

DRAFT FOR COMMENT

THE BIOLOGY, ECOLOGY, AND RESOURCE
OF THE SKIPJACK TUNA, KATSUWONUS PELAMIS

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THE BIOLOGY, ECOLOGY, AND RESOURCE OF THE SKIPJACK

TUNA, KATSUWONUS PELAMIS

I. INTRODUCTION

The harvesting of the skipjack tuna, Katsuwonus pelamis, in the world oceans has increased noticeably in the last few years, due to the increased attention given to this species based on indications that it is the only one of six principal market species of tunas (others are the yellowfin tuna, Thunnus albacares; the bigeye tuna, T. obesus; the bluefin tuna, T. thynnus; the southern bluefin tuna, T. maccoyii; and the albacore, T. alalunga) that can withstand heavier fishing pressure without immediate danger of being overfished. Recent studies of tuna longline catches (Kikawa et al, 1969; Rothschild and Uchida 1968; Hayasi et al. 1970; Suda 1971; Skillingman 1985), have indicated that except for the bigeye tuna in the Atlantic Ocean and possibly the albacore in the South Pacific Ocean, all tunas taken with the longline in the three major oceans are now being exploited at or near their maximum sustainable yields. As a result of this increased interest in the skipjack tuna, this species has become the greatest yield producer among the tunas.

Although further increases in the yield of this species are still possible, the time will come when management of the species becomes necessary to ensure continued high yields. To place future investigations and possible management measures on a rational and economically sound basis, we need more complete knowledge of the biology and ecology of the species, and of the origins and relationships of the groups of

skipjack tuna that are being harvested or may be harvested in the future. A first step in enlarging this knowledge is to review and assess all pertinent literature on the skipjack tuna and its populations so that emphasis in research may be directed properly. Reviews of the species had been made in the past (Waldron 1963; Jones and Silas 1963; Postel 1963; and Kawasaki 1965a, 1965b), but with the addition of new information in the past decade, it has become necessary to re-examine the status of our knowledge of the skipjack tuna. This paper reviews the past knowledge of the skipjack tuna and presents the status of the skipjack tuna and its fisheries in terms of more recent research and developments.

II. IDENTITY

Katsuwonus pelamis (Linnaeus 1758) has been widely accepted as the scientific name of skipjack tuna since it was first proposed in 1915 by Kishinouye, although at that time he used the spelling "pelamys." Prior to Kishinouye, the skipjack tuna was variously assigned the generic name of Scomber (Linnaeus 1758), Thynnus (Lesson 1830), Pelamys (Bleeker 1865), Orcynus (Goode and Bean 1879), Euthynnus (Jordan and Gilbert 1882), Gymnosarda (Dresslar and Fesler 1889).

In the 1950's and early 1960's there was a tendency towards replacing the name Katsuwonus with Euthynnus, retaining the specific name pelamis, but in the late 1960's, it reverted to Katsuwonus, when it was recognized that pelamis was generically distinct from the three species of Euthynnus (Collette 1966). Variations exist also in the use of the species name. A few authors used vagans for the Pacific form, but there are no factual data to support this view. While there have been no studies comparing the skipjack tuna from the three major oceans, the existing descriptions and data from these areas (Postel 1963; Jones and Silas 1963; Waldron 1963) do not differ enough to warrant separate species categories by oceans.

III. OCCURRENCE

Prior to 1959, the occurrence and distribution of the skipjack tuna had been determined essentially from records of captures in coastal waters and in those offshore areas subjected to commercial pole-and-line and purse seine fishing. Because the pole-and-line fisheries were constrained by their need for live bait to areas within easy access of bait supplies and the purse seine fisheries were confined to those areas which possess a relatively shallow mixed layer, a feature characteristic of the eastern sides of both the Atlantic and Pacific Oceans (Brock 1959), there were large gaps in our knowledge about the distribution of skipjack tuna in midoceanic areas of the Pacific Ocean. Even less was known about the occurrence and distribution of skipjack tuna in the Indian and Atlantic Oceans, where fishing for this species on a commercial scale had not developed as in the Pacific Ocean.

Since 1959 various authors (Brock 1959; Kasahara 1968; Miyake 1968; Matsumoto 1974, in press) have used the Japanese tuna longline data to determine the distribution of skipjack tuna in midoceanic areas. Although the catches made by the longline gear are small, they constitute evidence of the occurrence of skipjack at the sites of capture, and the information thus obtained have expanded our knowledge about the distribution of the species.

Fig. 1

Figure 1 illustrates the distribution of skipjack tuna in all the oceans. The distribution was derived from atlases of skipjack tuna catches in the Japanese southern water fishery for 196⁶~~4~~-67, 1970-71, and 1973 (Tohoku R. F. R. L. undated),^{2,5,4} Japanese tuna longline catch data for 1964-67 and 1969-71 (Matsumoto 1974, in press) and from the literature (Brock 1959; Jones and Silas 1963; Postel 1963; Robins 1952; Roux 1961; Sakagawa 1974; Wade 1950). The species generally occurs continuously from east to west across all ocean, and over a wide latitudinal range in the Atlantic and Pacific Oceans (darkly shaded areas, Fig. 1). Rare captures off Vancouver Island (Clemens and Wilby 1961) in the Pacific Ocean and off the British Isles, Scandinavia, and Denmark (Postel 1963) in the Atlantic Ocean (lightly shaded areas, Fig. 1) extend the limits of distribution to lat 50°N and nearly to lat 60°N, respectively. The skipjack tuna occurs also in the western basin of the Mediterranean Sea, but not in large concentrations as in the Atlantic Ocean (Postel 1963; Belloc 1955).

IV. BIOLOGY

A. REPRODUCTION

Studies on reproduction have followed two approaches:

(a) examination of gonad development and (b) collection of eggs and larvae. The two approaches complement each other for while (a) provides certain information concerning pre-natal development and reproductive conditions of individual adults, (b) provides evidence that spawning had actually occurred, pinpointing the time and place of spawning more accurately. Information not available by the latter method, such as fecundity and size of fish at first spawning, are provided by the former.

It should be noted that although a number of gonadal studies have been made in the past, the majority have been based on material collected in the Pacific Ocean. Relatively few studies have dealt with material from the Indian and Atlantic Ocean.

1. Sexual Maturity

Several methods have been used to determine the degree of sexual maturity of tunas. These include the classification of gonad development on the basis of (a) appearance of the gonads, (b) measurements of ova diameters, (c) a combination of the two, a and b, and (d) the relation between ovary weight and fish weight or length.

The most direct way to measure sexual maturity is by visual observation of the external appearance of the gonad, as was done by Matsui (1942), Marr (1948), Yao (1955) and Williams (1964),

among others. The external characters most used were size of gonad and degree of softness or turgidity. Others, such as Bunag (1956), Raju (1964^c) and Kawasaki (1965^a) believed that external characters alone were inadequate even for gross classification. Some improvements were made by including the description of ova in the various stages when the ova were developed sufficiently for observation by the unaided eye (Schaefer and Orange 1956; Bunag 1956; Raju 1964^c; Yoshida 1966; Simmons 1969; Batts 1972^c), but the classification still remained subjective and was prone to variations caused by each individual observer's interpretation of the various stages.

Bunag (1956) and Raju (1964^c) classified sexual maturity on the basis of ova diameter measurements, a more objective method than the one above, and their classifications were accompanied by descriptions of the ova. Others such as Yoshida (1966) and Batts (1972^c) also provided ova diameter measurements along with descriptions of ova, ovaries, or both. Yet the classification by these authors differed noticeably.

Such differences occur, regardless of the method used, since no standard scale defining the various stages of development has been established. Bunag (1956) made an attempt to classify the stages according to the International Maturity Scale⁵, but

no one else had followed his example. Table 1 contains the classification used by the various authors. Even from a table such as this, which shows such great diversity in classification, one could derive a reasonably acceptable maturity scale such as that shown in Table 2.

Any classification requiring the measurement of ova diameter involves a great deal of time and labor. Several authors have discussed the possibility of using relative ovary weight (ovary weight $\times 10^x$ / fish weight) as a measure of maturity of tuna (June 1953 ; Yabe 1954; Yuen 1955; Otsu and Uchida 1959). Schaefer and Orange (1956) also used the relative ovary weight to measure the maturity of tunas, the only difference being that they used the cube of fish length instead of fish weight (as did Kikawa 1953) and a factor of 10^8 to obtain a two-digit value. They called this relationship the "gonad index," which they defined as $G.I. = \frac{w}{L^3} \times 10^8$, where "G.I." is the gonad index, "w" the weight of the ovaries in grams, and "L" the length of fish in millimeters. By plotting the gonad index against the 95th centile of ova diameter frequency distribution and fitting a regression to the plots, they observed that the gonad index provided a useful estimate of ova size, even though the standard error of estimate was not small.

Orange (1961) employed the same index to determine the sexual maturity of skipjack, as well as yellowfin tuna, in the eastern Pacific and from it to determine the incidence of spawning and also the size of females at first spawning. He observed a slight increase in the gonad index with increased fish size and explained that this could be due to the occurrence of more immature females in the smaller size classes, the larger size classes being predominantly females in the resting stage, or because the gonads grow proportionately faster than the rest of the fish, or because

the cube of the fish length is not proportional to weight. However, he also felt that the value of the gonad index was not hindered because of this slight increase in gonad index with fish size. Raju (1964^c), using the same G.I. to fish from Minicoy waters obtained similar results.

That the regression of ova diameter on gonad index may not hold for index values, at least, above 36 was suggested by Yoshida (1966), who calculated gonad index of skipjack taken in the Marquesas and Tuamotu Islands. He used the mean diameters of the most developed group, instead of the 95th centile of the total ova diameter frequency distribution, but he felt the difference should not affect greatly the comparison of his results with those of Schaefer and Orange (1956). His gonad index ranged to a high of 96 (Fig. 2), compared to Schaefer and Orange's 36. Batts (1972^c) obtained an even higher index of 99.33 from a ripe fish in North Carolina waters and suggested that the skipjack tuna may attain gonad index values of 100 or more. Raju's (1964^c) data show that the regression of ova diameter on gonad index holds well through G.I. values of 50 or more (Fig. 3). To what extent the breakdown of the regression above, say, 50 affects the validity of the G.I. has not been determined. However, the fact that gonads with index values of 50 or more generally contain ova, at least, in the late maturing stages, support the use of the G.I. for determining sexual maturity.

Fig. 2

Fig. 3

2. Spawning Areas and Season

The determination of spawning area and season has been approached by two methods; i.e., the examination of gonads and the collection of newly hatched larvae. While both methods are deficient in certain aspects, used together, they complement each other well, so that a fairly accurate estimate of spawning can be made. Gonad studies generally have been made in areas subjected to commercial fishing, whereas larval studies have been made in areas both within and outside of the fishery.

Pacific Ocean.--Wade (1950) observed that fish with ripe ovaries were taken in Philippine waters throughout the year but mostly from April through July, and that fish with spent ovaries were taken from March through July. He thus concluded that skipjack spawning occurs in late spring and summer months. Off Japan Kishinouye (1923) reported that the skipjack spawns from May through August. Yabe (1954) found fish with high relative gonad weight ($>5\%$) from May through June and fish with spent ovaries in July and August in the waters south of Japan. Yao (1955) in the same area, did not find ripe ovaries but noted large numbers of fish with enlarged ovaries containing ova visible to the eye (probably late maturing stage) in May and June, with the largest ovaries in July. Further to the east, in the Marshall Islands area, Marr (1948) found fish considered to be ripe from April through August. Fish with spent ovaries were found in the latter half of August. In the central North Pacific, Brock (1954) noted

that fish with large ova first appeared in Hawaiian waters in late February, March, or April and were found continuously until September. He further noted that only few, if any, fish with spent ovaries were taken during the summer but spent fish were taken in increasing numbers in September. He thus concluded that in Hawaiian waters the spawning season extended from late February through September. Yoshida (1966) reported that in the Marquesas-Tuamotu Islands the major spawning season was from November through April (southern summer). In the eastern Pacific, Schaefer and Orange (1956) and Orange (1961) found fish with maturing ovaries near Revilla Gigedo Islands from April through November. They suggested that the main spawning season in the eastern Pacific was from July through November. In other areas further to the south, Cocos and Galapagos Islands, they found maturing fish from December through April. At least one skipjack with ripe eggs which could be extruded by external pressure was reported by Clemens (1956) from Cocos Island.

Captures of skipjack larvae in all the areas mentioned above have been reported by Wade (1951), Matsumoto (1958), Klawe (1963), Nakamura and Matsumoto (1967), Ueyanagi (1969) and Seckel (1972). In all areas, except the eastern Pacific, larvae have been reported in all the months in which ripe or spent ovaries had been recorded. Only occasional catches of skipjack larvae were reported from the eastern Pacific (Klawe 1963), which led Klawe to remark that very little spawning by skipjack occurs in

coastal and oceanic areas in the eastern Pacific. In addition to these, larval studies in other areas of the Pacific Ocean provide evidence (a) that the skipjack spawn in midoceanic areas in tropical and subtropical waters almost continuously across the Pacific, though at low levels in the eastern Pacific (see discussion on larvae), (b) that in the higher latitudes in the northern hemisphere (above lat 20°N in the western Pacific and above lat 15°N in the central Pacific) spawning occurs largely in the spring-summer period, whereas in the areas closer to the equator, spawning generally occurs throughout the year (Matsumoto 1958; Strasburg 1960; Ueyanagi 1969). A similar condition prevails in the southern hemisphere (Matsumoto 1958; Nakamura and Matsumoto 1967; Ueyanagi 1969).

Atlantic Ocean.--The spawning season of skipjack tuna has been reported from gonad studies as May to September near Cap Vert (Frade and Postel 1955~~7~~; Zhudova 1969), and from December through April and in September in the eastern tropical Atlantic (Simmons 1969). In the western Atlantic, gonad studies show spawning in Cuban waters to occur all year long with a peak from April to July (Rivero and Fernandez 1954; Gorbunova and Salabarría 1967); February through April, June, August, October and November in tropical waters (Simmons 1969); and June through August in waters off North Carolina (Batts 1972^c_n).

Larvae have been taken in the eastern tropical Atlantic from February through April and August through October (Richards 1969)

and in the period November through April (Ueyanagi 1971: no specific month of capture given). In the western Atlantic, larvae have been taken in April, May, July, August and October in the Florida Current (Klawe 1960); in May, August and September (Gorbunova and Salabarría 1967) and throughout the year (Rivero and Fernandez 1954) in Cuban waters; from February through April and August through October (Richards 1969) and in the period November through April (Ueyanagi 1971: no specific month of capture given) in the western tropical Atlantic.

From both gonadal studies and larval captures it appears that the skipjack spawn throughout the year in the tropical Atlantic waters between lat 10°N and 10°S and in Cuban waters, in the spring and summer in areas north of lat 10°N in the eastern Atlantic, and in the summer in areas north of Florida in the western Atlantic.

