Assessment of skipjack tuna (*Katsuwonus pelamis*) spawning activity in the eastern Pacific Ocean

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Abstract—An investigation of skipjack tuna, *Katsuwonus pelamis*, spawning activity was conducted to test an earlier established and widely accepted hypothesis that significant spawning of skipjack does not occur in the eastern Pacific Ocean (EPO). Skipjack tuna ovaries were collected, from fish greater than 50 cm in length, from commercial landings of purse seiners fishing in the EPO during 1995. A total of 76 samples, each consisting of approximately 25 females, were collected, processed, and analyzed. The characteristics used to classify the reproductive condition of the individual fish were the mean diameter of the oocytes of the most advanced mode and the presence or absence of residual hydrated oocytes. Results indicate that significant spawning of skipjack tuna, 50 cm or greater in length, occurs in areas of the EPO where sea surface temperatures are equal to or greater than 24°C.

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Skipjack tuna, *Katsuwonus pelamis*, are distributed throughout the Pacific Ocean in tropical and subtropical waters, where they are a primary target species of large-scale purse-seine fisheries. Total estimated catches now exceed one million metric tons. In the eastern Pacific Ocean (EPO), skipjack tuna have been fished from 34°N, off southern California, to 27°S, off northern Chile (Collette and Nauen, 1983; Matsumoto et al., 1984; Wild and Hampton, 1994). The fishery in the EPO was historically concentrated in two areas, a southern area at about 5°N to 10°S and east of 110°W, and a northern area at about 10°N to 30°N and west of 105°W to about 125°W. Estimated annual catches of skipjack tuna during the 1988 to 1997 period in the EPO averaged about 97 thousand metric tons, ranging from 63 to 159 thousand metric tons (Table 3 in Bayliff, 1999). The catches in the southern area have generally been twice as large as those in the northern area, and there have been large annual fluctuations in both areas. Since 1995, the greatest catches have been made by purse seiners setting on floating objects, including fish-aggregating devices (FADs), between about 10°N and 15°S from the coast of the Americas to about 140°W.

Schaefer (1963), reporting on population structure of skipjack tuna in the eastern Pacific, stated that "some, at least, of the West Coast population range far to the westward." He further stated that, "most important, there is little evidence of skipjack tuna spawning in the eastern Pacific fishing region, or near to it; most reproduction occurs farther westward." Rothschild (1965), however, hypothesized that "most skipjack taken by the eastern Pacific skipjack fisheries originate in the central Pacific." His hypothesis was based on available evidence, at that time, from larval distributions, gonad indices, size distributions, tag recoveries, catch predictions, and immunogenetic studies. This hypothesis, however, regarding the origin of skipjack tuna that occur in the eastern Pacific may not be completely valid. The results of research on the reproductive biology of skipjack tuna in the EPO (Schaefer and Orange, 1956; Orange, 1961) indicated some spawning off Central America and in the vicinity of the Revillagigedo Islands, Mexico. In addition, larval surveys have indicated that skipjack tuna spawning occurs in offshore waters and, to a lesser extent, in coastal waters of the EPO (Matsumoto, 1975; Matsumoto et al., 1984; Nishikawa et al., 1985).

In order to achieve a better understanding of the stock structure of skipjack tuna in the Pacific Ocean, an investigation of the spawning potential of skipjack tuna in the EPO was undertaken. The objective of this study was to test the hypothesis that significant spawning of skipjack tuna does not occur in the EPO.

Materials and methods

Field sampling

Skipjack tuna specimens were selected by staff members of the Inter-American Tropical Tuna Commission (IATTC) from the landings of purse seiners at processing plants in Manta (Ecuador), Ensenada and Mazatlan (Mexico), Mayaguez and San Juan (Puerto Rico), and Cumana (Venezuela). Sampling was restricted to catches from east of 150°W from January through December 1995. The sampling program was designed to select specimens greater than 50 cm in length, in order to efficiently sample sexually mature fish (Orange, 1961), if there were any.

