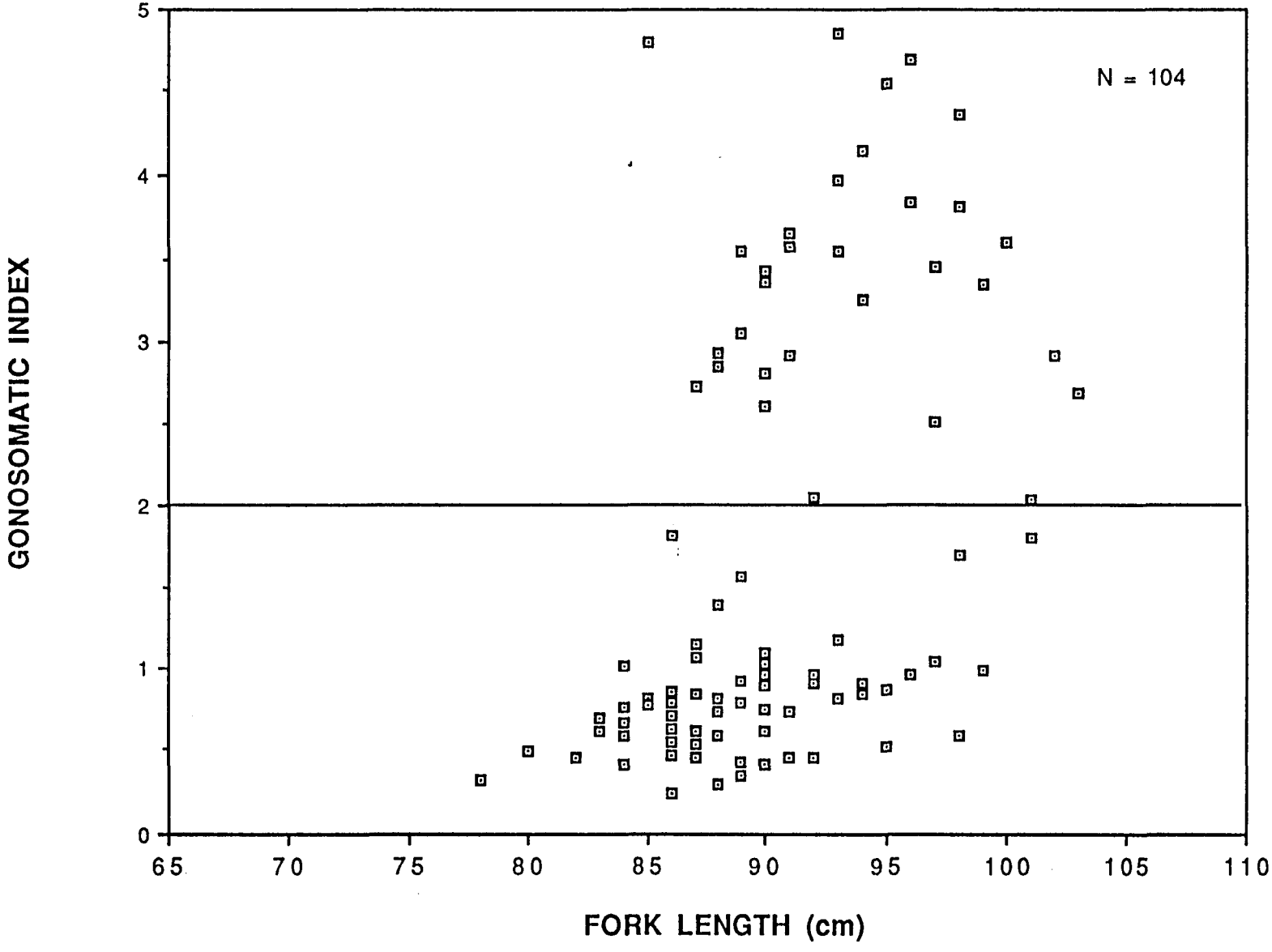

Figure 3a. Gonosomatic indices of female albacore from New Caledonia, May 1990 to February 1992.