Indian Ocean.--There is only limited information on gonad observations from the Indian Ocean. Williams (1964) has reported the capture of one ripe (~~immature~~) family skipjack in March and one with spent ovaries in July from waters off the east coast of Africa between lat 1°30'S and 10°30'S. Larval captures in the western Indian Ocean and off the east coast of Africa have been reported for December and January (Jones and Kumaran 1963).

In waters closer to India, around Minicoy Island, Raju (1964^c) reported that females with mature ovaries occurred from November through July, with high percentages of mature ovaries

occurring from February through July. He further noted that spent ovaries occurred in fair numbers in June and were more frequent in July and August and concluded that the spawning period around Minicoy Island was between February and July. Larval captures from the Laccadive Islands, which include Minicoy Island, extend the spawning period given by Raju (1964^c). Jones (1959) reported the capture of larvae from December to April.

Evidence of spawning in other areas of the Indian Ocean come entirely from larval captures. Skipjack larvae have been taken in the Bay of Bengal in January and February, in the central Indian Ocean, predominantly in the southern latitudes, in the period November to March, and in the eastern Indian Ocean west and south of Sumatra in September and October (Gorbunova 1963, 1965a, 1965b).

It is evident from these studies that spawning occurs in the Indian Ocean much as it does in both the Atlantic and Pacific Oceans--in the spring and summer in areas removed from the equator, roughly above lat 10° to the north and south of the equator, whereas it occurs throughout the year in the vicinity of the equator between lat 10°N and 10°S.

3. Size of Females at First Spawning

The minimum size of skipjack tuna at first spawning has not been defined, but a reasonable estimate can be made from the various published reports of fish with mature, ripe and spent ovaries, and of fish with ova diameters approaching 1.0 mm.

Pacific Ocean. Marr (1948), examining skipjack tuna from the Marshall Islands, recorded females as small as 400 mm fork length with spent ovaries (all fish lengths given are in fork length, unless specified otherwise). He also recorded a 439 mm fish with ripe ovaries and a 442 mm fish with spent ovaries. Wade (1950) listed two fish in the 400 to 409 mm size class with ripe and spent ovaries from Philippine waters, and reported the capture of a female in the 340-349 mm size class possessing ripe ovaries. Brock (1954) reported the capture of a 432 mm female skipjack in the Hawaiian Islands that possessed fully ripe ovaries with ova diameters averaging 1.125 mm. He further noted that the smallest fish that possessed maturing ova during the spawning season were around 400 to 450 mm. More recently, Yoshida (1966) reported that a great number of females in the 437 to 507 mm size group taken in the Marquesas-Tuamotu Islands possessed developing and advanced ovaries (=late maturing and mature). He also reported the capture of a skipjack with ripe ovaries containing ova with diameters ranging from 0.85 to 1.12 mm. Although its length was not recorded, he observed that this fish had come from a school containing fish 456 to 569 mm long.

Indian Ocean.--Raju (196^{4c}~~6~~) estimated the size of sexual maturity as about 400 to 450 mm from skipjack taken in waters around Minicoy Island. He derived his estimate from his observations that (a) the smallest skipjack that possessed ovaries with maturing ova during the spawning season was around 400 to 450 mm

and (b) remnants of mature ova were present in fish above 400 mm but none in fish below this size. He further felt that the sharp rise in the percentage of females with mature ovaries from 0 percent in the 376 to 400 mm size class to 30 percent in the 401 to 425 mm size class was an additional basis for his estimate.

Atlantic Ocean.--Simmons (1969) reported that the minimum size of females at maturity in the eastern tropical Atlantic was 435 mm, as determined from fish with developing ovaries (=late maturing), and that the minimum size in the western tropical Atlantic was 410 mm, as determined from fish with spawned or spent ovaries. Batts (1972^c) reported the minimum length of female skipjack attaining sexual maturity in waters off North Carolina as 454 mm. The minimum size of skipjack given by both authors fall within the size range estimated for both the Pacific and Indian Oceans.

From the above, it appears that the minimum size of female skipjack at maturity is 400 mm and that initial spawning can occur in fish between 400 and 450 mm or larger. The unusually small female (340-349 mm size class) with ripe ovaries reported by Wade (1950) could be a rarity or a case of erroneous staging of the gonads.

4. Frequency of Spawning

That the skipjack tuna spawns more than once during the season has been discussed by several authors. Brock (1954) was of the opinion that the multimodal distribution of ova diameter

during the spawning season and the absence at other times indicated that individual skipjack taken in Hawaiian waters spawns several times. As supporting evidence he cited the absence of an overall trend in ova diameters during the spawning season (Fig. 4) and the absence of spawned-out fish until after the end of the spawning season. Bunag (1956) determined multiple spawning by following the movement of ova diameter modes through the various stages of development as indicated by ova diameter frequency polygons

Fig. 4

Fig. 5

(Fig. 5). Raju (1964^c) determined multiple spawning of skipjack from the Indian Ocean by satisfying the four lines of evidence used by Clark (1934): (a) the presence of multiple modes in his diameter frequency polygons, (b) obtaining a high correlation in the progression of successive modes, (c) the presence of ova remnants in maturing ovaries, and (d) the decrease in the numerical ratio of ova between maturing and mature group.

From the results of these studies there seems to be little doubt that the skipjack spawns more than once during the season. How many times it spawns is not yet known, but from the reports by Brock (1954) and Bunag (1956), the number of spawnings can be estimated, at least for fish in Hawaiian waters.

Taking Brock's (1954) 1949 and 1951 data in Figure 4, we note that in Hawaiian waters, fish with immature ova (ova diameter 0.1 mm) occur in February, and in two months the ova develop into the mature state (ova diameter 0.7 mm). If development continues at this same rate, the ova should be in the ripe stage

(ova diameter 1.0 mm) in late April or early May. The commencement of the spawning season in Hawaiian waters indicated by the captures of larval skipjack has been shown to vary from late April in certain years to early May in others (Seckel 1972). Bunag (1956), as well as others, have observed that after the first batch of ripe ova has been spawned, the ovaries revert to the condition similar to that of ovaries in maturity stage III (Fig. 5), i.e., ova in the most advanced group are not much larger than about 0.5 mm. Again, from Figure 4, ova of this size would require at least six or seven weeks to reach the ripe stage, exclusive of a probable resting period after the initial spawning. The earliest that a skipjack can spawn a second time after having spawned once in early May would be in late July or early August. Since the spawning season in Hawaiian waters terminates in September (Brock 1954), it would be unlikely for this fish to spawn a third time in the area. This does not imply that a third or even a fourth spawning could not occur. For fish with ovaries developing more than two groups of ova (see Fig. 4, Brock 1954), migration of the fish to warmer waters in the fall could allow it to spawn a third or fourth time.

An added piece of information may be gleaned from the above discussion. If the first spawning occurs as described, then the duration of ova development from the immature to the ripe or spawning stage can be estimated as being from 3 to 3-1/2 months.

5. Fecundity

Relatively little has been published concerning the

Table 4

fecundity of the skipjack (Table 4). In all of these studies fecundity estimates have been based on the number of ova in the most advanced mode. As is obvious from Table 4, the fecundity estimates vary considerably between fish in similar size ranges. Yabe (1954) inferred that the number of ova increased with increasing fish size on the basis of five fish. Others with larger samples of fish (Joseph 1963; Raju 1964b; Simmons 1969; Batts 1972^C) demonstrated that fecundity was indeed related to fish size. Although regressions of fecundity on fish length were calculated by the latter authors, the narrowness of the length ranges had restricted them to fit straight rather than the expected curvilinear lines. The regression lines are shown graphically in Figure 6.

Fig. 6

On the basis of better data in terms of both

number of observations and coverage over the size range below 650 mm (only two observations were above this, near 700 mm) Raju's (1964b) regression line (Fig. 7) could be close to representing the true fecundity-length relationship of fish in the smaller size range. The calculated fecundity estimate of fish at minimum spawning size (400 mm), using Raju's regression is 80,000 ova. Raju, as well as Simmons (1969), obtained a slightly better fit by using fecundity-(length)³ relationship. The fecundity estimate calculated from this relationship for fish 400 mm long is 110,000 ova. Both figures are reasonably close to the 100,000 ova estimated

Fig. 7

by Yoshida (1966) from a 430 mm fish. Reasonable fecundity estimated for fish well above 700 mm cannot be made from the regressions given in Table 4. It can be noted, however, that the 2,000,000 ova estimated by Yoshida (1966) could be near the maximum for the skipjack.

The estimates of fecundity given above are only for ova in the most advanced mode. To obtain estimates of total ova spawned during the entire season, ova from more than one modal group must be included. No one has yet examined whether there is a diminishing of fecundity with successive spawnings within the same season for the skipjack. Joseph (1963) has done this for the yellowfin tuna in the eastern Pacific and has stated that there may be some decrease in fecundity at successive spawnings, but that such decreases are difficult to detect in the presence of high variability due to other factors. For this reason and also because of the lack of understanding fully the true relationship between fecundity and fish size, any attempt to estimate total ova spawned during the season is futile.

B. LIFE HISTORY

1. Eggs

Ripe ovarian eggs are spherical, smooth, and transparent, and usually contain a single yellow oil droplet (Brock 1954; Yabe 1954; Yoshida 1966). The eggs are 0.80 to 1.17 mm in diameter, with mean diameters ranging from 0.96 to 1.125 mm. The oil droplet varies greatly in size; Yabe (1954) reported a range of 0.22 to 0.27 mm, Brock (1954) gave a range of 0.22 to 0.45 mm, and Yoshida (1966) reported an average of 0.14 mm. That eggs of this size range are gully ripe and capable of being fertilized has been shown by Ueyanagi et al. (1973 and 1974). The former reported egg diameters of 0.88 to 1.22 mm, with oil droplets measuring 0.20 to 0.24 mm in diameter, whereas the latter gave egg diameter measurements ranging from 0.93 to 1.09 mm and that of oil droplets ranging from 0.21 to 0.25 mm.

Eggs of other species of scombrids that have been successfully fertilized artificially and reared through the hatching stage (Harada et al. 1971; 1973a, 1973b; Ueyanagi et al. 1973) also are comparable in size and appearance as those of skipjack. Egg diameter ranges given by these authors as 0.85 to 0.98 mm for frigate mackerel, Auxis thazard, 0.80 to 1.0 mm for A. rochei (A. tapeinosoma of Harada et al. 1973b), and 0.90 to 1.04 mm for yellowfin tuna. Consequently, tuna eggs collected at sea by plankton net tows are extremely difficult to identify to species.

The spawned eggs of skipjack are thought to be buoyant in nature since the largest catches of eggs recognizable as those of tunas are invariably caught in plankton net tows made at the surface (personal observation), and since artificially fertilized eggs of A. thazard, A. rochei and yellowfin tuna were found to be so (Harada et al. 1971; 1973a, 1973b). Kikawa (1953), during experiments in rearing artificially fertilized yellowfin tuna eggs, observed that most of the eggs, presumably dead, turned opaque and sank to the bottom, but those still viable were transparent and buoyant. The opaque eggs were found to be in arrested stages of cleavage, whereas the viable eggs contained developing embryos.

2. Incubational Period

The incubational period for skipjack tuna has been determined by observing artificially fertilized eggs through the hatching stage (Ueyanagi et al. 1973; 1974). Ueyanagi et al. (1973) reported that hatching occurred in 26 to 31 hours after fertilization in 23° to 25°C water, in 21 to 32 hours in 24.2° to 27.0°C water, and in 21 to 22 hours in 26.0° to 29.0°C water in three batches of eggs held in tanks of different sizes. Ueyanagi et al. (1974) also reported that hatching occurred in 22 to 27 hours in 27.0°C water in a fourth batch of eggs reared primarily to observe the development of the embryonic and larval stages. Although the data do not show conclusively that incubational period is related inversely to water temperature, they at least suggest it.

3. Development of Larvae and Juveniles

The newly hatched larva is about 2.6 mm in total length (Ueyanagi et al. 1974), comparable to the size estimated by Matsumoto (1958). According to Ueyanagi et al. (1974), the larvae absorbed their yolk sac within two days after hatching, but due to unsuccessful initial feeding, they were dead within five days.

Fig. 8

The development of the larvae is shown in Fig. 8.

Ueyanagi et al. (1974) described the earliest stages of the larvae thus: "Yellow pigment spots on the finfold were conspicuous in the prelarval stage. Small melanophores appeared on the dorsal edge of the trunk in the early prelarval stage and moved toward the ventral edge [where they] tended to converge toward the caudal peduncle." The conversion of these melanophores at the caudal peduncle suggest the eventual formation of a single, distinct

Fig. 9

black spot (Fig. 9), one of the principal characters used in the past to identify the skipjack larvae. Other characters describing the larvae have been reported in Wade (1951), Yabe (1955), Ishiyama and Okada (1957) and Matsumoto (1958). These include a disproportionately large head bent slightly downward in relation to body axis; appearance of 2 or 3 melanophores over the forebrain area when the larvae are about 7 mm long and increasing to about 12 in larvae about 14.5 mm in length; heavy pigmentation over the midbrain area throughout all sizes; and the appearance of the first dorsal fin spines at about 7 mm in body length and increasing

to about 13 spines at a body length of 11 mm; and pigmentation on the first dorsal fin limited to scattered melanophores near the outer edge of the fin (Fig. 9). The full complement of 16 spines and 15 rays in the first and second dorsal fins, respectively, and 15 rays in the anal fin are developed by the time the larvae are about 12 mm in length. At this stage the young are considered as juveniles.

The juvenile stage is characterized by the development of the body in assuming a more fusiform shape and by a general increase in pigmentation over all parts of the body. Juveniles up to 47 mm (Fig. 10) are easily identified by the concave outline of the first dorsal fin and its characteristic pigmentation, the moderately long snout, and the number of vertebrae (20 precaudal and 21 caudal). The first dorsal fin has scattered melanophores on the first 3 or 4 interspinal membranes and along the distal edge of the remaining membranes. The only other genus in which the juveniles are known to have similar-shaped first dorsal fin is Euthynnus (Schaefer and Marr 1948; Wade 1950; Mead 1951). In Euthynnus, however, the first dorsal fin is either completely or almost completely pigmented. Also, unlike Euthynnus, juveniles of skipjack do not develop dark vertical bands over the dorsal half of the body.

Juveniles below the size of first spawning (<400 mm) have not been described and there is no information in the literature describing the initial appearance of the longitudinal black stripes along the side of the body below the lateral line.

Fig. 10

4. Adults

The adult description has been given in detail by Jones and Silas (1963). The body is robust and rounded in cross-section; about 40 teeth are present on each jaw, but none on the vomer and palatine; the corselet is well defined with hardly any scales on rest of body; the interspace between the first and second dorsal fins hardly exceeds the eye diameter; the margin of the first dorsal fin is strongly concave; and the lateral line has a decided downward curve below the second dorsal fin.