The area sampling strata (Fig. 1) used by the IATTC for length data (Tomlinson et al., 1992) were also used for sampling skipjack tuna specimens for the present study. The sampling was designed to collect 25 recognizable ovaries from a single purse-seine set from each area and month stratum for one year. A quota was stipulated of no more than three such samples, for a total of 75 ovaries, from each area and month stratum from which skipjack tuna were caught and unloaded. A total of 76 samples (including 11 replicates), each consisting of approximately 25 female skipjack tuna, for a total of 1822 ovaries, were collected and processed. Skipjack tuna specimens were not available for sampling from various area and month stratum during this sampling period because of the distribution of fishing effort.

Each fish was measured to the nearest centimeter with calipers. The gonads were removed, sex was determined, and the ovaries placed in a plastic bag with identification labels and frozen. The capture locations, dates, set specifications, and sea surface temperatures (SSTs) were obtained from records of scientific observers or abstracts of the vessel logbooks made by IATTC employees, or from both.

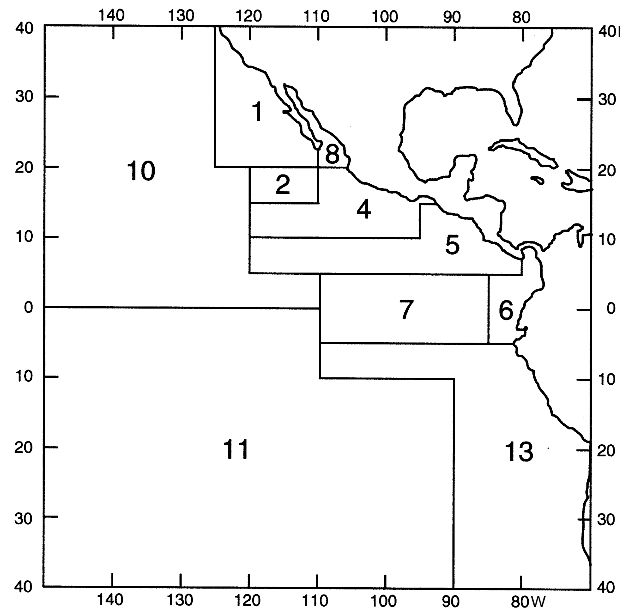

Figure 1

Areas of the eastern Pacific used for sampling skipjack tuna gonads.

Analysis of ovaries

Chi-square contingency tests were employed to compare distributions of oocyte diameters from tissue samples from the rostral, medial, and caudal regions of both ovaries from 30 fish. Because no significant differences were found ($P>0.5$), oocytes from an approximately 1-g tissue sample from the medial region of the right or left ovary were measured to the nearest 0.03 mm at 27· magnification with an ocular micrometer in a dissecting microscope. The mean diameter (random axis) was determined from 10 oocytes per fish (with oocytes >0.21 mm) present in the most advanced mode of oocytes. Ovaries were slit longitudinally and the ovarian lumen examined microscopically for the presence of residual hydrated oocytes, indicative of recent spawning activity.

Female skipjack tunas can be classified as immature, maturing, reproductively active, or resting. Skipjack have asynchronous oocyte development and are considered to be multiple or batch spawners (Schaefer, 1998; Schaefer, in press). Histological and morphological descriptions of oogenesis in the ovary of skipjack tuna (Cayré and Farrugio, 1986; Goldberg and Au, 1986; Stéquert and Ramcharrun, 1996) were used for classification of reproductive condition of individuals in the present study. The characteristics used to classify the reproductive condition of the individual fish were 1) the mean diameter of the oocytes of the most advanced mode and 2) the presence or absence of residual hydrated oocytes. A fish is classified as immature if the mean diameter of the most advanced group of oocytes is less than or equal to 0.2 mm and if there are no residual hydrated oocytes present.