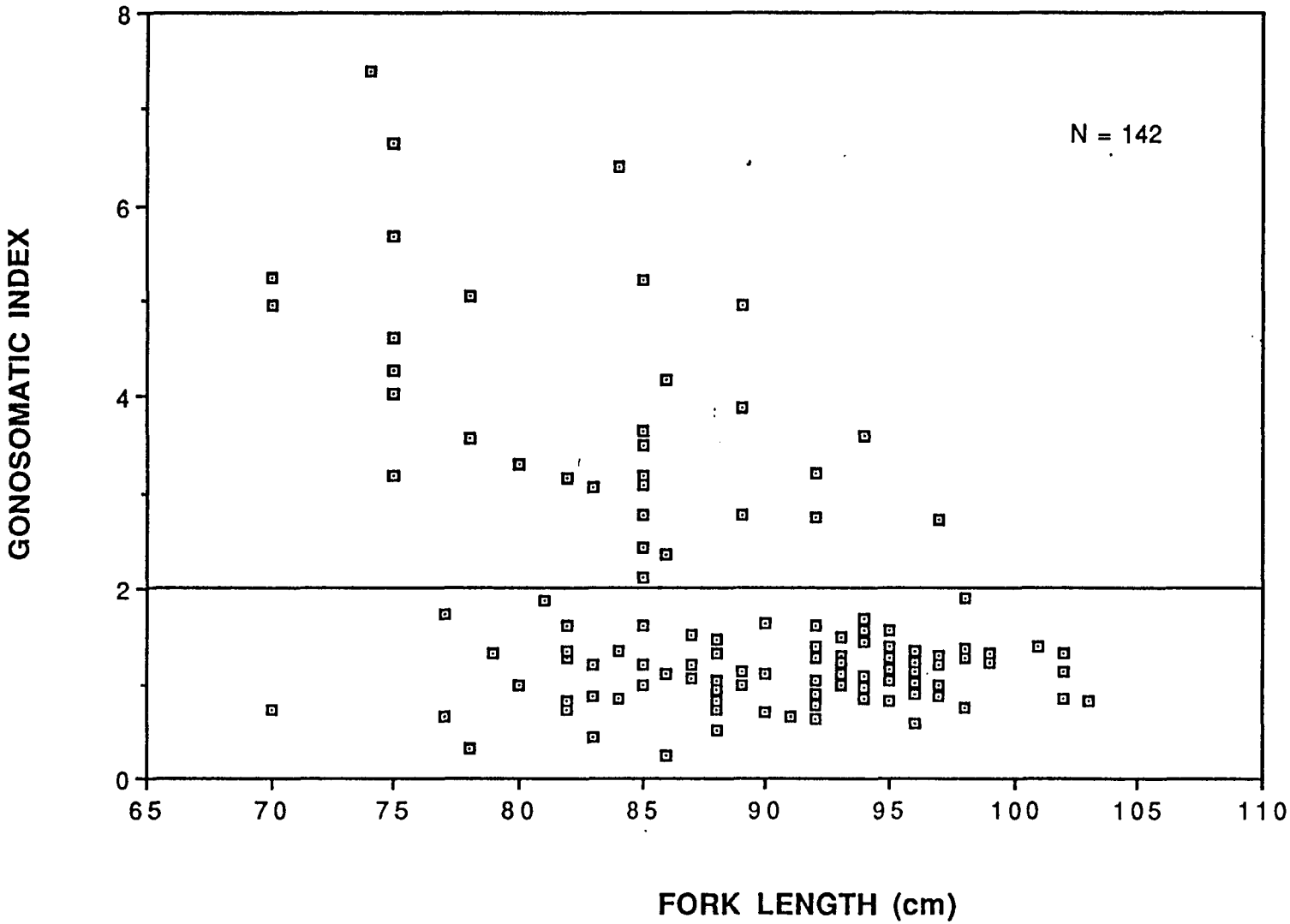

Figure 3b. Gonosomatic indices of female albacore from Tonga, January 1990 to February 1992.