Color in life is steel blue, tinged with lustrous violet along the dorsal part and decreasing in intensity on the sides to the level of the pectoral fin base; half of the body, including the abdomen is whitish to pale yellow; evanescent vertical light bars are seen on the sides of the body immediately after capture; conspicuous four to six longitudinal dusky to black stripes are present below the lateral line on each side of the body; and light greyish tinge on the underside of the mandible merges posteriorly with whitish color of lower half of the body.

The meristic counts for specimens from all oceans are given in Table 5. There seems to be no difference in the counts of fish from the Pacific and Indian Oceans and in at least two characters, first dorsal spines and gill-rakers, of fish from all oceans.

Table 5

C. GROWTH AND AGE

1. Estimate of Growth

The literature contains a number of studies of skipjack tuna growth, nearly all of which concerning skipjack in the Pacific Ocean. Various methods have been used to determine the growth of skipjack tuna, including analyses of annual marks on hard parts such as vertebrae (Aikawa 1937; Aikawa and Kato 1938; Yokota et al. 1961; Chi and Yang 1973) and first spine of first dorsal fin (Shabotiniets 1968; Batts 1972^b), the temporal progression of modal sizes (Brock 1954; Kawasaki 1955a, 1955b, 1963, 1965^a; Schaefer 1961^b; Yokota et al. 1961; Joseph and Calkins 1969; Yoshida 1971; Chi and Yang 1973), and data from tagged fish (Schaefer et al 1961; Rothschild 1967; Joseph and Calkins 1969). The results are confusing because of a wide variety of estimates of growth rates, asymptotic lengths and lengths at age. Reviews of some of these studies prior to 1967 were given by Shomura (1966) and Rothschild (1967) and a more recent one of studies prior to 1969 was given by Joseph and Calkins (1969). Chi and Yang (1973) also compared the results of their study with those of studies made prior to 1969.

A summary of the results of growth studies made of skipjack tuna is presented in Table 6 and the growth curves from these studies are shown in Figures 11-13. It is obvious from both the table and Figure 11 that the growth determined from vertebral rings is generally underestimated. The estimate by Aikawa and Kato (1938) indicate a considerably smaller size at age and a much higher attainable age

Table 6
Figs. 11-
13

than any of the growth estimates made for fish of the eastern and central Pacific. As Rothschild (1967) suggested, there is a possibility that Aikawa and Kato's estimates are in error since no serious attempt was made to validate the rings as annual marks. Subsequently, Chi and Yang (1973) observed that two rings were formed during the year, one in summer and the other in winter, in skipjack tuna taken from waters around Taiwan. If Aikawa and Kato's estimates are corrected on the basis of rings being formed semiannually, their estimates coincide with that of Chi and Yang.

The figures also show that growth estimates based on modal progression are slightly higher than estimates based on vertebral rings or tag returns. The question arises as to whether growth estimates based on modal progression are overestimated or growth estimates based on tagged fish are underestimated. Rothschild (1967) suggested that Brock's (1954) estimate of growth based on modal progression of length frequencies of skipjack tuna from Hawaiian waters may be too high and that there was a possibility that Brock's modal length of age 2 fish was overestimated. According to Rothschild, this could result if Brock's "2-year-old" group is based on an overlapping "poly-age" distribution, or if the "2-year-old" fish are not fully recruited into the Hawaiian fishery.

More recently a study of growth of skipjack tuna in Hawaiian waters based on otoliths was made by Uchiyama and Struhsaker (MS).^{6,7} In a study prior to this (Struhsaker and Uchiyama, *in press*)⁵ they found direct evidence that growth increments in the engraulid Stolephorus purpureus, a common tuna baitfish in Hawaii, represented daily growths. Similar structures in the otoliths of 50 skipjack tuna from 3.6 to 80.5 cm FL in the central Pacific yielded a growth curve as shown in Figure 12. The growth estimate is nearly similar to Brock's, although slightly higher after the first year.

The similarity in the two curves and the fact that the estimated growth from otoliths is derived from individual fish rather than from large numbers to determine modal groups negates Rothschild's (1967) suspicion that the modal length method used by Brock (1954) overestimated the length of "2-year -old" fish in the Hawaiian fishery as a result of partial recruitment of fish of this age and on the overlapping of "poly-age" distribution.

On the other hand, Rothschild suggested that estimates from tagging may underestimate the actual growth and gave two reasons for believing so; first, that tagging may have reduced the growth of the tagged fish and second that size-specific movements may have caused an undersampling of the faster-growing fish, which might not remain in the fishery as long as the slower growing ones. Joseph and Calkins (1969), in their study of the growth of skipjack tuna from the eastern Pacific, also suggested that estimates of growth from tagged fish may be minimal since it has been shown for some

species of fish that tagged individuals exhibit reduced growth rates compared to untagged fish from the same population (Sette 1950; Broadhead 1956).

Fig. 14

Figure 14 shows three growth curves obtained from modal progression of fish in the eastern, central, and western North Pacific and the curve obtained from otoliths of fish from the central Pacific. If the growth estimates obtained from the modal progression method are valid, there is reason to believe that the growth rates of skipjack tuna may not be uniform in all parts of the Pacific Ocean. In the North Pacific, at least, the growth rates appear to be similar in the eastern and western parts, but slightly higher in the central part. The existence of differences in growth by areas has been observed by Kearney⁷⁴ of fish in the Papua New Guinea region. He observed a growth of approximately 7 cm per year among tagged fish between 52 and 61 cm, only slightly more than half the growth of fish of similar sizes in the eastern Pacific estimated by Joseph and Calkins (1969: Table 6).

Studies of skipjack age and growth in the Indian and Atlantic Oceans have been minimal. Shabotiniets (1968) determined the size at age of skipjack tuna in the Indian Ocean from growth marks in the first spine of the first dorsal fin (Table 6); however, he did not validate these marks as annuli. The size at age he obtained thus appears questionable. Batts (1972)^b also made a study of the growth and age of skipjack tuna from growth marks in the first dorsal spine of fish from the western Atlantic Ocean. He, too, failed to show

that the growth marks were annuli. His sizes at ages 1 through 4 essentially represent a straight line and differ greatly from those obtained in modal progression or tag return studies by others (Table 6).

2. Length-Weight Relation

The length-weight relationship of skipjack tuna has been studied by various investigators. In all of the published reports the original calculations have been based on the usual relationship:

$$W = aL^b \text{ or } \log_{10} W = \log_{10} a + b \log_{10} L,$$

where W is the weight in gram, kilogram, or pound, L is fork length in centimeter or millimeter, and a and b are constants. A summary of these studies is presented in Table 7 and a typical curve describing the relationship is given in Figure 15, the latter based on data from the largest sample size and widest size range (Nakamura and Uchiyama 1966). There are several discrepancies between Table 7 and a similar table by Nakamura and Uchiyama (1966). The latter's $\log a$ value for Hennemuth (1959) is incorrect and they selected the erroneous a values from Ronquillo's (1963) figures 26 and 27, thus resulting in erroneous $\log a$ values and length unit. The correct $\log a$ values are given in Ronquillo's regression equation in his figure 25 with the length unit in centimeters. The calculated weights of fish of a common size, based on the regression statistics of the various authors, show close agreement (column 9, Table 7), except for that obtained from Uda's (1941) length-weight relationship.

Table 7

3. Maximum Size and Longevity

The L_{∞} estimate theoretically gives the maximum size attainable, but the estimate can vary depending on the available data as witnessed in Table 6. To determine a reasonable estimate of maximum size, therefore, one has to look at the largest skipjack tuna taken. Miyake (1963), in his table 8 showing the length-frequency distribution of skipjack tuna taken on the tuna longline gear on Japanese research cruises to the equatorial Pacific, lists one fish in the 106.5- to 108.4-cm size class. Though he made no special reference to this fish, it could well be the largest recorded to date. A fish of this size class, using the length-weight relation developed by the Honolulu Laboratory (Nakamura and Uchiyama 1966), would weigh between 32.5 and 34.5 kg (= 71.6 and 76.0 lb). On the basis of growth parameters giving L_{∞} nearest to this size class, i.e., growth parameters from modal progression by Joseph and Calkins 1969 (Table 6), such a fish would be at least 12 years old.

D. NUTRITION

1. Food of Skipjack Tuna

The food of skipjack tuna have been described by various authors: Kishinouye (1923); Suyehiro (1938); Welsh (1949), Ronquillo (1953), Hotta and Ogawa (1955), Postel (1955), Tester and Nakamura (1957), Yuen (1959), Waldron and King (1963), Alverson (1963), Raju (1964^a), Thomas (1964), Nakamura (1965), Sund and Richards (1967), Dragovich (1971), Roberts (1972), and Batts (1972^a). In addition

there are other reports with brief mention of the composition of food of the skipjack tuna. The most comprehensive studies to date are those by Hotta and Ogawa (1955), Alverson (1963), Waldron and King (1963), [and Nakamura (1965) in the Pacific Ocean; Dragovich (1971) and Batts (1972)^u in the Atlantic Ocean; and Raju (1964)^u in the Indian Ocean.

Table 8

The major food items fall into three groups: fishes, crustaceans and molluscs (Table 8). Although fishes comprise the most important source of food for the skipjack tuna in most of the oceans, variations in the order of importance of the major groups of food organisms are found within and between the different oceans. In the western and central Pacific, the fishes ranked first in importance, followed in order by molluscs and crustaceans⁸; in the western South Pacific (New Zealand), crustaceans were the predominant food, with fish being of minor importance; and in the eastern Pacific, the crustaceans ranked first, followed in order by fishes and molluscs. With the exception of the western South Pacific, a similar situation exists in the Atlantic Ocean. In the western Atlantic, fishes ranked first, followed in order by molluscs and crustaceans, except at Oregon Inlet, where both fishes and molluscs were about equal; whereas, in the eastern Atlantic the crustaceans ranked first, followed in order by fishes and molluscs. In the central Indian Ocean the crustaceans ranked first, followed in order by molluscs and fishes, a situation opposite to that found in the western and central Pacific.

Table 9

The food of skipjack tuna includes a wide variety of organisms representing 11 invertebrate orders and 80 or more fish families, collectively (Table 9), in all the major oceans. Past studies show that of the invertebrates the decapods (crustaceans), stomatopods, octopods, and squids were found in stomachs from nearly all localities. The fish families represented in stomach contents vary considerably. Skipjack tuna taken in the Pacific Ocean, by far, had the greatest number. Hotta and Ogawa (1955) listed 48 families, Waldron and King (1963) listed 42 and both Ronquillo (1953) and Nakamura (1965) listed 33. On the Atlantic Ocean, Dragovich (1970) listed 28 fish families in the western and 21 in the eastern sectors. Raju (1964^u) listed only 10 fish families in the stomachs of skipjack tuna from the central Indian Ocean. The small number of fish families listed by Raju could be due to sampling skipjack tuna from inshore waters (4 to 6 miles). Of the fish families represented in the diet of the skipjack tuna, only two Carangidae and Balistidae, were common to all areas of all oceans. Others that were common to most of the areas were Exocoetidae, Syngnathidae, Holocentridae, Bramidae, Chaetodontidae, Gempylidae, Scombridae (including Thunnidae), Ostraciidae, and Tetrodontidae.

The wide variety of food organisms and the variations in the order of importance of the major food groups have led to the conclusion that the skipjack tuna do not exhibit food preference, but will feed upon whatever prey organisms are available to them. The incidences of cannibalism exhibited by the skipjack tuna bears this

out. In the central Pacific Ocean, Nakamura (1965) reported that of the stomachs containing food, 143 (31.2%) contained juvenile tuna, while 57 (12.4%) contained juvenile skipjack tuna. He also reported that juvenile skipjack tuna were found in 55 (7.8%) of the stomach samples examined by Waldron and King (1963).

2. Variation in Feeding With Fish Size

It is reasonable to expect that food requirements and the capacity to satisfy the requirements, such as larger mouth and stomach, increase as the size of fish increases. All studies of this relationship (Yuen 1959; Alverson 1963; Waldron and King 1963; Raju 1964; ^a~~N~~ Nakamura 1965) agree that the average volume of food in skipjack tuna stomachs increase with size of fish. Differences in diet have also been found among the various sizes of skipjack tuna. Generally, the smaller skipjack tuna rely mainly on crustaceans for food; the larger skipjack tuna on juvenile fishes. In the central Pacific (Hawaii), Yuen (1959) observed that the percent either by volume or occurrence of fish in skipjack tuna stomachs increased with an increase in size, whereas, the percentage of molluscs and crustaceans decreased. Similar observations were noted for skipjack tuna in the Marquesas Islands (Nakamura 1965), eastern Pacific (Alverson 1963), central Indian Ocean (Raju 1964^a), and western Atlantic Ocean, off Hatteras, North Carolina (Batts 1972). Two exceptions were noted. First, in the western Atlantic Ocean, Batts (1972) found that in waters around Oregon Inlet, approximately 60 km northeast of Hatteras, the frequency of fish in skipjack tuna stomachs decreased with size, whereas, the frequency of crustaceans and molluscs increased in

intermediate-sized skipjack tuna and then decreased in larger fish. Second, in the Pacific Ocean, Waldron and King (1963) reported that there was no difference in the percentage of occurrence and volume of the major food categories between small (<60 cm) and large (>60 cm) skipjack tuna. The only difference they found was that with an increase in fish size the feeding on crustaceans shifted from crab larvae to the more pelagic amphipods and euphausiids and on juvenile fishes from carangids and mullids to scombrids and nomeids, the latter two groups in both categories being more oceanic in occurrence than the former.

3. Variation in Feeding With Distance From Land

Thus far there are only two reports which provide information concerning the relation of stomach contents with distance from land. Nakamura (1965) has examined stomach contents of skipjack tuna taken from inshore (up to about 30 miles from shore) and offshore (up to 225 miles from shore) waters around the Marquesas Islands area. He found no relationship between stomach content volumes and distance from land. However, he did find that the percentages of food items considered as reef-originating forms (i.e., organisms that spend the adult life on reefs or nonpelagic areas, but whose larvae or juveniles are in pelagic waters) decreased significantly in the inner, middle, and outer 75-mile sectors of four 225-mile survey tracks. The percentages were 62, 40, and 9, respectively, in the three sectors.

Waldron and King (1963) examined stomachs from skipjack tuna taken in Hawaiian waters at distances set arbitrarily from 0-9, 10-24, 25-49, 50-99, 100-199, and 200+ miles. They found that the average volume of stomach contents increased in an offshore direction up to a distance of 50 miles and then varied irregularly at further distances offshore. Stomach samples from 100-199 miles had the lowest volumes. According to the authors, the declining trend was due largely to a decrease in the volume of fishes, which were the dominant element in the food. They also found that among the various fish families represented, Scombridae, Gempylidae, and Exocoetidae were important at the 100- to 199-mile distance; that Scombridae was dominant in the 25- to 49-mile distance, followed by Carangidae, Gempylidae, and Holocentridae; and that the important fish families in the diet of skipjack tuna taken closest to shore were Scombridae, Mullidae, and Carangidae.