Results

Sex ratios

There were 65 purse-seine sets on schools of skipjack tuna in which a minimum of 24 fish and a maximum of 87 fish, equal to or greater than 50 cm in length, were sampled (mean=52.5 cm, SE=1.44 cm). The percentage of males in the samples ranged from 26.5 to 71.3 (mean=51.5, SE=1.21). A total of 3284 fish, of which 1737 (52.9%) were males and 1547 (47.1%) were females, were sampled. The overall sex ratio for the pooled data from the 65 samples was significantly different ($\chi^2_{0.05,1}$=10.99) from the expected 1:1 ratio. Chi-square tests of males and females grouped into 5-cm length classes for the pooled data (Table 1) indicated a significant deviation in the 50–54.9 cm class (56.0% males), and the 65–69.9 cm class (57.0% males).

Replicate samples

For the 11 replicate samples collected, chi-square tests indicated no significant differences in the proportions of reproductively active female skipjack tuna specimens among the paired replicates ($P>0.05$). Thus, the sample sizes of approximately 25 female skipjack tuna from a single purse-seine set appeared to be adequate for assessing the reproductive status of the fish from the sets sampled. The data from the replicate samples were not used in any of the subsequent analyses.

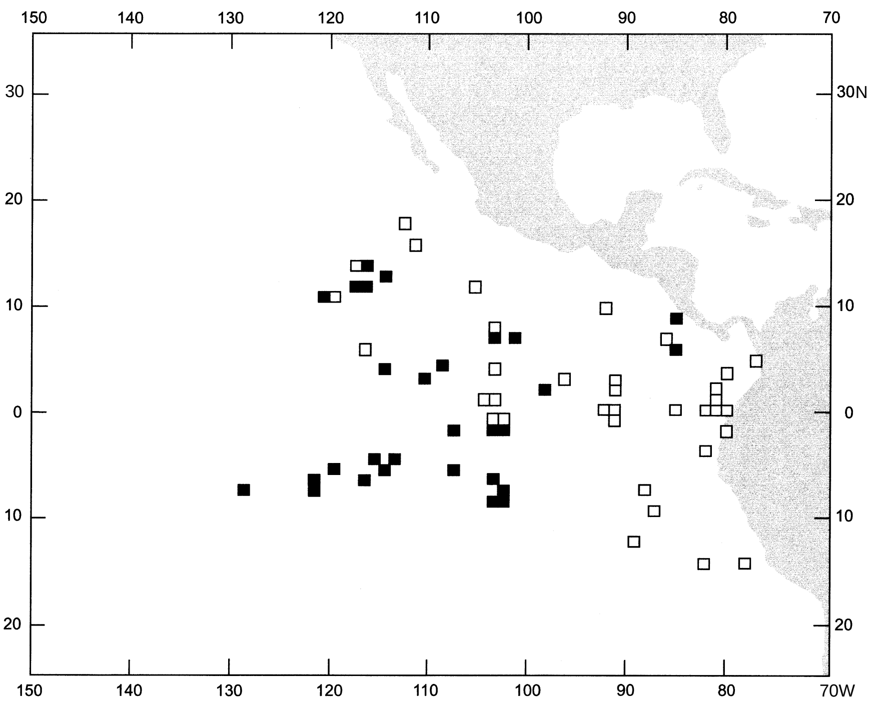

Figure 2

Distributions of reproductively-active (solid squares) and inactive (open squares) female skipjack tuna sampled during 1995.

Spatiotemporal patterns in spawning

Reproductive activity is certain for the females with advanced yolked oocytes that are equal to or greater than 0.55 mm in diameter. Of these, 429 (28%) were classified as reproductively active, and reproductively active females were found in 27 of the samples (42%) (Table 2). Of the 429 skipjack tuna with advanced yolked oocytes, 232 (54%) also had residual hydrated oocytes in the lumen of their ovaries, indicative of recent spawning. Based upon the distribution of these samples, skipjack tuna spawning in the EPO appears to be fairly widespread from around 15°N to 10°S and from the coast to about 130°W (Fig. 2). Reproductively active skipjack tuna were present north of the equator throughout the year and south of the equator during the first three quarters of the year, and there were no apparent seasonal peaks in either stratum (Fig. 3). No samples of mature fish were collected during the fourth quarter south of the equator. The length-frequency distribution of the females from the 65 independent samples is shown in Figure 4.