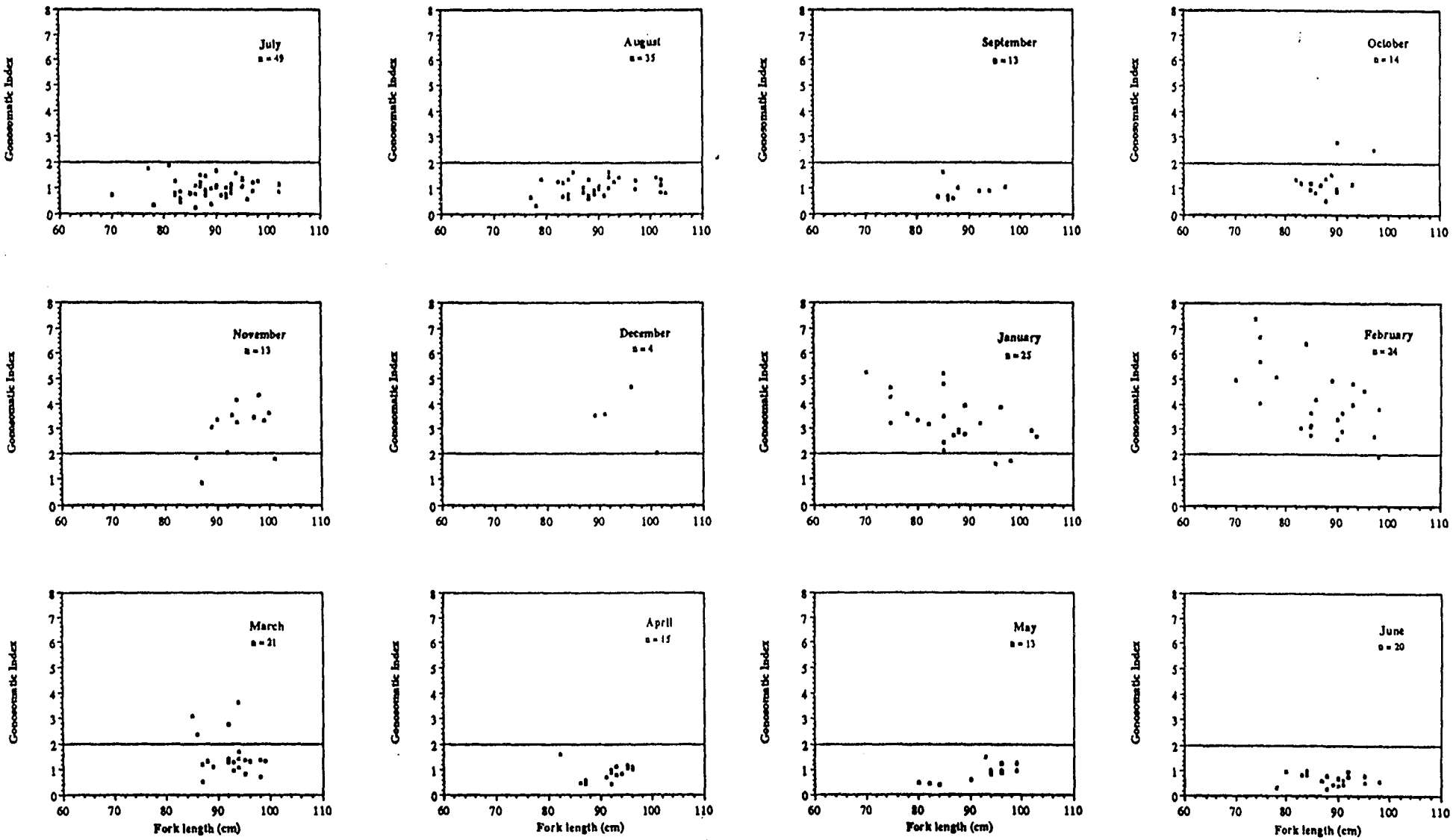

Figure 4. Gonosomatic index values for all female albacore, January 1990 to February 1992.