4. Time of Feeding

Feeding by skipjack tuna follows a more or less regular pattern. From studies of stomach contents, Waldron and King (1963), Nakamura (1965), and Dragovich (1971) determined that the skipjack feeding peaks in the early morning from about 0800 to 1200, drops to a low between 1300 and 1600, and peaks again in late afternoon roughly from about 1600 to sunset (Figure 16). From the figure it is obvious that the peak and low periods may differ by 1 to 2 hours, depending upon the area sampled. Nakamura (1965) associates the diurnal feeding pattern with the availability of food.

Fig. 16

"Zooplankters moved downward during the early daylight hours, presumably to reach a preferred level of illumination. Since they serve as food for the forage organisms, some of the latter, also seeking lower levels of illumination, will tend to move downward and thus minimize their availability to the surface-dwelling skipjack. The minima occur around noon, the period when sunlight penetration is greatest, when zooplankters are deepest, and when forage fish are least available to skipjack. During late daylight hours the zooplankters and forage fish begin their upward movement. Skipjack begin feeding heavily in the late afternoon hours before dark as food becomes more available."

Nakamura also suggested that the diurnal variation in the volumes of stomach contents may also reflect the effects of satiation to food. He reasoned that "Skipjack, starting the day with their stomachs empty, feed actively during the early morning hours, and food consumption reaches a peak sometime before noon. A period of satiety occurs midday while digestive processes reduce the stomach contents. As the stomach empties, skipjack, forage again, and the volume reaches a second peak prior to darkness." That this may not be the case is suggested by the hourly catches of skipjack

Fig. 17 tuna in the Hawaiian fishery (Figure 17). The figure shows catches of skipjack tuna by time of day as observed on a number of Hawaiian bait boats during the 1956 and 1957 fishing season, May through September (data from Yuen 1959). If the fish were satiated near midday, then chumming with bait, which would involve more feeding, should not result in large catches, yet the figure shows that the highest average catches occurred at about that time. Hence, his prior observation that feeding pattern is associated with the availability of food is preferable to the latter.

Seasonal variation in stomach content volumes differ by localities. Although Waldron and King (1963) were not able to compare stomach contents over all the seasons in Hawaiian waters, they observed a noticeable decrease in the average volumes of food in stomachs collected during midsummer as compared to stomachs collected in late spring and early fall. The trend of the average volume followed that of forage fish very closely. Nakamura (1965) observed that though the occurrence of forage did not vary from season to season in skipjack tuna stomachs from the central equatorial Pacific, the proportions of the three major food categories did so. Crustaceans were low in fall and highest in summer, and molluscs were lowest in spring and highest in fall. In waters around Minicoy Island, Raju's (1964⁶) data show that total average volume showed a peak in early spring and a lesser peak in the fall. The trend followed closely that of crustaceans, which dominated the food category, the samples all having been taken close to shore.

5. Digestion and Food Consumption

The passage of food through the alimentary canal and the food consumed during a whole day by skipjack tuna held in captivity were studied by Magnuson (1969). The skipjack tuna ate the equivalent of about 8.6% of the body weight. About 10% of the original quantity eaten passed from the stomach each hour during the first 8 hours and the stomach was essentially empty within 12 hours. The content of the intestine reach a maximum after about 5 hours and the intestine was empty within 14 hours.

Food consumption experiments showed that although a period of intensive feeding occurred between 0630 and 0830, the skipjack tuna did not fill their stomachs to capacity the first or even the second or third time they were offered food, but filled their stomachs slowly over a 2-hour period. Although the maximum capacity of the stomach was about 7% of the body weight, the fish consumed an equivalent of 15% of their body weight. Skipjack tuna ate more food and digested it more rapidly than other fish for which data are published.

E. BEHAVIOR

1. Feeding Behavior

Only a few studies have been made of the feeding behavior of skipjack tuna both in the wild and in captivity. These, however, have provided a wealth of information. Nakamura (1962), from his study of skipjack tuna in captivity found (1) that when fed hourly until satiated, the skipjack tuna exhibited an initial high consumption followed by feeding of small amounts throughout the day;

(2) that all interest of food was lost at onset of darkness; (3) that the skipjack tuna had difficulty in seizing the food at night; (4) that new fish introduced into tanks learned to feed faster from fish already in the tanks; (5) that food particles were always taken at the surface or middepth, never off the bottom, and that the skipjack often accelerated their swimming prior to taking the food; (6) that after ingesting a few pieces of whole shrimp or squid, they refused such food; but when the rejected pieces were cut up into smaller pieces, they again accepted the foods; and (7) that the captive skipjack tuna were never seen to prey upon small fish such as the nehu, Stolephorus purpureus, the principal baitfish used by fishermen in Hawaii.

To determine feeding behavior in greater details, Magnuson (1969) also conducted several experiments with skipjack tuna in captivity. In one experiment, skipjack tuna were fed at 0700 after 24 hours of deprivation and then fed again at intervals to determine how much they would eat before their stomachs had completely emptied. He found that skipjack tuna began feeding before their stomachs had completely emptied and even ate more than had already passed through from the stomach. For example, 4 hours after a meal they ate 75% of the amount eaten at the earlier meal, whereas only 50% of the earlier meal had emptied from the stomach. In a second experiment, to determine diel changes in the quantity of food eaten, he found that when skipjack tuna were fed at 15-minute intervals throughout the day, a period of intense feeding occurred between 0630 and 0830 (Figure 18). During this period of intensive feeding the fish did not fill their

Fig. 18

stomachs to capacity the first or even the second or third time they were offered food, but filled their stomachs slowly over the whole 2-hour period. The maximum capacity of the stomach was about 7% of the body weight, but during the whole day the fish ate an equivalent of 15% of their body weight. Finally, the stomachs were estimated to be completely empty by dawn. In yet another experiment, skipjack tuna that had been deprived of food for 24 hours were fed at a uniform rate for 45 minutes from 0900 to 0945. The stomach contents approached a maximum after about 30 minutes (Figure 19-I). The proportion of food particles attached decreased as the stomachs filled (Figure 19-II), but very little change was noted until the contents exceeded 50% of the stomach's capacity, at which time the likelihood that a skipjack would attack a food particle decreased rapidly, indicating that satiation had occurred. The fish responded to food particles (i.e., food particles responded to but not attacked) even when the stomach was full (Figure 19-III).

Fig. 19

Another aspect of feeding behavior, though not exclusively confined to it, is the appearance of banded color patterns on the skipjack tuna. Strasburg and Marr (1961) reported on the appearance of such coloration on the skipjack tuna weighing from 1 to over 14 kg, but the bands or bars were not observed on all members of a school. As they explain it, the bands are formed when the dark horizontal stripes are interrupted by light vertical bars. The transitory barred or banded appearance are likely under various and are produced presumably by the contraction of melanophores. The vertical bars were

noticed from a subsurface viewing chamber particularly during the chumming of fish schools. Nakamura (1962) confirmed the relation of the appearance of the bars to feeding among skipjack tuna held in captivity. In his feeding experiments he noted that, in addition to excited swimming behavior during feeding, the skipjack tuna exhibited such bars or bands which disappeared when the fish were no longer interested in food.

Similar markings have been reported for Pacific bonito, Sarda chiliensis (Magnuson and Prescott 1966), little tunny, Euthynnus affinis (Nakamura and Magnuson 1965), and the dolphin, Coryphaena hippurus (Strasburg and Marr 1961).

2. Courting Behavior

Iversen, Nakamura, and Gooding (1970) observed that they believed to be courting behavior in Hawaiian waters from an underwater sled towed from the RV Charles H. Gilbert. They observed a pair of skipjack tuna from the sled and another pair from the deck of the vessel. The paired fish, approximately 50 cm long, remained close together while swimming back and forth in front of the sled. They noticed that twice while swimming side by side, the bodies would tilt about 30° from the vertical in opposite directions with the ventral portions of their bodies almost touching each other. At another time they saw what appeared to be tail-nosing by the following fish. The latter fish would be slightly below the lead fish and would approached it closely from the rear, its snout coming within a few

centimeters of the caudal fin of the lead fish. At the closest point of approach, the following fish would display dark vertical bars on its side, similar to that displayed during feeding. At about the same time, a second pair of skipjack tuna were observed from the deck of the vessel. On two occasions the lead fish was seen to wobble from side to side and the following fish would exhibit vertical bars along its flanks. These fish showed no interest in the baitfish thrown into the water, so that the appearance of the bars were not likely connected with feeding. This is supported by observations by commercial fishermen in Hawaii, who claim that fishing for skipjack tuna from schools such as this was futile, since the fish were spawning and would not take either chum or hook.

3. Visual Acuity

Nakamura (1968) studied the visual acuity of skipjack tuna and little tunny, Euthynnus affinis, in an experimental tank by training the fish to respond to targets displaying vertical and horizontal black and white stripes of varied widths. Visual acuity, i.e. the ability to see clearly the fine details of objects as the objects became smaller and closer together, was calculated by taking the quotient of one-half the width of the stripes and the distance between the eyes and target, which equaled the tangent of one-half of the visual angle, and converting it to minutes of arc. The reciprocal of twice the minutes of arc gave the visual acuity.

He found that at lower luminescences of the white stripes the visual acuities of two species were similar, but at higher luminescences, the skipjack tuna had a greater visual acuity. The maximum visual acuity obtained for skipjack tuna was about 0.180 and for little tunny about 0.135 at an illumination of 170 luxes (Figure 20). The luminescence of the stripes at the distance of the crossbar (eyes of the fish) was calculated by:

Fig. 20

$$B_d = B_o e^{-\alpha d}$$

where B_d = luminescence of the white stripes in feet-lamberts at the crossbar, B_o = luminescence of the white stripes in feet-lamberts at object, α = volume attenuation coefficient, and d = distance between crossbar and object in meters.

The role of visual acuity in the life of pelagic fishes may involve, in addition to the detection of prey and predators, the recognition of transient body marks, such as the vertical bars exhibited by the skipjack tuna during feeding (Nakamura 1962; Nakamura and Magnuson 1965; Strasburg and Marr 1961) or during courtship (Iversen, Nakamura, and Gooding 1970), as well as other permanent body markings. Nakamura (1968) calculated the distances of resolution of prey or body marks as 36 m, if the skipjack tuna were in waters having the same visibility conditions as that in the experimental tank. He also determined that the skipjack tuna could prey on objects as small as 0.9 mm, based on the minimum size of food particle that could be retained by the gill rakers, and that it would be able to resolve the prey of this size at a maximum distance of 54 cm. The

transient vertical bars on the flanks of skipjack tuna, being about 2 cm wide, would be resolved at a maximum distance of 12.4 m, whereas the permanent black longitudinal stripes on the belly, being 0.5 cm wide, would be resolved at maximum distances of 3.1 m again in waters having the same visibility conditions as that in the experimental tank. These conditions would be met in the ocean with an unobserved sun at an altitude of 65° so that the illumination at the surface of the sea was 107,000 luxes and with an alpha of 0.18 natural log/m.

4. Response to Stimuli

Tester (1959) summarized the experiments on the response of tuna to stimuli made by the Honolulu Laboratory in past years. The experiments were directed particularly at devising a substitute for skipjack tuna baitfish by testing the response of tuna in captivity to visual, auditory, chemical, and electrical stimuli and to edible and inedible lures. While the captive fish (yellowfin tuna and little tunny) learned to respond to various stimuli, tests at sea on skipjack tuna schools indicated that (1) the sense of smell plays little, if any, part in natural feeding, and (2) that vision played an important part in natural feeding and the mobility of a lure, whether living or dead, whether edible or nonedible, was an important stimulus to the skipjack tuna. The response to auditory and electrical stimuli were not adequately investigated.

In other studies, Strasburg and Yuen (19⁶⁰~~58~~) observed that blood sprayed in water or blood and slime allowed to drain from deck while fishing a school did not affect the behavior of the skipjack

tuna. Nor did throwing of a dead skipjack tuna, with arteries severed, in the midst of a school being fished. However, the skipjack tuna avoided any deeply stained mass of water produced by spraying dense concentrations of red food coloring.

In one experiment Strasburg and Yuen (1958) observed that noise produced by hammering on the ship's hull did not affect the behavior of the skipjack tuna being fished. Uno and Konagaya (1960) also attempted to determine auditory response of the skipjack tuna on the premise that if the fish responded to the sounds produced by another, it could utilize this for chasing prey or escaping from predators. However, they were unable to detect any sound when the skipjack tuna approached its prey.

5. Schooling

It is well known that the skipjack tuna have a strong tendency to form schools; yet, very little is known about the ~~mechanism~~ mechanism involved in schooling nor the reasons which compel this species to school. Sette (1950) suggests that schooling of predators may assist in the capture of prey, whereas Breder and Halpern (1946) discuss the possibility that schooling may confer some protection from predation. Brock and Riffenburgh (1960), in treating the predator-prey relationship quantitatively, also are of the opinion that schooling of fish is considered a mechanism for protection against predation. The study of the courting behavior of skipjack tuna (Iversen, Nakamura, and Gooding 1970) suggests yet another drive or need for schooling.

These studies, thus, point to at least three basic drives that could be responsible for causing fish, including the skipjack tuna, to school.

a. Types of schools

Over the years skipjack tuna schools of various kinds (in appearance) have been observed by pole-and-line and purse seine fishermen. The schools have been categorized in various ways by (a) the presence or absence of birds, (b) their association with drifting objects, sharks, mammals or other tuna species, and (c) their behavior at the surface, such as milling, breezing, jumping, or feeding, or (d) a mixture of a, b, and c. The following list includes the various types of schools likely to be encountered in the oceans:

- (1) Schools without birds
 - (a) Milling or swirling in slow circular paths
 - (b) Breezing or traveling
 - (c) Jumping
- (2) Schools with birds or bird flock
 - (a) to (c) As above
- (3) Schools with drifting objects
- (4) Schools with sharks
- (5) Schools with whales

Among these, the last three types may be accompanied occasionally by birds or bird flocks, and all types could be of either pure or mixed school, i.e., schools made up entirely of skipjack tuna or mixed with other tuna species.