Based upon the SST data collected in conjunction with catch information for each of these samples, it appears that skipjack tuna are sexually inactive at SSTs less than 24°C. Of the 65 samples, 20, or 31%, were taken from skipjack tuna captured at SSTs less than or equal to 24°C (Fig. 5). In other words, just over half of the 38 samples that did not contain reproductively active fish were obtained from skipjack tuna captured at SSTs below those at which spawning occurs.

Table 1

Sex ratios of skipjack tuna, *Katsuwonus pelamis*.

Length (cm)	Number observed: Male	Number observed: Female	Percent male	Chi-square
50.0–54.9	873	687	56.0	22.18*
55.0–59.9	365	387	48.5	0.64
60.0–64.9	252	285	46.9	2.03
65.0–69.9	226	170	57.0	7.92*
70.0–74.9	21	18	53.8	0.23
Total	1737	1547	52.9	10.99*

* = $P < 0.05$.

The frequency distributions of the estimated sizes, in metric tons, of the skipjack tuna schools sampled, along with the subset of those that were classified as spawning, are shown in Figure 6. The prominent mode in each distribution was around 25 metric tons; the ranges in each mode were from about 5 to 270 tons.

Discussion

It is evident from the results of this investigation that significant spawning of skipjack tuna, 50 cm or greater in

Table 2

Reproductive status of female skipjack tuna caught in the eastern Pacific Ocean and sampled at canneries during 1995. Area boundaries are shown in Figure 1.

	Area								
	2	4	5	6	7	10	11	13	Total
No. of samples collected	2	8	10	8	20	4	6	7	65
No. of ovaries collected	29	170	232	196	493	100	150	177	1547
No. of samples with reproductively active females	0	4	4	0	7	3	6	3	27
Percentage of samples with reproductively active females	0	50	40	0	35	75	100	43	42
No. of active females	0	44	72	0	67	55	117	74	429
Percentage of active females	0	26	31	0	14	55	78	42	28

length, occurs in areas of the EPO where the SSTs are equal to or greater than 24°C. Skipjack tuna spawning occurs throughout the year in tropical waters and seasonally in subtropical waters in all major oceans (Matsumoto et al., 1984; Nishikawa et al., 1985; Schaefer, in press). The latitudinal range in the spawning distribution of skipjack tuna has been shown for the Pacific and Atlantic Oceans to coincide with the area delineated on the north and south by the 24°C isotherm (Ueyanagi, 1969; Cayré and Farrugio, 1986). In the western part of the equatorial Indian Ocean skipjack tuna spawning also occurs throughout the year (Stéquert and Ramcharrun, 1996; Timohina and Romanov, 1996).

Earlier research on the reproductive biology of skipjack tuna in the EPO indicated spawning off Central America and off Baja California, Mexico, near the Revillagigedo Islands (Schaefer and Orange, 1956; Orange, 1961). It was concluded from these studies that skipjack tuna spawning occurs mainly offshore in the EPO, and the estimated minimum size at maturity in the vicinity of the Revillagigedo Islands is about 55 cm and about 40 cm off Central America. The present study also indicates spawning of skipjack tuna in the EPO appears to be more concentrated offshore, west of 95°W longitude (Fig. 2). It should be noted that during the 1950s and early 1960s the fishery for tunas in the eastern Pacific occurred within a few hundred miles of the mainland and in the vicinity of a few offshore islands and banks (Alverson, 1960, 1963). Thus, skipjack tuna gonad sampling for those earlier studies was confined to those areas.