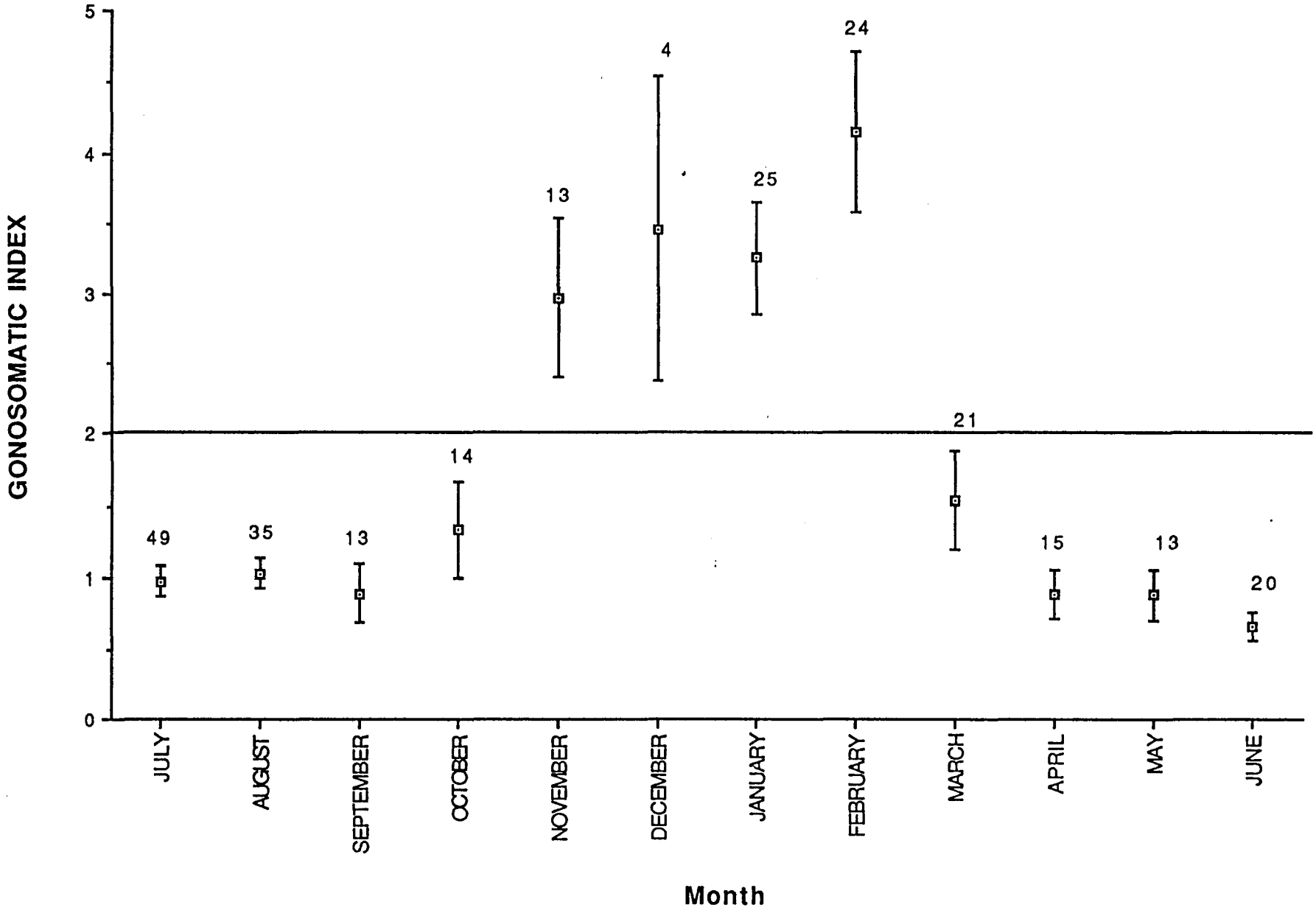

Figure 5. Mean monthly variation of gonosomatic indices for female albacore sampled from New Caledonia and Tonga, 1990 to 1992. (+/- 2 standard error; N = 246).

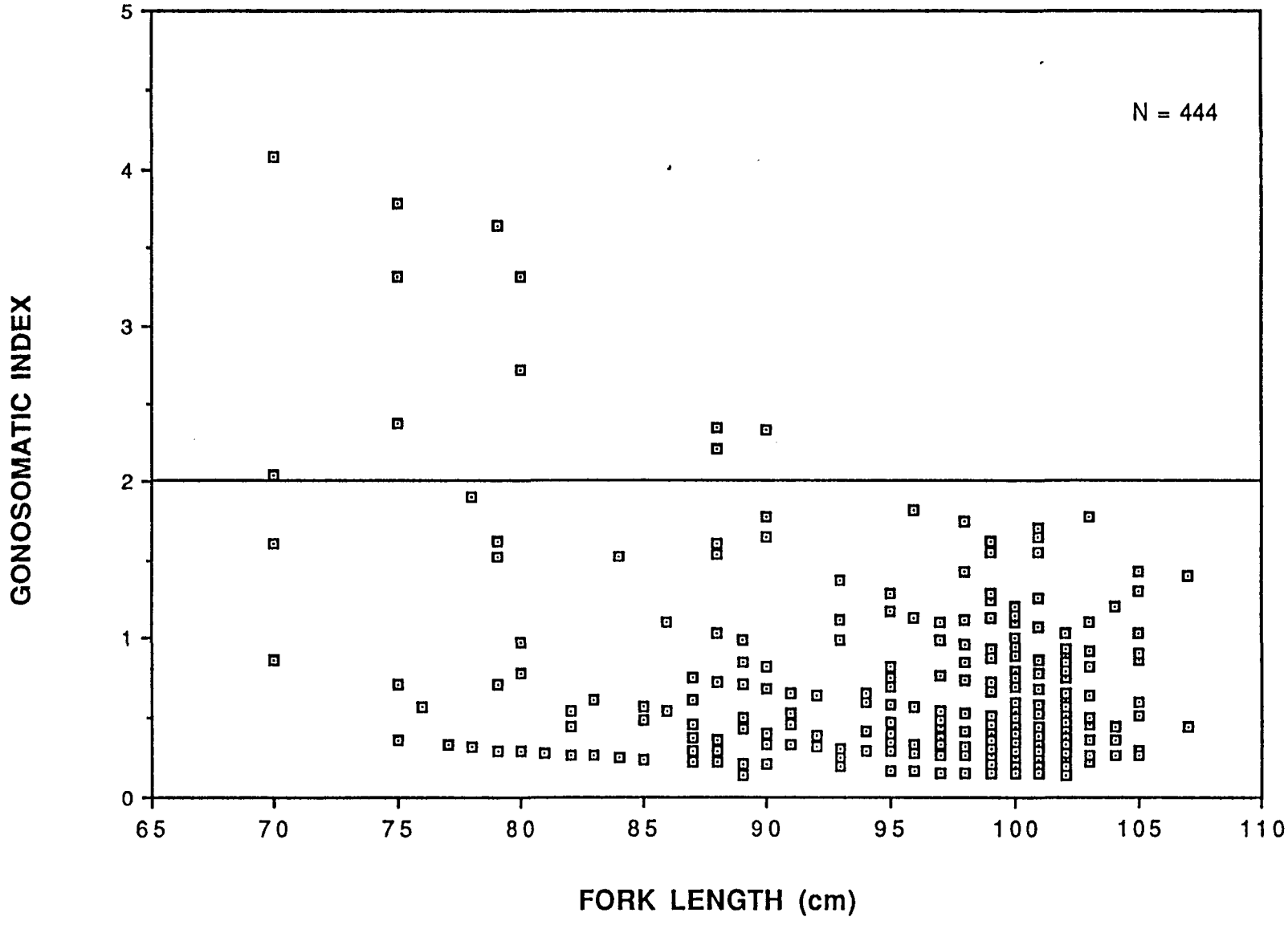

Figure 6. Gonosomatic indices of male albacore from Tonga, January 1990 to February 1992.