Schooling behavior is relatively easy to observe at the surface, but such is not the case for skipjack tuna in waters beneath the surface. There is ample evidence that the skipjack tuna also school at depth. Schools of skipjack tuna have been recorded on the echo sounder at depths from 20 to 150 m (Kimura, Iwashita, and Hattori 1952). Strasburg, Jones, and Iversen (1968) reported seeing a school of 250 skipjack tuna at depths well over 100 m from a small submarine.

b. Associations

The association of birds with tuna schools is based on a common interest in the same concentration of prey. Birds were observed to follow tuna schools and to prey upon small fish chased to the surface by the schools (Godsil 1938; Royce and Otsu 1955). Since birds are more readily seen at a distance than fish schools, it is not surprising that the majority of skipjack tuna schools sighted are those accompanied by birds (Kimura 1954).

Skipjack tuna are frequently sighted at sea in the presence of other tunas (Orange, Schaefer, and Larmie 1957; Broadhead and Orange 1960; Waldron 1963), with logs (Uda and Tsukushi 1934; Imamura 1949; Yabe and Mori 1950; Kimura 1954; Kuroda 1955; Inoue et al. 1963, 1968; Hunter and Mitchell 1967); rafts (Kojima 1960; Gooding and Magnuson 1967); other flotsam, such as ship's material, airplane fuel tanks, carcass of dead whale, etc. (Inoue et al. 1963); sharks (Uda 1933; Imamura 1949; Kimura 1954; Kuroda 1955; Tominaga 1957); and whales (Uda 1933; Godsil 1938; Imamura 1949; Kimura 1954;

Kuroda 1955; Tominaga 1957). The occurrence of these associations vary markedly with geographical area and time of year (Uda 1933; Uda and Tsukushi 1934; Kimura 1954). Uda (1933) reported that in the western Pacific skipjack tuna schools associated with birds, whales or logs generally appear in greatest number in the main Kuroshio system in May and June, whereas schools associated with sharks appear for the most part in warm water pockets where the Kuroshio and Oyashio systems impinge upon each other in July and August.

The occurrence of mixed schools containing skipjack and other tuna species is relatively common. In the eastern Pacific where the mixed schools are composed of skipjack and yellowfin tunas, Orange, Schaefer, and Larmie (1957) and Broadhed and Orange (1960) report that 72% to 62% of the yearly catches of skipjack tuna by purse seiners and bait boats, respectively, are made from pure schools or conversely, 28% to 38% from mixed schools. Kawasaki (1959, 1965^a) reports that aside from mixed schools containing yellowfin tuna, fish species most frequently found with skipjack tuna are the little tunny; frigate mackerel, Auxis sp.; bluefin tuna; albacore; bigeye tuna; and dolphin, Coryphaena hippurus. Yabe and Mori (1950) reported other fish, wahoo, Acanthocybium solanderi; rainbow runner, Elegatis bipinnulatus; amberjack, Seriola intermedia; triggerfish, Canthidermis rotunadatus; and jack, Caranx equula, taken along with skipjack tuna associated with driftwood in waters off southern Japan, but it is doubtful whether these fish were truly mixed with the skipjack tuna schools. More likely, these fish may have been attracted mainly to the driftwood itself.

Associations of fish with floating objects have been studied by a number of workers. While protection from predators or availability of food were given as the reason for attraction by some (Hardenburg 1950; Kojima 1956; Soemarto 1960; Gooding and Magnuson 1967), food was considered unimportant by others (Yabe and Mori 1950; Senta 1966). The importance of shade was discounted by all. As for the skipjack, Gooding and Magnuson (1967) found them to be transients. Hunter and Mitchell (1967) found little evidence to support the mechanisms postulated by others, i.e., attraction to food, response to shade, shelter from predators, presence of spawning substrate, and parasitic-cleaning symbiosis. They suggested two mechanisms: (1) that the objects function as schooling companions and (2) for fishes not adapted to pelagic life, the objects function as substitutes for reef or substrate.

Uda (1933) stated that skipjack ~~tuna~~ congregate around whale sharks (Rhinodontidae) in fear of spearfish. Tominaga (1957) also reported that skipjack tuna associate with ~~basking~~ sharks (Cetorhinidae) for protection from spearfish. His observations of this relationship indicate that the shark is the likely leader and the skipjack tuna the followers, and that the attachment of the skipjack to the shark is quite strong. The skipjack tuna "swim in front, behind, to the sides, above and below the shark. When attacked by a spearfish, the skipjack close in toward any part of the shark's body. Upon chumming such a school, the skipjack will come toward the bait, but if the shark moves away from the ship, the skipjack will proceed after the shark immediately."

Association of skipjack tuna with whales is also for protection, but is not as close as that with sharks (Tominaga 1957). According to Tominaga, the association usually occurs with one or two whales, seldom with a herd. When attacked by spearfish the skipjack tuna merely comes in the vicinity of the whale. In this association, the skipjack tuna always precede the whales, and while fishing such schools, the skipjack tuna may suddenly abandon the whale.

c. Distribution of types of schools

The distribution of the various types of schools differ by area and time. In the western Pacific Uda (1933) reported that in the waters off northeastern Japan skipjack tuna schools associated with birds, whales or logs generally appeared in greatest number in the main Kuroshio system, while schools associated with sharks appeared for the most part in warm water masses (pickets) where the Kuroshio and Oyashio impinged upon each other. He also noted that schools associated with whales were seldom found in the southern portion of the Kuroshio. Kimura (1954) in a larger study obtained additional details: (1) Schools unaccompanied by birds were more often found at the boundaries of the Kuroshio and Oyashio, (2) schools associated with sharks also occurred south in warmer waters slightly south of the two current boundaries, and (3) schools associated with birds were seldom seen in offshore waters (~500 miles). He further determined the percent occurrence of the various types of schools observed over six seasons by 10-day intervals and plotted the average occurrence of the three most common types of schools in

Fig. 21

the area (Figure 21). Schools associated with birds were abundant in May and June but were relatively scarce during the peak of the season, July to September. Schools associated with sharks first appeared in early June, were predominant in July and disappeared in October. Schools unaccompanied by birds were abundant in August and September and predominant in October.

In areas to the south, west of the Boin Islands (lat. 19° - 24° N, long. 136° - 147° E), schools associated with whale sharks have been reported in October 1967 and schools associated with logs in February 1968.²⁴ Further south, in the area lat. 2° - 5° N, long. 134° - 150° E, schools associated with logs regularly occur with schools associated with birds from December through February, and in waters south of the equator around New Guinea and the Solomon Islands schools are generally associated with birds, with few instances of association with sharks and logs.^{4, 80}

A vastly different situation prevailed in the central Pacific, where almost all of the fish schools sighted are accompanied by birds. Murphy and Ikehara (1955) observed that about 85% of all fish schools sighted in waters around and between the Hawaiian, Line, and Phoenix Islands were accompanied by birds and Royce and Otsu (1955) reported that on two scouting cruises around the Hawaiian Islands during the spring of 1953 every one of 253 fish schools sighted was accompanied by birds and were found by means of birds. Undoubtedly this dependence on birds arises partly from their prevalence and partly also from the almost constantly choppy areas with white caps

in Hawaiian waters which make it extremely difficult to see the wake of a school or jumping fish at any appreciable distance from the vessel. Schools associated with sharks, whales or logs are not mentioned in either report. This is as expected since of those sharks normally associated with skipjack tuna, the basking shark is not found in these waters and to date there has been only a single report of the whale shark (Gosline and Brock, 196⁰~~6~~). Drifting logs also are encountered only sporadically (personal observation) in Hawaiian waters.

A report by Waldron (1964) summarized skipjack tuna schools and bird flocks observed in the greater central Pacific area bounded by lat. 30°N-20°S and lat. 110°W-180° during 128 cruises by vessels of the National Marine Fisheries Service, Honolulu Laboratory, between 1950 and 1961. The results shown in Figures 22 and 23 indicate that (1) high rates of sighting of both skipjack tuna schools and bird flocks were most prevalent in time-area units containing island groups, (2) there were distinct seasonal changes in sightings between island groups (Figure 24), and (3) the rate of sighting in the general Marquesas Islands area was much higher than for other areas of ~~simi~~ similar size.

d. Length distribution of schools

Brock (1954), in examining the length frequency of skipjack tuna taken from single schools in the Hawaiian fishery, ~~noted~~ a comparatively small range of lengths within a school which was in contrast to the range of lengths in the landings as a whole. The

Figs. 22,
'23

Fig. 24

mean range of lengths for single school samples was 11.3 cm, with 5 and 21 cm being the least and greatest, respectively, whereas the range for the seasonal landing was 47 cm. On the basis of this, he concluded that the skipjack tuna school was highly size-selective, and hypothesized that the segregation by size was likely due to the maximum speed attainable by fish of the same size.

Kawasaki (1964) compared the length frequency distributions of skipjack tuna taken from various types of schools in Japanese waters and noted that the variations in length within each school type increased in the following order: pure school (without birds), bird-associated school, whale-associated school, shark- or driftwood-associated school. Although Kawasaki's classification of pure- and bird-associated schools is confusing, a pattern is discernible here, viz, the less mobile the object of association, the greater the size range of fish associated with it. This is, thus, consistent with Brock's (1954) hypothesis, since schooling under slow moving objects does not require uniform swimming ability.

In the eastern Pacific, Schaefer (1948), from a limited amount of data collected off Central America during the first 4 months of 1947, suggested that the tendency of tunas to aggregate by size might, in some cases, be stronger than the tendency to aggregate by species. With the availability of considerably more data from 42 pure yellowfin tuna schools, 64 pure skipjack tuna schools and 57 mixed-species schools fished by bait boats, Broadhead and Orange (1960) examined the size relationships within and among schools.

They observed that the frequency distributions of the lengths of skipjack tuna from schools of pure and mixed schools were similar, but those of yellowfin tuna differed noticeably. Yellowfin tuna from pure schools appeared to be larger than those from mixed schools (Figure 25). A comparison of the variation in the sizes of tuna from pure schools with that of tuna from mixed schools indicated that the variances for samples from pure yellowfin tuna schools were considerably greater than the variances for samples of yellowfin tuna from schools also containing skipjack tuna, and conversely, the variances of samples from pure skipjack tuna schools were smaller than variances of skipjack tuna from schools also containing yellowfin tuna. The analysis of variance indicated that these differences for both species were significant, but upon examining the coefficients of variation for each species, the authors concluded that the difference in variances was not the result of difference in lengths of fish in the samples. The data thus clearly indicated that the yellowfin and skipjack tunas do school by species as well as by size. Schooling by size, however, is evidently modified by the species relationships, as yellowfin tuna from schools of mixed composition were (1) smaller and varied less in range than yellowfin tuna from pure schools, and (2) larger than skipjack tuna from such schools.

e. Size of school

Estimation of school size has been attempted in the eastern Pacific by Orange et al. (1957), based on the catch-per-set by purse seiners, and by Broadhead and Orange (1960), based on the

catch-per-school by bait boats. Of the two methods, school size can be better estimated from catches made by purse seiners, since a greater percentage of fish can be taken from a school by seining than by bait fishing. It is known, however, that whole schools are not always caught by the purse seine (Orange et al. 1957), so that the size of schools are largely underestimated.

Fig. 26

The frequency distribution of catch-per-successful set plotted by Orange et al. (1957) is shown in Figure 26. The distributions (of pure skipjack tuna schools) are skewed very strongly toward ~~small~~ small catches, with more than 50% of the sets falling in the two smallest size classes, i.e., 0.25 to 4.9, and 5 to 10 tons. The average catch~~per~~per-set of pure skipjack tuna schools for the 4 years is 13.5 tons, with a range of 1 to 130 tons (from their Table 2). Along the northeastern coast of Japan the average catches per successful set of one-boat and two-boat purse seines are 6.3 tons and 8.6 tons, respectively (Inoue 1959). Either the schools in the eastern Pacific are larger than those in waters off Japan, or the fishing environment and technique are more conducive to greater catches from similar-sized schools in the eastern Pacific. There is ~~also~~ the possibility that seiners in the eastern Pacific pass up setting on small schools much more than seiners off Japan. On the basis of Figure 25 one can say that the occurrence of skipjack tuna in small schools (<20 tons) is the rule and that large schools over 50 tons occur only rarely.

Fig. 27

Broadhead and Orange (1960) plotted the frequency distribution of the catch-per-school from pole-and-line fishing for the period 1956-58 (Figure 27). The frequency distribution is skewed strongly toward the small catches, as in the case for purse seiners. The majority of the catches (about 65%) from pure schools again fell into the first two smallest size category, 0.5 and 1.5 tons, and the mean catch for all schools was 2.8 tons. The difference in the mean catches by bait boats of 2.8 tons as compared with that of purse seiners of 13.5 tons likely reflect the inefficiency of pole-and-line fishing and the likelihood that the purse seines may avoid setting the net on small schools.

Broadhead and Orange (1960) also plotted the distribution of catches from skipjack tuna schools fished by Hawaiian bait boats using data from Yuen (1959). They obtained a similar "J" shaped curve but the points fell well below those obtained for the eastern Pacific area. The mean catch-per-school was about 1 ton (1.1 ton from table 10, Uchida and Sumida 1971) compared with 2.8 tons from schools fished in the eastern Pacific. On the basis of this comparison, they felt that skipjack tuna schools fished in the eastern Pacific area are, on the average, larger than those fished in Hawaiian waters, assuming that the bait boats captured the same percentage of each school fished in the two regions. The assumption is incorrect, however, since the catch in bait fishing depends greatly, among other things, on the number of men fishing (Yuen 1959; Uchida and Sumida 1971). This is already seen in a comparison of the number of men

fishing and the resulting catches. In the Hawaiian fishery an average of 6.8 men fishing yield an average of 1.1 tons per school fished (Uchida and Sumida 1971). In the eastern Pacific an average of 13 men fishing (estimated from Godsil 193⁸) yield an average of 2.8 tons per school fished. In the western Pacific off northeastern Japan an average of 19 men fishing (estimated from [Japan.] Ministry of Agriculture, Statistics and Survey Division 1971) yield an average of 5.8 tons per school (Inoue 1959). A plot of these sets of data suggests that catch-per-school increases roughly proportionately to number of men fishing. The differences in the average catch-per-school in the three areas thus may not necessarily indicate differences in school size.

f. Schooling at night

Some evidence that the skipjack tuna school at night are available in the literature. Nakamura (1962) observed that skipjack tuna in captivity swam slowly about the perimeter of the pool, often with their bodies normal to the light rays from the floodlight. Fish were observed once at night without the floodlight. On this occasion moonlight was sufficient to allow the fish to be seen. They remained in a school and swam slowly around the pool. Other evidence come from Yuen (1970). While tracking skipjack tuna tagged with ultrasonic tag, he observed that a school of skipjack tuna was often visible at the position of the tagged fish. On several occasions,

both day and night, switching the sonar to the active mode disclosed many fish targets in the vicinity of the tag.

g. Locomotion

Swimming behavior of skipjack tuna in captivity has been described by Nakamura (1962) and Magnuson (1973). Nakamura observed that skipjack tuna usually swam leisurely around the pool's edge with the pectoral fin slightly extended, the first dorsal and pelvic fins retracted and the caudal fin vibrating. The second dorsal and anal fins were directed posteriorly at about a 30° to 45° angle. To change swimming direction, the first dorsal fin and pectoral fins were extended and all fins were extended to their fullest for sudden deceleration.