Larval surveys have also indicated that skipjack tuna spawning occurs in offshore areas of the EPO and may be restricted in coastal areas (Klawe, 1963; Matsumoto, 1975; Matsumoto et al., 1984). One of the objectives of the EASTROPAC expeditions of 1967 was to look at the distribution of scombrid larvae over a vast expanse of the EPO. During EASTROPAC I (Ahlstrom, 1971), larvae of skipjack tuna (17 occurrences, 214 larvae) were collected predominantly in the offshore southern portion of the EPO at about 7°S and 120°W. Likewise, few yellowfin tuna larvae (19 occurrences, 40 larvae) were collected during EASTROPAC I, even though the spawning distribution of yellowfin tuna has been shown to be widespread throughout the EPO (Schaefer, 1998). Scombrid larvae were markedly less abundant during EASTROPAC II; few skipjack tuna (2 occurrences, 2 larvae) and yellowfin tuna (2 occurrences, 2 larvae) were collected (Ahlstrom, 1972). Catch rates of larval skipjack tuna adjusted for different size nets and different towing methods in a band of water from 10°S to 20°N indicated that skipjack tuna larval abundance was highest between 160°E and 140°W, moderate between 100°W and 140°W and between 120°E and 160°E, and low in the EPO east of 100°W (Matsumoto, 1975). The extensive compilation of data on larval scombrids by Nishikawa et al. (1985) also indicates that east of 150°W between 10°S and 10°N there is widespread spawning of skipjack tuna, mostly west of 110°W. Although there is also a distinct tendency of increasing abundance of skipjack tuna larvae from the EPO to the WPO, these authors caution that this tendency is perhaps overstressed due to a potential bias in the data.

Tag release and recapture studies have shown that considerable mixing of skipjack tuna exists in the Pacific Ocean (Hunter et al., 1986). There is a large volume of information on skipjack tuna movements in the western Pacific Ocean (WPO). Although there were numerous long-distance movements of individual tagged skipjack tuna observed, the overall percentage of recoveries having displacements of greater than 200 nmi was only 17% and there are few probable migration routes revealed from the recovery of tagged skipjack tuna (Wild and Hampton, 1994). Furthermore, when considering skipjack tuna on a Pacific-wide basis, particularly the areas of tagging operations in the WPO, it was concluded that skipjack tuna did not appear to migrate toward specific areas for feeding or spawning but appeared to move in more or less random directions within broad limits (Hunter et al., 1986). There have been no recoveries in the EPO from skipjack tuna tagged in the central or WPO. The assumed eastward migration routes of juveniles described in the skipjack tuna migration model (Rothschild, 1965) lack validation, and hypotheses about the energetic advantages of migration to the EPO using the North