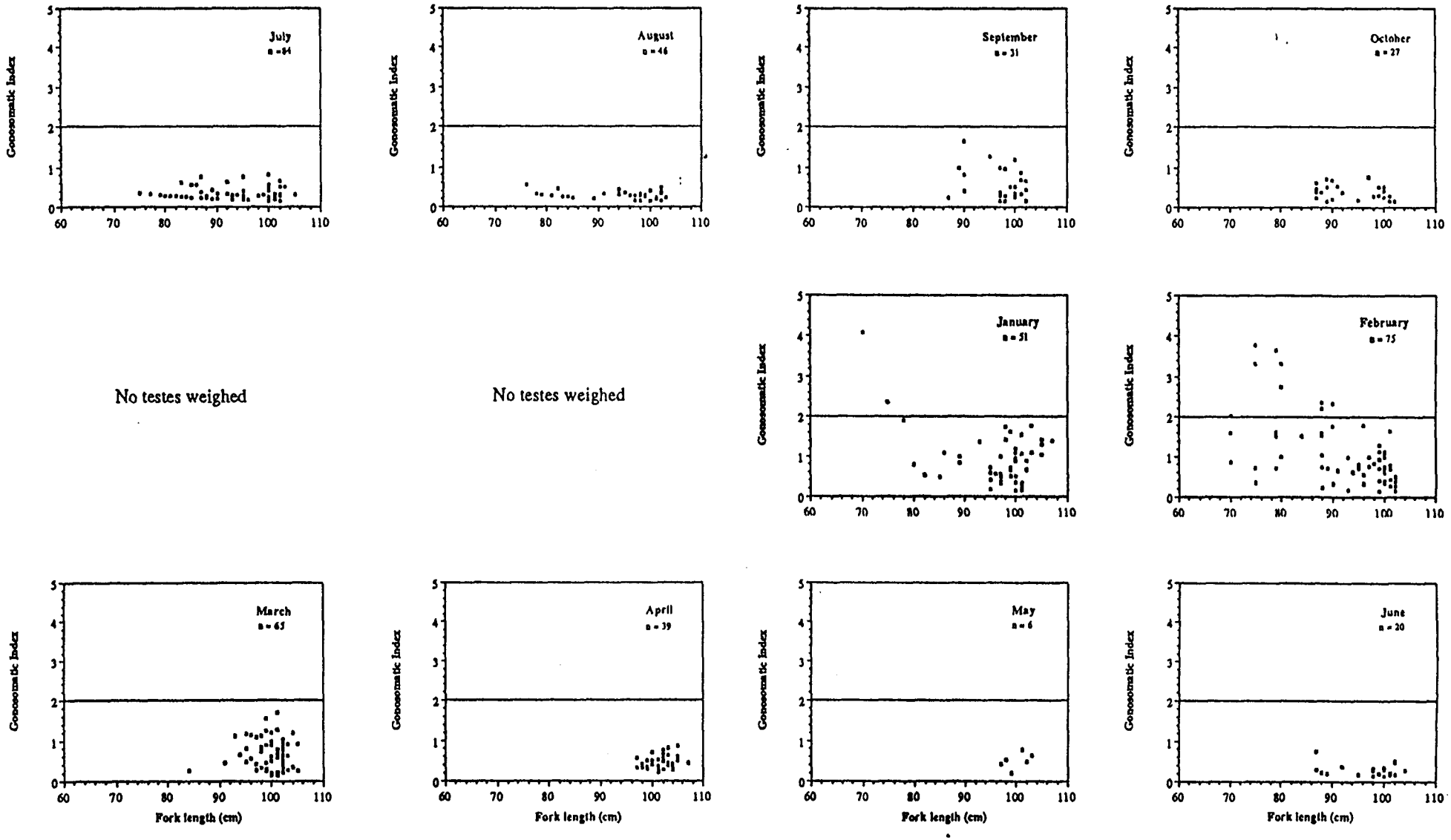

Figure 7. Gonosomatic Index values for all male albacore, January 1990 to February 1992.