Magnuson (1973) in his study on features associated with swimming of scombroid and xiphoid fishes, observed that ~~the minimum~~ typical swimming speeds in a pool differed among sizes and between fish of similar sizes (Figure 28). The speed of three skipjack tuna (38, 39, and 48 cm) converted to meters per second, ranged from 0.43 m/sec (0.8 knot) to 1.03 m/sec (2.0 knots), with a mean of 0.72 m/sec (1.4 knots). Neill et al. (MS),⁹¹ working with skipjack tuna 0.4 to 3.5 kg, report that free-swimming skipjack tuna swam continuously at 1.5 to 3.0 body lengths per second, or approximately 0.82 m/sec (1.6 knots) to 1.65 m/sec (3.2 knots) for the largest fish (55 cm). Chasing the fish caused them to swim at speeds in excess of 10 body lengths per second, or 5.5 m/sec (10.7 knots) for the largest fish.

Fig. 28

An even faster swimming rate has been observed of skipjack tuna in the open ocean. Watanabe (1942) has clocked the speed of feeding schools alongside of the vessel at 6.4 to 7.7 m/sec (12.6 to 14.9 knots) and Strasburg and Yuen (19~~68~~⁶⁰) reported that medium sized fish made rapid dashes to the surface while being chummed at speeds of about 25 knots (12.9 m/sec).

h. Activity and movement of schools

That skipjack tuna school at depths in excess of 100 m was shown by Kimura, Iwashita, and Hattori (1952). From vessels equipped with echo sounders, fish schools were located between depths of 20 and 150 m. The vertical movements of these schools were traced on the recorders and identified as skipjack tuna schools by fishing them as they reached the surface. In some instances chumming with baitfish caused the schools to rise to the surface from depths as great as 100 m within 45 seconds at a speed of 2.2 m/sec (4.3 knots).

The tracking of skipjack tuna using ultrasonic tags (Yuen 1970) has disclosed that skipjack tuna that are associated with banks have the ability to navigate and have a sense of time. A 44-cm skipjack tuna, with a tag placed in its stomach and tracked for 8 days, made nightly journeys of 25-106 km away from the bank, and with one exception, returned to it each morning (Figure 29A, B, C). On the excepted morning it was 9 km from the bank. It remained there all day and returned to the bank the next morning (Figure 29D, E). Two observations, first, that skipjack tuna over 600 cm long have different food preferences from those less than 50 cm long

Fig. 29

(Yuen 1959) and second, that the swimming behavior of the tracked fish was typical of that of foraging fish, suggested that food preferred by the small skipjack tuna is found at the banks and that the small skipjack tuna frequent the banks for the purpose of feeding (Yuen 1970).

Underwater observations of skipjack tuna schools by Strasburg and Yuen (19~~58~~⁶⁰), Strasburg (1961) and Yuen (1970) provide further insight into the behavior of skipjack tuna schools. Strasburg and Yuen (19~~58~~⁶⁰) observed that the activity of schools varied with fish size. First, small skipjack tuna (~20 cm) schooled in large numbers (in the thousands). Such schools responded instantaneously to stimuli, individuals were closely spaced and maneuvered with precision. These schools were never entirely disrupted, even during feeding. Second, in medium-sized skipjack tuna (45-65 cm) the activity was frenzied and most semblances of schooling were lost during feeding. The fish made rapid dashes to the surface (about 25 knots or 12.9 m/sec), either singly or in pods of half a dozen, at great speeds. Their swimming was seldom horizontal but oscillated vertically in pattern resembling a series of sine curves, and third, large skipjack tuna (70-80 cm) appeared lethargic in comparison to small skipjack tuna. There were no signs of schooling during feeding and the fish never appeared to swim faster than about 10 knots (5.1 m/sec). More often the fish cruised at 2-4 knots (1.0 to 2.1 m/sec), swimming nearly horizontally, with surface dashes being relatively unhurried.

Strasburg and Yuen (19~~68~~⁶⁰) also noted that (1) water sprayed on surface while chumming bait caused more fish to be caught by increasing feeding frenzy, (2) fast chumming (twice normal) resulted in decreased catches, (3) slow chumming or insufficient bait resulted in loss of skipjack tuna, either through scattering of fish or reforming into schools, and (4) neither sound, blood or skin extracts appeared to have much effect on actively feeding schools.

One other school activity was observed by Strasburg (1961). During experimental fishing in Hawaiian waters he noted that a school being fished would abruptly dive vertically and vanish from view. Examination of stomach contents of fish from such schools showed that they had consumed postlarval Synodus variegatus and juvenile Holocentrus lacteoguttatus, both reef type fishes, and that the occurrence of these fish in the stomachs was significantly related to diving frequency. Observations on a number of diving schools indicated that diving was the rule rather than the exception. The number of dives per school ranged from 0 to 8 (Figure 30) with a mean of 2.7. The schools were away from the surface as briefly as 3 sec or as long as 28 minutes. In a later report (Strasburg, Jones, and Iversen 1968) reef type fishes, such as those found in the stomachs above, were observed from a small submarine at depths of 107 to 192 m, suggesting that skipjack tuna schools dived in pursuit of these natural prey.

i. Biting response of schools

The factors influencing the biting response of skipjack tuna schools has been studied by a number of scientists. These factors include (1) state of hunger, (2) behavior of prey, (3) maturity of gonads, (4) distance from land, (5) time of day, and (6) weather.

(1) State of hunger, as determined by the amount of food in the stomachs.--Uda (1933), Suyehiro (1938) and Hotta et al. (1959) noted that skipjack tuna responded to bait well when their stomachs were empty, and poorly when full. Uda further stated that skipjack tuna with stomachs between the extremes of fullness and emptiness tended to respond more poorly when their stomachs were emptier. The last statement, however, is contrary to Yuen's observation (1959) that skipjack tuna schools responded to bait longer when the major food items in the stomachs were in the earlier stages of digestion and the stomachs were emptier, nor to Magnuson's observation (1969) of skipjack tuna in captivity that attacks on food particles decreased rapidly only after the stomach contents exceeded 50% of the stomach's capacity.

(2) Behavior of prey.--Skipjack tuna feeding on fast-swimming fish such as bromeids, thunnids, carangids, and gempylids, exhibit a more favorable biting behavior than skipjack tuna feeding on slower-swimming chaetodontids, scorpaenids, molids, and acanthurids (Yuen 1959).

(3) Maturity of gonads.--Brock (1954), commenting on the rarity of skipjack tuna with fully ripe gonads and the lack of spawned-out ovaries within the spawning season in his extensive sampling of fish in the Hawaiian skipjack tuna fishery, suggested that fish with ova diameters over 0.7 mm become progressively less available to the fishery. In effect implying that such fish may abstain from feeding, hence reducing the chances of being caught, during the spawning period. Yuen (1959) also found that maturation of the ovary did not appear to affect biting response, except in fish with ripe eggs. That the skipjack tuna likely undergo a period of fasting is borne out by fishermen's remarks (see discussion on feeding behavior) concerning the infutility of fishing such schools.

(4) Distance from land.--Suyehiro (1938) measured biting quality on the number of fish caught per man in 100 minutes, designating 16 fish or less as poor biting and 17 fish or more as good biting. Applying this to schools fished in Japanese waters by vessels from 17 prefectures in 1935 he determined that skipjack tuna schools in the open sea generally bit well, whereas those occurring around islands bit poorly. He interpreted this to mean that schools bite poorly in coastal waters because of an abundance of natural food and bite well in offshore waters because natural food is less abundant. A similar relationship was found for skipjack tuna in the central Pacific. Yuen (1959) reported that the peak catch rate of fish in the Hawaiian skipjack tuna fishery showed a positive significant correlation with distance from land. However, the correlation was true only for large (>60 cm) fish.

(5) Time of day.--Uda (1940) reported that there is a relation between time (hour of catch) and total catch and between time and catch-per-school. The curve for total catch shows three peaks, a primary peak between 0500 and 0900, a secondary peak between 1800 and 1300 and a tertiary peak between 1600 and 1800. Uda determined that about half of the day's catch was made between 1500 and 0900 and about two-thirds of the day's catch occurred prior to noon. He explains the catch curve thus: "the fish school and feed most actively in the early morning, and once their stomachs are filled their appetites decline, but around noon, for reasons connected with the time required for digestion, their appetites again increase and they become slightly active." He presumes another such phenomenon is exhibited in the evening just before sunset. While his explanation above agrees with the results obtained by Magnuson (1969) from feeding experiments conducted on skipjack tuna in captivity (see Feeding Behavior), similar peaks were not reflected in the catch rates obtained in two of the four years examined.

A similar study was done in the central Pacific by Uchida and Sumida (1971), but rather than using catch and catch rates as the variants, they used number of schools sighted and number of schools fished successfully. Plots of the variants against time of day (Figure 31) resulted in curves not unlike that obtained by Uda (1940~~d~~). However, their interpretation of the curves differed. Fishing success (i.e., schools yielding catches) increased rapidly from daybreak to a peak at 0901-1000, dipped slightly at 1001-1100, and followed by

two peaks at 1201-1300 and 1401-1500. The authors attributed the dip at 1001-1100 to reduced scouting effort due to time taken for lunch. They suggested that the time taken for breakfast and dinner also may have partly affected the reduced sighting and successful catches near sunrise and sunset. Additionally, unlike the Japanese fishery, where most of the day's catches were made prior to noon, most of the day's catch in the Hawaiian fishery occurred after midday (Table 10).

Table 10

(6) Weather.--To what degree weather affects the biting behavior of skipjack tuna schools has not been clearly determined. Suyehiro (1938) reported that in the western Pacific biting seemed to be better in cloudy than in clear weather, and that biting appeared equally good in rain and fog as in clear weather. He noted, however, that the reliability of the latter was questionable due to few data. He also reported that wind velocity was not related to biting quality. In the central Pacific Yuen (1959) observed that weather conditions were predominantly uniform and biting behavior did not change even on unusual days. The few darker days affected fishing only in decreasing the chances of sighting schools.

(7) Other aspects of biting behavior.--Uda (1940) shows that in the western Pacific most of the schools fished and most of the catches are made between 10 and 40 minutes of fishing, that the catch rate, expressed as catch-per-school, increases in direct proportion to the increase in fishing time up to 80 minutes, and that when fishing time exceeds 80 minutes, neither the total catch nor catch rate shows any increase. Similarly, in the central Pacific,

the fishing duration of most schools are between 5 and 40 minutes (Yuen 1959; Uchida and Sumida 1971) and the catch-per-school increases proportionally to fishing duration (Figure 32).

Fig. 32

Yuen (1959) measured various factors which seemed to influence the catch. Of these, (1) postpeak duration, (2) fishing duration, (3) peak catch rate, (4) mean number of hooks per minute, and (5) rate of increase of prepeak catch rates were all found to be related significantly to total catch (Table 11). Of these (1) and (3) were subsequently used as measures of skipjack tuna response on the premise that postpeak duration would measure the duration of interest and peak catch rate would measure the degree of interest or intensity in feeding.

Table 11

Yao (1962) examined the biting qualities as judged and recorded on fishing reports by Japanese fishermen. In these reports biting qualities were judged as good when:

- (a) fish were attracted in large numbers immediately upon ~~chumming~~ and accompanied by a sudden initial increase in catch;
- (b) the number of fish increased beyond the fishermen's capacity to catch them;
- (c) duration of fishing above a minimum catch rate was long;
- (d) when catch per school was large; and,
- (e) when maximum catch was attained quickly.

Yao calculated ^{the} biting qualities ^{of} schools, employing Yoshihara's theory (1960) on the mechanism of skipjack tuna fishing, ~~represented~~ by the equation

$$W = N [1 - (1 - \lambda t) e^{-\lambda t}]$$

where \underline{W} is number of fish caught, \underline{t} is fishing duration, N is number of fish in school, and $\underline{\lambda}$ is the biting coefficient expressed as the reciprocal of the length of time until the catch rate reaches a maximum. Yao's calculations indicate that (1) through (4) tend to be judged higher as school size increases, even when the degree of biting were the same. Ignoring school size, he found no statistical differences in the mean biting coefficient between schools judged as good, average and poor by the fishermen.

Yao also observed the mean biting coefficient, 0.135, for schools below 1,000 fish was extremely high, as compared with the mean coefficient, 0.085, of schools above 2,000 fish. He suggested that the high mean coefficient for small schools was due to reporting by the fishermen of only good biting schools, since only such schools, usually, actually fished, whereas both good and slow biting large schools were fished.

Summarizing the above, it seems that fish respond well to chum when their stomachs are less than half filled and when ~~they are~~ feeding on fast-swimming prey; that schools in offshore areas respond better than those inshore; that fish, particularly females, respond poorly during spawning; that the response reaches a peak in the early morning between 0800 and 1000; that there may be more than one feeding peak during the day; that the response generally lasts from 5 to 40 minutes, depending on school size and state of hunger; and that weather may not influence feeding behavior.

F. PHYSIOLOGY

1. Body Temperature

Tunas are the only teleosts known to maintain their body temperature much above that of the surrounding waters. These fish possess a system of counter-current heat exchangers located in the circulation between the gills and the tissues (Carey et al. 1971). The heat exchangers act as a thermal barrier, so that heat generated as a by-product of metabolism is retained, causing the temperature in the muscle mass and nearby tissues to rise. Carey et al. (1971) described two types of heat exchanger, lateral and central. Lateral heat exchangers (Figure 33) are best developed in the Thunnus where they consist of four sets of longitudinal subcutaneous arteries and veins, each with adjoining layers of retial vessels that penetrate the red muscle near the midplane (Kishinouye 1923; Gibbs and Collette 1967; Carey et al. 1971; Graham 1975). Central heat exchangers (Figure 33), found in Euthynnus, Katsuwonus and Auxis, are located below the vertebral column, in the haemal arch, and consist of a large vertical rete formed from branches of the dorsal aorta and the posterior cardinal vein (Kishinouye 1923; Godsil 1954; Carey et al. 1971; Graham 1973, 1975).

Fig. 33

Body temperature measurements of skipjack tuna have been made by various researchers (Fukushima 1953; Barrett and Hester 1964; Carey and Teal 1969; Stevens and Fry 1971). The excess red muscle temperature, i.e. muscle temperature minus ambient water temperature, obtained by these authors ranged from 3.1° to 11.1°C. Stevens and

Fry (1971) also obtained excess white muscle temperature from 29 skipjack tuna that ranged from 5.9° to 11.4°C and excess brain temperatures that ranged from 1.9° to 5.6°C. They believed that 13°C was the lower lethal ambient temperature, since a test skipjack tuna had died suddenly when the water temperature was cooled to this level.