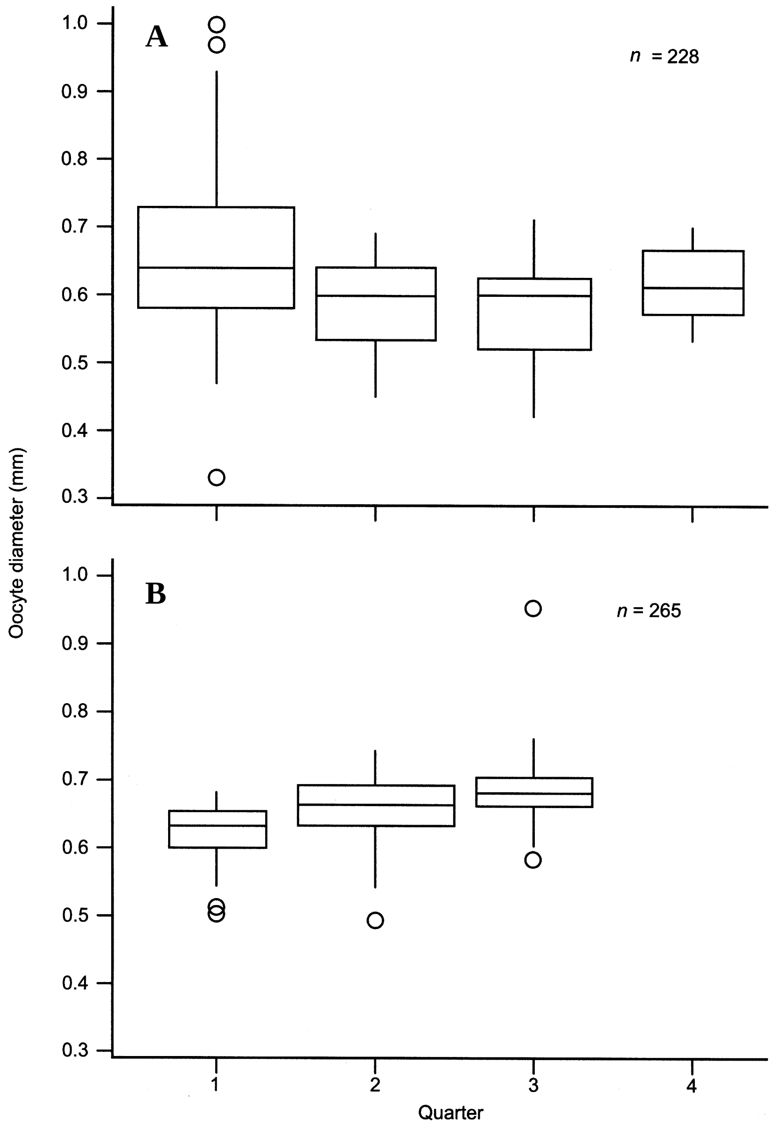

Figure 3

Seasonal variation in oocyte diameters from the most advanced modal group of oocytes from (**A**) skipjack tuna collected from north of the equator and (**B**) skipjack tuna collected from south of the equator during 1995. Immature fish were excluded from this analysis. The width of the box is proportional to the number of samples in the group. The horizontal line within the box is at the median. The bottom of the box is at the first quartile (Q_1) and the top is at the third quartile (Q_3) value. The lines extend from the top and bottom of the box to the adjacent lowest and highest observations within the lower and upper limits defined as $Q_1 \pm 1.5\ (Q_3 - Q_1)$. Outliers are points outside the lower and upper limits and are plotted as circles.

Equatorial Countercurrent and the Equatorial Undercurrent (Williams, 1972) are unsubstantiated.

Numerous tagging studies have also been conducted in the EPO to investigate movements of skipjack tuna (Fink and Bayliff, 1970; Bayliff, 1984). It appears from these studies that skipjack tuna show some consistency of directed movement in the nearshore regions off Central America and northern South America. In the northern region around the Revillagigedo Islands and the west coast of Baja California, there is a northern and then southern movement of the fish between 20°N and 30°N in response to the seasonal movements of the 20°C surface isotherm between about

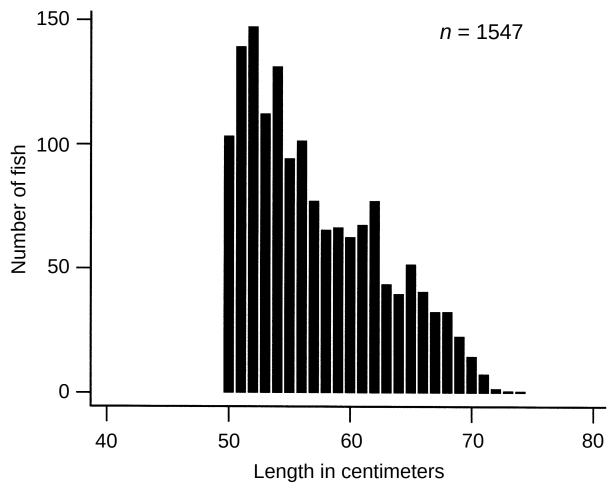

Figure 4

Length distribution for female skipjack tuna sampled in the eastern Pacific Ocean during 1995.