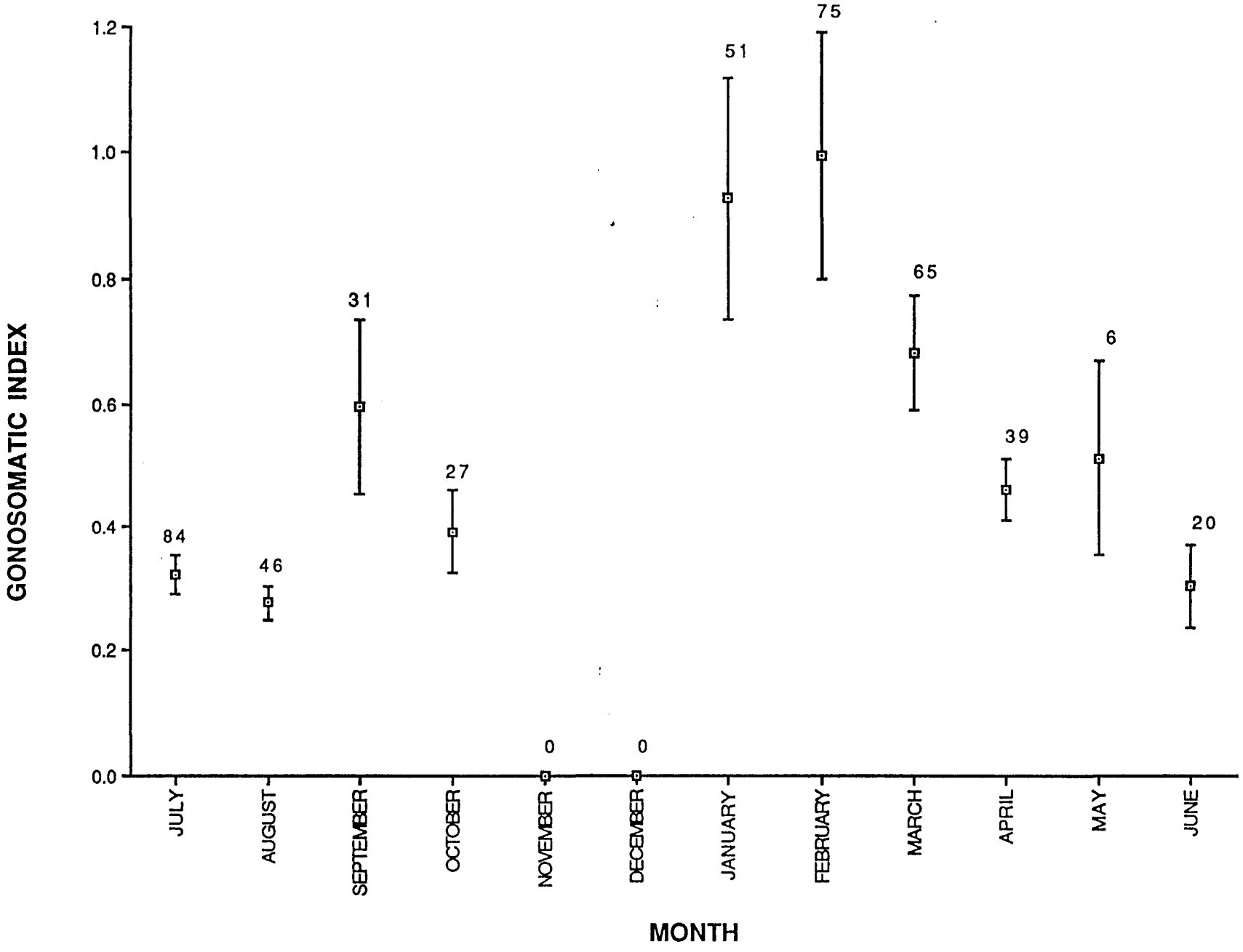

Figure 8. Mean monthly variation in gonosomatic indices for male albacore sampled from 1990 to 1992. (+/- 2 standard error; N = 444).