Neill et al. (1959)⁹ conducted heat exchange experiments with sedated and free-swimming (unsedated) skipjack tuna and explored the role of large thermal inertia in tuna ecology. The heat exchange experiments yielded the following results:

- (1) Inertial resistance to cooling and warming were virtually unaffected over the same span of temperature (18° to 30°C) for fish between 0.4 and 3.5 kg in weight.
- (2) Thermal inertia of red muscle, white muscle, and brain was proportional to weight of fish.
- (3) White muscle, brain and ventricular blood equilibrated with a changed environmental temperature about 1.1, 3.3, and 20 times as rapidly as red muscle.
- (4) The countercurrent heat exchanger was about 95% efficient as a thermal barrier between gills and red muscle; consequently, only about half the total heat transfer between the red muscle and the environment occurred across the gills.

- (5) Under conditions of thermal equilibrium, the red muscle and white muscle of sedated fish were warmer than the environment by amounts independent of environmental temperature but proportional to weight; in contrast the excess temperature of the brain was independent of fish weight but bore a weak, positive relation to environmental temperature.
- (6) In two free-swimming fish stimulated to violent activity by chasing, the red muscle warmed up at rates up to $0.3^{\circ}\text{C M}^{-1}$, ultimately attaining temperatures 1.5° and 3.4°C above pre-chasing equilibrium levels.

They further noted that skipjack tuna exchange core heat with the environment only about 60% as rapidly as do typical teleosts, and that there was no short-term physiological thermoregulation in skipjack tuna. From calculations based on thermal inertia, excess temperature, and rate of warming they determined that minimum and maximum rates of metabolism in the red muscle of skipjack tuna were about 4 and $25 \text{ cal g}^{-1} \text{ hr}^{-1}$, respectively. Similar considerations suggested to them that large thermal inertia and high rates of metabolism could pose an ecological problem for skipjack tuna as they grew in body mass; i.e. excess core temperatures could become so large as to cause the muscle of the fish to overheat, especially during period of greatest activity in warm waters. They, therefore calculated hypothetical limiting upper environmental temperatures

Fig. 34

for skipjack tuna as a function of body size based on an average metabolic rate (suggested) in the red muscle of a normally active fish. The limiting upper environmental temperatures they obtained were 30.2°C at fish weight (W) = 1 kg, 2/15°C at W = 10 kg, and 15.8°C at W = 22 kg (Figure 34). These calculations implied that "large skipjack tuna must occupy cooler waters if they are to be as active as smaller fish. This could be achieved by large fish living at higher latitudes or at greater depths than smaller fish. Low rates of heat exchange in large skipjack tuna would permit forays of several minutes' duration into surface waters warmer than maximum ambient temperature, if the fish were initially at thermal equilibrium with deeper, cooler water."

Other studies (Dizon et al. 1974; Dizon et al. MS¹⁰) show that restrained skipjack tuna could perceive abrupt temperature increases (1°C/sec) and decreases (0.5°C/sec) as small as 1°C and that the oral-branchial cavity was more sensitive to temperature stimuli than antero-dorsal quadrant of the body surface or the nasal cavity.

2. Oxygen Requirement and Uptake

Metabolism of free-swimming skipjack tuna weighing 0.4 to 3 kg was reported by Neill et al. (MS⁹) to be minimally 0.5 to 0.6 mg-O₂ g⁻¹ hr⁻¹ and exceeded 2 mg-O₂ g⁻¹ hr⁻¹ under conditions of moderate swimming activity. These values were stated to be 3 to 5 time larger than those for non-scombroid teleosts of similar size.

In an experiment to determine heat production by red muscle, Neill et al. chased two skipjack tuna, 1.21 and 1.78 kg body weight, in a pool for varying lengths of time. The larger fish died after 15 minutes of continuous chasing. The smaller fish was chased for 4.5 minutes and for 2 more minutes, after a rest period of 18.5 minutes, before it died. The metabolic rates of red muscle prior to chasing were $1.4 \text{ mg-O}_2 \text{ g}^{-1} \text{ hr}^{-1}$ in 1.21 kg fish and $1.0 \text{ mg-O}_2 \text{ g}^{-1} \text{ hr}^{-1}$ in the 1.78 kg fish. The maximum rate of metabolism was slightly over $7 \text{ mg-O}_2 \text{ g}^{-1} \text{ hr}^{-1}$ for both fish (Figure 35). According to the authors such a large demand for oxygen could not be met aerobically, thus leading to a lethal oxygen debt.

Fig. 35

Brown and Muir (1970) considered the ventilation of the gills by skipjack tuna to be analogous to the ramjet engine and thus applied the theory of the ramjet mechanics to the gill ventilation by the skipjack tuna. Their analysis provided estimates of the pressure losses as the water passes through the gill spaces, and of the resistance force that must be overcome by the swimming muscles. For a 44 cm skipjack tuna swimming at its basal speed of 66 cm/sec, the gill resistance was estimated to be 1090 dynes/cm^2 or 7% of the total swimming resistance. They noted that if oxygen consumption doubled, gill resistance increases to 27% of the total. They estimated the energetic cost of respiration to lie between 1 and 3% of the total metabolism at basal swimming speed.

Stevens (1972) attempted to relate some measurements of the variables affecting respiration to the theoretical analysis by Brown and Muir (1970). Using these measurements he calculated the oxygen uptake of skipjack tuna. He observed that the skipjack tuna can extract 50% of the oxygen from the water at gill flow rates about four times as high as other fishes. The absolute value of oxygen uptake (692 mg/h kg) he obtained was much higher than in any other resting or perfused fish. This value was similar to the minimum metabolic rate ($0.5-0.6 \text{ mg O}_2 \text{ g}^{-1} \text{ h}^{-1}$) of free-swimming skipjack tuna reported by Neil et al (MS).⁹

Stevens (1972) also measured the partial pressure of oxygen in blood afferent and efferent to the gills and used it to calculate the effectiveness of oxygen removal from the water. This value was 90% for the skipjack tuna. He reported that values for other fishes from the literature range only from 10% to 30%, and that the high value for skipjack tuna stresses the great efficiency of skipjack tuna gill in removing oxygen from the water.

3. Role of Red and White Muscles

Raynor and Keenan (1967) monitored the electrical activity of both the red and white muscles in two skipjack tuna, 1.5 and 1.7 kg in weight, by attaching electrode probes and observing the behavior of the fish. From the records obtained, they concluded that basal swimming of free-swimming skipjack tuna was brought about entirely by the red muscle system. The white muscle appeared to represent a reserve power for short bursts of high activity as in feeding and escape behavior.

V. ECOLOGY

A. LARVAE

1. Geographical Distribution

Subsequent to the publication of the synopses of biological data of skipjack tuna in the Pacific (Waldron 1963), Atlantic (Postel 1963) and Indian Oceans (Jones and Silas 1963), additional captures of skipjack larvae have been reported to enlarge the area of distribution (Fig. 36). The reports include Klawe (1963), Nakamura and Matsumoto (1966), Ueyanagi (1969, 1970), Ahlstrom (1971), and Chen and Tan (1973) for larvae taken in the Pacific Ocean; Klawe (1960), Suarez-Caabro and Duarte-Bello (1961) Gorbunova and Salabarría (1967), Juárez (1974), Richards (1969), Richards and Simmons (1971), Zhudova (1969), and Ueyanagi (1971) for larvae taken in the Atlantic Ocean; and Gorbunova (1963, 1965a), and Ueyanagi (1969) for larvae taken in the Indian Ocean.

Fig. 36

Larvae of skipjack tuna thus have been found over a wide range in all the major oceans, including the Gulf of Mexico and throughout the Indo-Pacific archipelagoes. In the Pacific Ocean the known distribution of skipjack larvae now extends over a wide range from near lat. 35°N off Japan to as far south as lat. 37°S off the southeastern part of Australia. The distribution remains wide eastward until slightly past the Hawaiian Islands in the northern and the Society Islands in the southern hemisphere. It then narrows abruptly toward the equator at about long. 145°W and remains within 10° to 15° of latitude on either side of the equator to the

Central and South American coasts. Both the northern and southern boundaries of distribution in the Pacific Ocean may be accepted as firm, based on the numerous sampling cruises made to date.

In the Indian Ocean the distribution extends southward to the southern tip of Africa to lat. 36°S , nearly similar to that in the Pacific Ocean. Unlike the distribution in the Pacific, however, the southward extension is also wide in the eastern part of the ocean, reaching to lat. 30°S . The southern boundary could be modified slightly with further sampling, particularly in the central sector. The northern boundary is limited to about lat. 12° to 15°N by the Asian continent.

The distribution in the Atlantic Ocean differs somewhat from that in the Pacific. Although the distribution is wide in the western side, resembling that in the Pacific Ocean, the extension southward does not reach much beyond lat. 20°S . The northern extension also falls short of the limit shown for the Pacific Ocean. The large dip in the boundary in the region of the Sargasso Sea may be due to lack of sampling data. The greatest difference in the distribution pattern between the two oceans is in the eastern sector. Whereas the distribution narrows and the concentration of larvae diminishes greatly in the eastern Pacific (Klawe 1963), the distribution is wider and the abundance of larvae is much greater (Richards and Simmons 1971) in the eastern Atlantic Ocean.

2. Occurrence Relative to Distance From Land

Larvae of skipjack tuna, as is true of larvae of most tunas, are found mainly in open ocean far removed from land. However, spawning by tunas can and often does occur close to shore under ideal conditions. In the Hawaiian Islands skipjack larvae have been taken as close to shore as 450 m (data Honolulu Laboratory).

3. Occurrence Relative to Surface Temperature

The skipjack, as well as other tunas, require warm water for spawning. Consequently the distribution of larvae is governed greatly by water temperature. The limits of larval distribution agree best with the 24°-25°C isotherm (Fig. 36). This is not to say that skipjack larvae are not found in waters below 24°C, for they have been taken in waters as cool as 22.1°C (Matsumoto 1974).

It seems that both the minimum and optimum temperatures for skipjack larvae differ by areas. For example, in the western Pacific between lat. 30°N and the equator, a summary of surface night tows from 10 cruises by the Shoyo Maru (data from Ueyanagi 1969) shows that all except one larva were taken in waters 25° to 29°C (Table 12). The one exception was a larva taken in 30°C water. The most productive tows were made in 28°C water, while the lowest temperature in which skipjack larvae were caught was 23.5°C, in a subsurface tow at 20-30 m (not included in table). In the central North Pacific around the Hawaiian Islands, nearly all the larvae caught had been from waters 23° to 26°C (Table 12),

Table 12

and the most productive tows in terms of occurrence and in number of larvae caught were in 25° and 24°C water, respectively. The lowest surface temperature in which skipjack larvae were caught was, as stated above, 22.1°C.

4. Occurrence Relative to Surface Currents

Fig. 37

The influence of surface currents on the distribution of skipjack larvae is obvious from Figures 36 and 37. Although the latter shows current conditions in the northern winter (also southern summer), and the former gives the summer distribution of larvae in both hemispheres, it does not materially affect the discussion. In both the Atlantic and Pacific Oceans the prevailing currents flow away from the equator in the west and toward the equator in the east. The pattern of flow thus causes the warm water area, favorable for skipjack spawning, to expand in the west and to constrict in the east. Similarly, the larval distribution is also expanded in the western part of the oceans and narrowed in the eastern part.

5. Vertical Distribution

Vertical distribution of tuna larvae has been studied by various researchers. Matsumoto (1958) found no definite evidence showing that larvae of any species of tuna occurred in waters deeper than 50 m in the central Pacific. Klawe (1963), likewise, found no evidence of tuna larvae in waters deeper than the thermocline (15-48 m) in the eastern Pacific. Strasburg (1960), who used opening and closing nets, found six times more skipjack

larvae at the 0-60 m depth than at the 70-130 m depth, and practically none (only one larva) at the 140-200 m depth. He also found that surface tows caught twice as many skipjack larvae as the 0-60 m depth tows. Finally, Ueyanagi (1969) found that tows made simultaneously at the surface and at 20-30 m depth showed there was little difference in the catches. It is evident from these information that skipjack larvae are concentrated mostly in surface waters, at least to a depth of about 60 m, and that only a small portion are found in depths greater than 60 or 70 m.

The absence of skipjack larvae below the thermocline in the eastern Pacific (Klawe, 1963) could be a valid local phenomenon or simply a result of generally poor occurrence of larvae there. In the central Pacific, the situation is quite different. Figure 38 provides evidence that a few skipjack larvae were present in waters well below the thermocline. The figure also provides evidence that skipjack larvae can and do occur in depths greater than 140 m.

Fig. 38

6. Larval Abundance

Skipjack larvae, as well as larvae of other fishes, are largely planktonic in the early stages of growth and therefore are commonly taken in fine mesh plankton nets. Because the catches have been so small and variable and the size of nets and towing methods used have differed in various sections of the ocean, it has been difficult to assess larval abundance over the entire

ocean in a meaningful way. Nevertheless, certain areas of high abundance can be recognized.

Based largely on the studies by Matsumoto (1958) and Yabe and Ueyanagi (1962), Kawasaki (1965^a) suggested that the center of abundance of skipjack larvae in the Pacific Ocean was in the area bounded by lat. 5°N and 4°S and long. 160°E and 140°W. Kawasaki (1972) revised his western boundary to long. 120°E, most likely on the basis of Ueyanagi's (1969) study, which showed a peak in larval abundance at long. 120°E-150°E along a band of water lat. 10°N. to 0°. Matsumoto (in press), after adjusting the catches of larvae made with different sized nets and different towing methods (Table^{x-} 12) in a band of water lat. 10°S to 20°N, reported that the center of abundance of skipjack larvae lay between long. 160°E and 140°W (Fig. 39), similar to Kawasaki's first estimate; that the abundance was moderate between long. 100°W and 140°W and between long. 120°E and 160°E; and that the abundance was low in the eastern Pacific east of long. 100°W.

Fig. 39

Other areas north of lat. 20°N with relatively high larval abundance include the waters around the Hawaiian Islands, where the catches in night surface tows using a 1-meter net during the spawning season averaged 4.1 larvae per ton (data from Seckel 1972) and in the waters to the south of Japan between lat. 25°N-30°N, where the catches in subsurface tows (20-30 m) using a 2-meter net averaged nearly 4.0 larvae per ton (Ueyanagi 1969).

In the Atlantic Ocean larvae are apparently more abundant in the eastern half of the ocean between lat. 10°N and 10°S (Richards 1969). There are no other report from the Atlantic Ocean that provide measures of abundance. The same is true of studies on larvae conducted in the Indian Ocean.