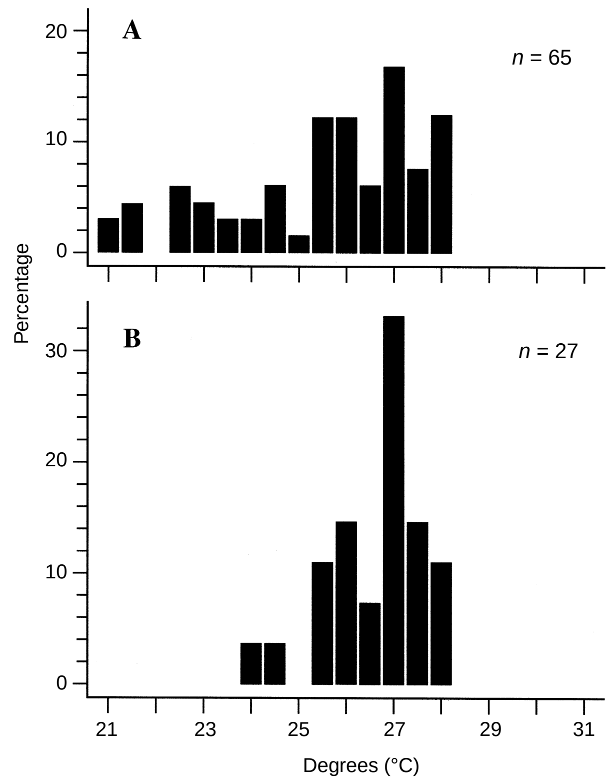

Figure 5

Sea surface temperatures at which (**A**) all skipjack tuna schools were sampled and (**B**) spawning skipjack tuna schools were sampled in the eastern Pacific Ocean during 1995.

May and December. There is also some movement of fish between the northern and southern areas of the fishery in the EPO. However, from well over 100,000 skipjack tuna tagged in the EPO and several thousand returns, only 27 skipjack tuna have been recovered in the central Pacific or the WPO, and 21 of those were recaptured around the Hawaiian Islands (Bayliff, 1988). Of those fish recovered, 19 were tagged off Baja California, 4 fish off the Revillagigedo Islands, 2 fish off Clipperton Island, and 1 fish well offshore at about 4°N and 119°W. Only 1 skipjack tuna tagged in the near shore waters off Central America, within the area of the primary fishery, has been recovered in the central Pacific around Hawaii. Before the recovery of this tagged skipjack tuna there was no evidence from tagging that fish of the southern group migrate to the central Pacific.

Although the information has been largely ignored, morphometrics research has shown significant statistical differences between skipjack tuna from the EPO and the central Pacific (Hawaii and French Polynesia) (Hennemuth, 1959). These differences could indicate a low level of mixing of skipjack tuna populations between the central Pacific and the EPO.

Reliable estimates of the skipjack tuna spawning biomass in the EPO are presently unavailable. However, some indication of the relative abundance of skipjack tuna spawners in the EPO can be derived from considering the estimated total catch of skipjack tuna by length intervals from the surface fishery in the EPO (Fig. 7). It is apparent for 1993 to 1998 that there were significant amounts of skipjack tuna greater than 50 cm in length present in the EPO. These data for skipjack tuna catch by length, combined with the data presented in the present study of spawning activity of skipjack tuna females greater than 50 cm in length, provide strong evidence to support the concept of a significant skipjack tuna spawning biomass in the EPO. It also seems reasonable to consider that the subsequent survivors, resulting from skipjack tuna spawning in the EPO, constitute a significant component of the skipjack tuna population in the EPO.

Skipjack tuna do not appear to be a migratory species such as Pacific, Atlantic, and southern bluefin tunas (*Thunnus orientalis, T. thynnus*, and *T. maccoyii*) that have discrete spawning locations (Schaefer, in press). Too much emphasis has been placed on long-range movements of a few tagged skipjack. The tagging data for skipjack tuna only supports extensive offshore–onshore movements as well as north–south movements in the EPO. Based upon what is known about skipjack tuna life history (Matsumoto et al., 1984; Wild and Hampton, 1994), it would seem that skipjack tuna need to be opportunistic in their reproductive strategy, taking advantage of the suitable environment in the EPO. Once skipjack tuna reach sexual maturity, they probably spawn throughout their distribution, whenever water temperatures rise above 24°C.