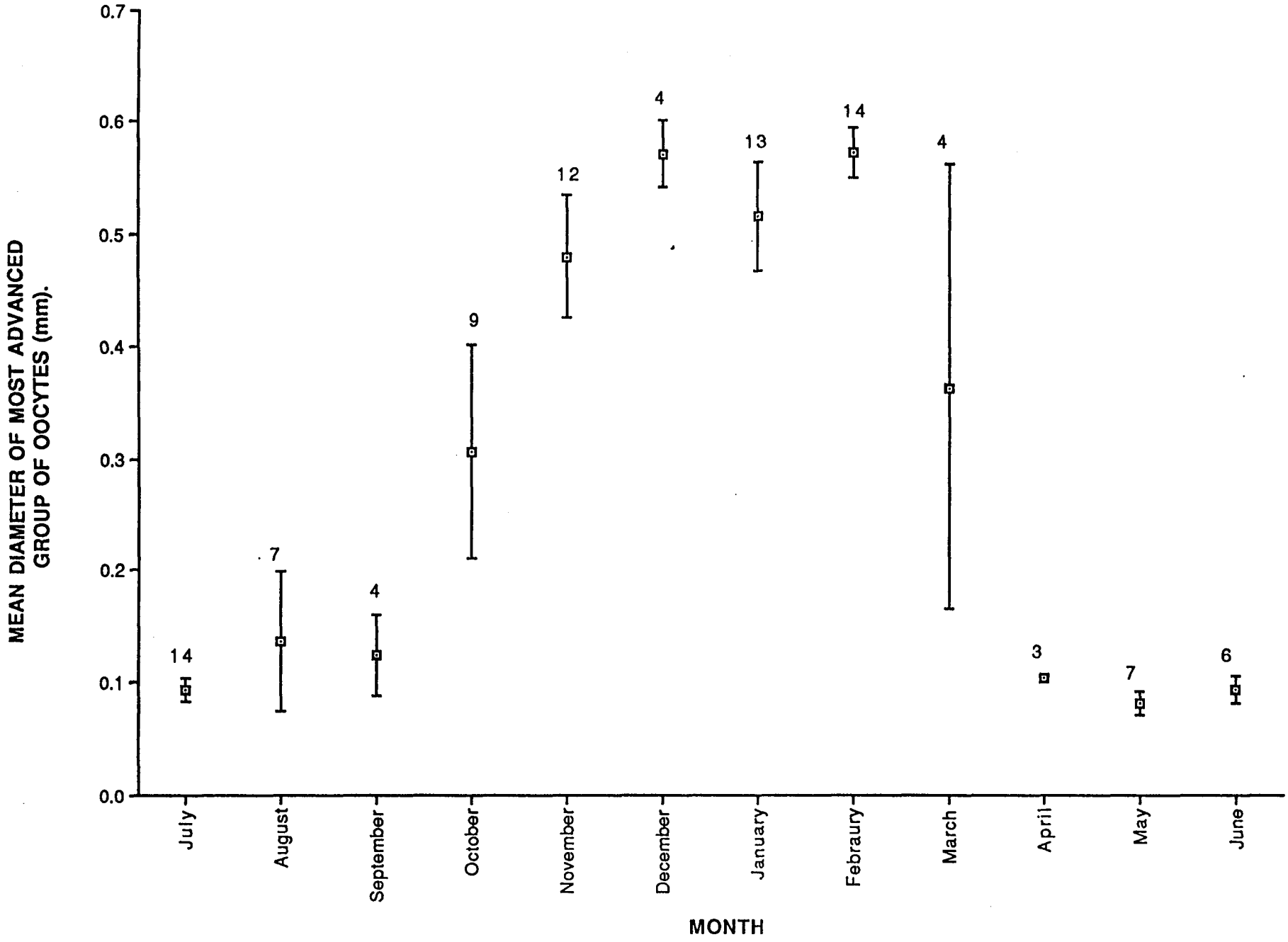

Figure 9. Monthly variation in ova diameters of albacore sampled from January 1990 to February 1992. (+/- 2 standard error; N = 97).

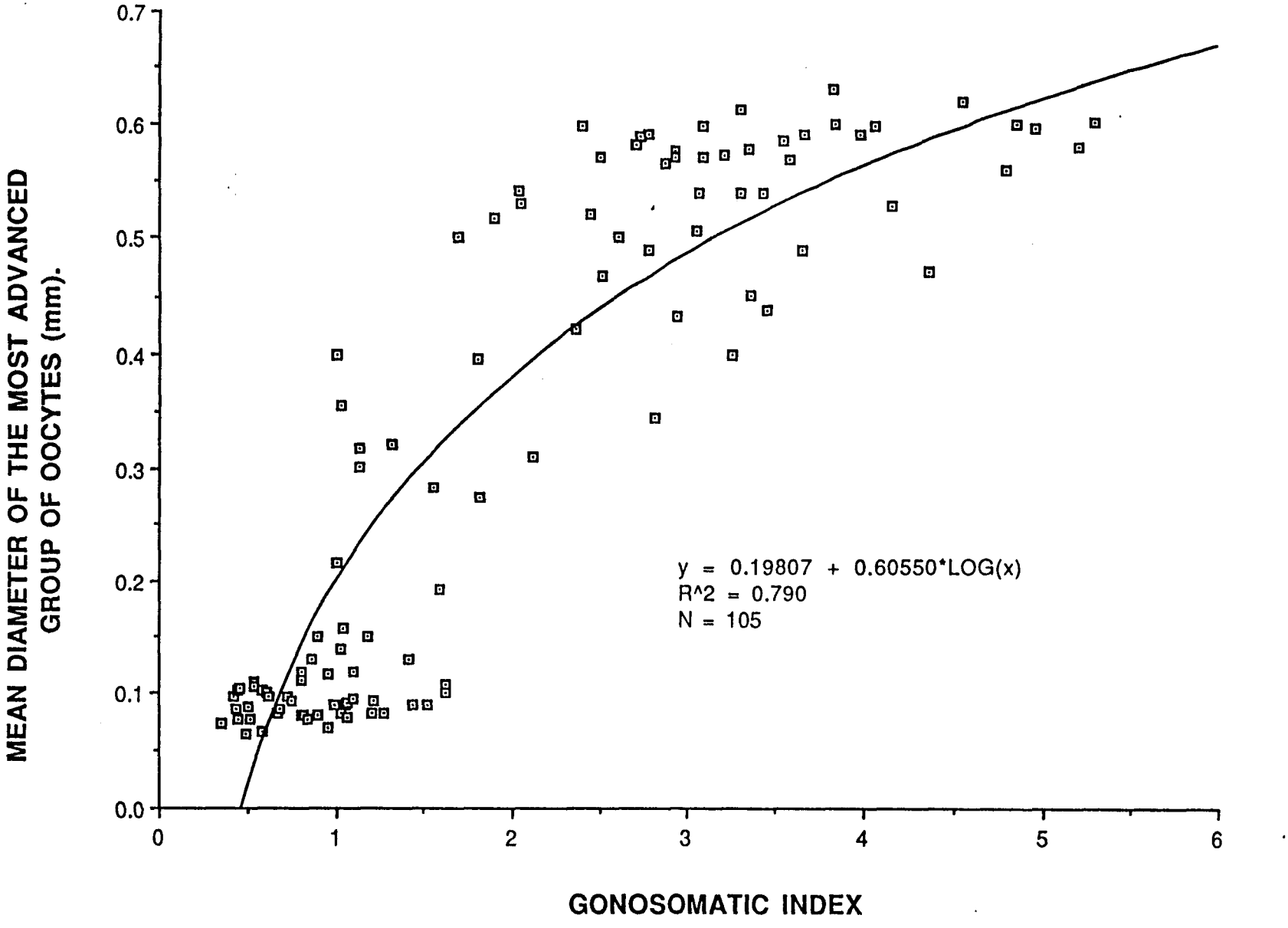

Figure 10. Relationship between the mean diameters of the most advanced groups of oocytes and the gonosomatic indices of albacore from New Caledonia and Tonga 1990 to 1992.

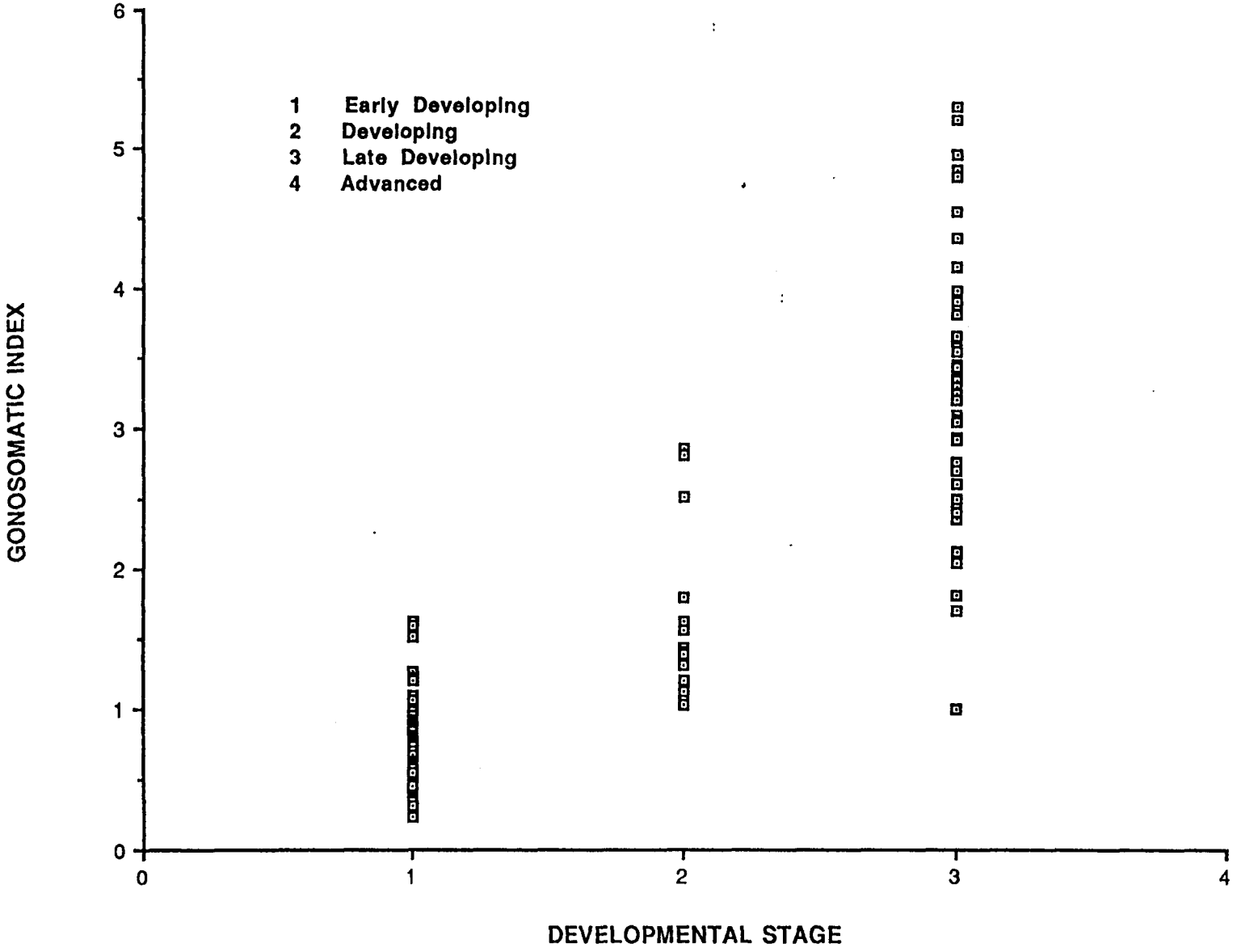

Figure 11. Relationship between the gonosomatic index and developmental stage of sampled albacore ovaries (N = 149)