The long-standing premise that skipjack tuna in the EPO are merely short-term transients, originating from spawning in the central Pacific or WPO, should be seriously reconsidered. This issue has important international management implications. Although the stock in the EPO is not a closed unit, as a result of the highly mobile and op-

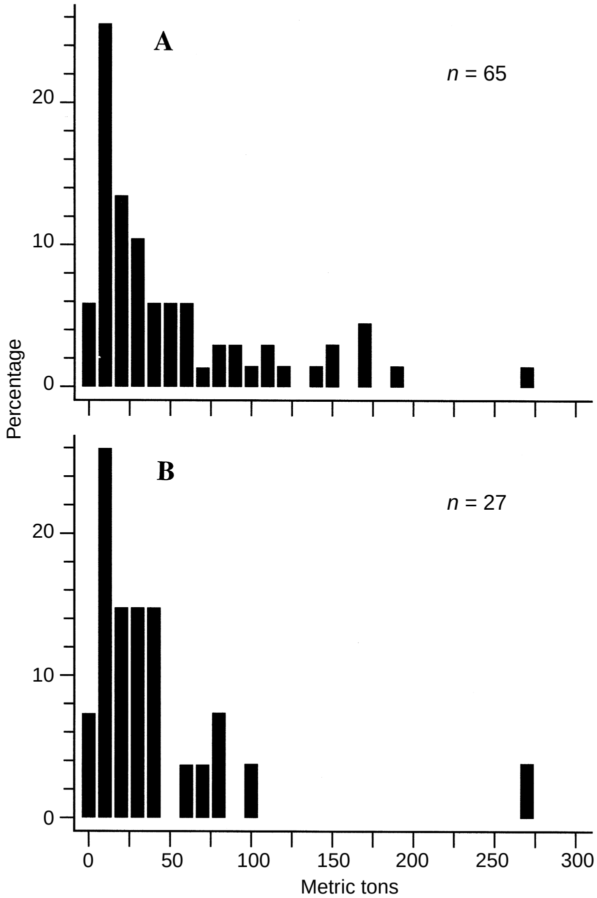

Figure 6

Sizes of (**A**) all skipjack tuna schools sampled and (**B**) those containing spawning females.

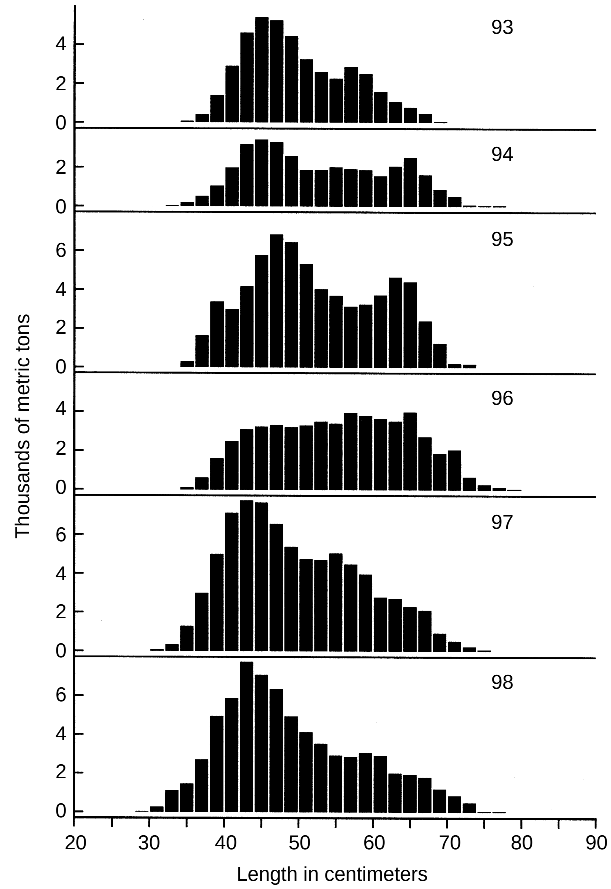

Figure 7

Estimated length compositions of the total skipjack tuna catch, by 2-cm intervals, in the eastern Pacific Ocean. These histograms are based on the catch statistics and length-frequency samples of skipjack tuna, for each year of the 1993–98 period, compiled by the Inter-American Tropical Tuna Commission.

portunistic nature of this species, assessments should nevertheless be conducted for the skipjack tuna stock within this geographical region. Ideally, stock assessment models for skipjack tuna should incorporate spatial and temporal variability in the size-specific parameters for age, growth, movement, mortality, and reproduction. A more comprehensive investigation of the reproductive biology of skipjack tuna in the EPO is in progress.

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