B. JUVENILES

1. Occurrence and Distribution

Existing information on the captures of juvenile skipjack (fork length 12-350 mm), including juveniles of other tunas, have been summarized for the Atlantic Ocean by Simmons (1969) for the years 1959-67, and for the Pacific Ocean by Higgins (1967) for the years 1916-66. It is obvious from these two studies that the collecting of juvenile tunas has been more intensive in the Pacific than in other oceans. Simmons lists 164 juvenile skipjack from the Atlantic Ocean and Higgins lists 603 juveniles from the Pacific Ocean. More recently, Yoshida (1971) examined 1,313 juveniles obtained in the Hawaiian Islands and in the Samoa-Society Islands area (lat. 5°S-35°S; long. 135°W-180°), and the National Marine Fisheries Service's Honolulu Laboratory (unpublished data) has collected an additional 631 skipjack juveniles in midwater trawl hauls in 1969-70. This brings the total juvenile skipjack either collected or recorded in the Pacific Ocean to 2,560. In the Indian Ocean Jones and Kumaran (1963) and Gorbunova (1963) have reported the captures and distribution of skipjack larvae. Included in their larval catches

were a number of specimens ranging in lengths from 12 to 27 mm, which should be considered as juveniles. Jones and Kumaran published the details of capture by station, which included the position of capture as well as the size ranges of material collected. Gorbunova also reported the size range, but this was for all skipjack taken by areas.

Fig. 40

Figure 40 shows the locations, in 5° square areas, of known captures of skipjack juveniles. It is obvious that efforts to collect juveniles have been spotty in all oceans, despite the large numbers. In the Pacific Ocean, however, a semblance of the wide distribution of the larvae is recognizable. From recent information obtained about the extremely rapid growth of skipjack and other tunas reared from artificially fertilized eggs through the juvenile stages (Mori et al. 1971; Harada et al. 1971a, 1973a, 1973b; Ueyanagi et al. 1973), it would not be unexpected to find juveniles of skipjack in all the localities where larvae are found.

2. Vertical Distribution

A systematic sampling of juvenile tunas with a small-mesh midwater trawl net by Higgins (1970) in Hawaiian waters provide information concerning the vertical distribution of juvenile skipjack. Shallow tows (maximum depth 20 m) at night tended to catch the most juveniles and deep tows (100 m) at night, the fewest. Catches during the morning were not significantly different from those at night, but shallow morning tows tended

to be less productive than shallow night tows and deep morning tows tended to be more productive than deep night tows. Daytime catches were about the same in shallow and deep tows. The differences in the catch rates for juvenile skipjack tuna between shallow and deep tows at different times of the day were assumed to be the result of diel vertical migration.

Higgin's (1970) study also showed that skipjack juveniles were significantly larger in deep tows (average standard length 14.4 mm) than in shallow tows (average SL 11.1 mm). Although the apparent tendencies were not significant, night and morning tows at the deeper depth also tended to catch larger juveniles than day tows. Higgins tentatively concluded that the smaller skipjack juveniles live primarily in the upper isothermal layer, whereas the larger juveniles tend to occur in or migrate to deeper water.

C. ADULTS

1. Distribution of Skipjack

Although the northern limit of occurrence was previously shown to be north of lat. 55°N in the Atlantic Ocean and lat. 50°N in the Pacific Ocean, based on a few rare captures, the more usual distribution is limited to much lower latitudes (Fig. 1). Nevertheless, the distribution, both latitudinally and longitudinally, is still very extensive. Within this distributional range, the skipjack tuna occur in varying densities, depending on certain environmental conditions favorable for their existence. Areas of

moderate to high densities quite often are defined by the existence of a fishery and may be sizeable in extent. In the Pacific Ocean, such areas extend from north of lat. 40°N to 5°S, possibly more, in the western side and from about lat. 35°N to 25°S in the eastern side. Such an area, which extends from lat. 20°N to 15°S, is also found in the eastern side of the Atlantic Ocean. Smaller areas of moderate to high densities also occur around islands indicated in Figure 1 and around other islands, not shown due to undeveloped stage of large scale fishing. Within these areas the density of skipjack fluctuates accordingly with changes in the environment.

2. Occurrence of Skipjack Tuna Relative to Environmental Factors

a. Temperature

The temperature range within which the skipjack appear to be restricted has been reported on a world scale by Laevastu and Rosa (1963) as 17° to 28°C, and for presence in major fisheries as 19° to 23°C. Reference to individual regions of the world oceans not only show some variations, but extend the range further. Uda (1957) gave the range off Japan of 17.5° to 30°C for all occurrences and 20° to 24°C for occurrences in the fishery; Broadhead and Barrett (1964) reported a range of 17° to 30°C in the eastern Pacific, with 20° to 24°C for occurrences in the major fishery off South America, and Jones and Silas (1963) reported regular catches of skipjack off

southern India from 27° to 30°C water, with the most frequent temperatures being from 28°-29°C. Robins (1952) reported skipjack taken in temperatures of 14.7°C to 20.8°C, with the most occurrences being in waters between 16° and 18°C in Tasmanian waters. Although skipjack are not fished commercially there, they are frequently very abundant. Thus, the temperature range of skipjack occurrence could be taken as 14.7° to 30°C. Figure 1 shows the mean 15°C isotherms which adequately demark the range of skipjack tuna occurrence. It should be noted that the 15°C isotherms are for the warmest month of the year in both hemispheres and hence represent the average maximum poleward displacement.

That skipjack tuna seek preferential temperatures is indicated by occurrences in the fishery. These also vary by regions: 20° to 24°C in the northwestern Pacific and the eastern Pacific southern fisheries, 28° to 29°C off southern India and 16° to 18°C off Tasmania. Besides seeking preferential temperatures skipjack also avoid certain temperatures in specific areas. Blackburn [~~and Associates~~] (1962) noting the absence of skipjack catches in the warm water cell off southern Mexico concluded that skipjack probably avoid surface waters of very high temperature (above 28°C) in this region.

It is evident then that although the skipjack tuna dwell in waters with surface temperatures ranging from below 15° to 30°C, the preferred range seems to be from 20° to 29°C.

While temperature is an important factor affecting the distribution of skipjack tuna, its influence on distribution is usually not obvious in the tropics where it is relatively uniform throughout the year. Matsumoto (in press) in his study of skipjack tuna taken by the Japanese tuna longline fishery from 1964-67, showed that the high catch rate areas in the equatorial central Pacific remained relatively unchanged during the year. At the northern and southern extremes of distribution, however, the skipjack respond directly to seasonal temperature changes (Matsumoto ^{in press} ~~1968~~; Schaefer 1961^b; Kawasaki 1965^a; Uchida 1970).

b. Surface currents

The circulation features of the main currents in both the Pacific and Atlantic, described previously in connection with larval skipjack distribution, largely applies to the distribution of adults as well. The flow towards the equator of cool currents on the eastern side of the oceans tend to restrict the distribution of fish in that region. Surface currents affect the occurrence of skipjack in other ways. In currents flowing meridionally the tuna, including skipjack, is considered to be distributed along the axis of the current and in greater abundance than in adjacent waters (Blackburn 1965). Such a relation with the Kuroshio Current was reported by Kawasaki (1958) and Uda (1962a). They both reported that good fishing in waters off Japan develops when the Kuroshio is well developed in intensity. The latter further stated that the broader the areal coverage of

the warm Kuroshio, the more abundant the migrants of skipjack into the northeastern area of the fishery.

c. Water masses

Within a current system tuna tend to aggregate in areas where warm and cold water intrusions are well developed, in eddies, in areas of turbulent mixing, all of which occur at oceanic fronts of water masses, and other hydrographic features (Uda 1961; 1962a, 1962b). Kawasaki (1958) also noted that skipjack fishing grounds developed when the warm Kuroshio water spread thinly over colder water and when the Kuroshio current meandered in a complicated pattern.

The relation of skipjack occurrence to water mass was shown for the area around the Hawaiian Islands by Seckel (1963). He found that skipjack is more abundant in the Hawaiian fishery in summers when the California Current Extension bathes the islands than in summers when it lies further south. He found also that the availability of skipjack was also associated with the time of initial warming of the water. Whenever this occurred in March, landings were average, whereas when it occurred in February, landings were above average (Fig. 41).

Fig. 41

3. Vertical Distribution

Based on studies of tuna caught on the longline Yabe, Yabuta and Ueyanagi (1963) indicated that the tunas are distributed by depth layers with the skipjack tuna occupying the shallowest layer followed in order by the bluefin, yellowfin,

bigeye tuna and the albacore. Skipjack tuna was assumed to occupy the shallowest depth layer largely on the basis that they are taken in commercial quantities almost entirely by fishing gear that require the fish to be at or very near the surface, and also with the knowledge that the skipjack are taken only incidentally on the longline.

Results from the use of echo-sounders (Kimura, Iwashita and Hattori 1952; Yamanaka, Kurohiji and Morita 1966) and underwater observations from small submarines (Strasburg, Jones and Iversen 1968) have shown that the skipjack tuna not only occur over a much greater depth range than previously realized, but also in depths occupied by other tunas. Kimura et al. (1952) and Yamanaka et al. (1966) observed fish schools at depths of 140 and 120 m, respectively, which they identified as skipjack when the schools subsequently rose to the surface. Strasburg et al. (1968) encountered skipjack schools at depths of 98 to 152 m during their numerous dives in the submarine. These depths are well within the depth range in which the yellow-fin tuna are usually caught on the longline.

4. Hypothetical Habitat of Skipjack Tuna

Recent acquisition of new information on the temperature and dissolved oxygen requirements of the skipjack tuna have enabled Barkley, Neill and Gooding (MS) ¹¹ to consider three environmental conditions that would likely determine the distribution of skipjack tuna. The conditions were (1) a lower

temperature limit, which varies with prior conditioning but is near 18°C; (2) a lower limiting concentration of dissolved oxygen, at or somewhat below 3.5 ml/L; and (3) a speculative upper temperature limit, ranging from 33°C for the smallest skipjack normally caught by fishermen to 20°C or less for the largest. Based on these limits and on oceanographic data from the eastern Pacific Ocean, they presented a hypothetical habitat for the skipjack tuna.

Fig. 42

Figure 42b shows the hypothetical habitat of skipjack

tuna of two sizes, those which can tolerate water up to 26°C,

Fig. 43

and larger fish restricted to water of 22°C or less. Figure 43

shows the areas of marginal or zero habitat thickness in the

eastern tropical Pacific. According to Barkley et al. (MS),¹¹

skipjack tuna larger than 11 kg should find no habitat within

the shaded area; fish 4 kg in size would find no habitat within

the smallest contoured area, with water temperatures above 26°C

at depths shallower than the lower limit of dissolved oxygen;

and fish 3 kg or less should find some thickness of habitable

water, within or just below the upper mixed layer, everywhere

in the eastern Pacific Ocean.

VI. RESOURCE

A. FISHERIES.

1. Gear.

The largest proportion of tuna landed on a worldwide basis is taken by the longline gear as deployed primarily by Japan, the Republic of China (Taiwan), and the Republic of Korea. This gear, of course catches the larger species of tunas and incidentally some skipjack tuna. The second largest catch of tunas and tuna-like species is taken by bait boats (Joseph 1973), and this catch consists largely of skipjack tuna. Japan is the primary bait boat fishing nation in the world today, and their vessels vary from small, under 50 gross ton (GT) vessels up to 300 to 400 GT vessels. The smallest vessels fish primarily in the coastal waters off Japan while intermediate sized vessels fish further offshore, and both participate in joint ventures that Japanese companies have set up with various governments in the Pacific, Indian, and Atlantic Oceans (Figure 44). The largest vessels (Figure 45) in the range from 250 to 400 GT are the best of their fleet and fish in the offshore waters of Japan and south into their "southern water" fishery (lat. 24°N-5°N and west of long. 160°E). Other interpretations of the bait boat have been developed by the USA for fishing in the Pacific Ocean and by France and Spain for fishing in the Atlantic Ocean. In the USA, west coast albacore bait boats initiated the skipjack-yellowfin tuna fishery in the eastern tropical Pacific and evolved to the tuna clipper that enjoyed its greatest success in the 1950's (Figure 46). Then in Hawaii, there is the aku sampan (Figure 47), which was originally

Figs. 44,
45

Fig. 46

Fig. 47

designed in the early 1900's after the Japanese sampan, that has evolved into an effective vessel for fishing the choppy waters of the Hawaiian Islands.

The third largest catch of tunas, and second largest catch of skipjack tuna, is taken by purse seiners. Although purse seining for tunas first began off the North American continent in the 1920's, the modern tuna clipper first appeared when bait boats began converting to purse seiners in the late 1950's (Figure 48). The remainder of the skipjack tuna catch is small and is accounted for by gear such as harpoons, traps, beach seines, gill nets, canoes (powered and sailing), and trolling.

Fig. 48

Each of the two major gears used in taking skipjack have their advantages and disadvantages. First, a bait boat fishery is actually two fisheries, one for skipjack tuna that is dependent on the success of the other, the bait fishery. Much has been written on this topic and will not be repeated here. Also, obtaining enough fishermen and the high cost of this labor has become a real problem, and Japan has attacked this problem by trying to develop various types of automatic fishing gear (Inoue, 1966; Iwashita, Inoue, Igeta, Yoshida, Amano, and Kodama 1967). The gear that seems most successful is the automatic fishing pole (Suzuki Tekko¹² Kabushiki Kaisha 1970). This gear has been used successfully on many Japanese vessels and has been tried in Australia, Hawaii, and the U.S. West Coast. Advantages of bait boat fishing are the relatively small capital investment involved, ability to harvest

small schools of fish, ability to operate out of small ports with a minimum of technical support, and ability to utilize unskilled, "local" labor.

Disadvantages of purse seine fishing are relatively large capital investment required, inability to fish in rough waters, inability (currently) to fish in waters with deep thermoclines, require rapid unloading facilities, require rather sophisticated support facilities. Advantages of purse seining are independence from bait sources, lower requirements for manpower, highly efficient catch rate per man and per vessel.

2. Area and Catch.

While the larger species of tunas comprise the major segment of catches of tuna and tuna-like species on a worldwide basis, it can be seen from Figure X47 that the skipjack tuna in 1971 accounted for 26.8% of this catch and 36.1% of the catch of the principal market species (Joseph 1973). In addition, it may be seen from Figure X48 that skipjack tuna catches in the Pacific Ocean made up in 1971, 72% of the world catch of skipjack tuna, in the Atlantic Ocean 19%, and in the Indian Ocean 9%. From Table 13 (from Matsumoto 1974; the FAO statistics given are "uncorrected" relative to those given by Joseph 1973), it can be seen that within the Japanese catch in the "northwest" (the Japanese coastal, offshore, and "southern water" fishery) makes up 63% of the world catch and 72% of the Pacific catch of skipjack tuna. A more detailed breakdown of the catches is provided in Table 14 (Uchida, in press a) for

Fig. X47

Fig. X48

Table 13

Table 14

Table 15 the more traditional fisheries and in Table 15 (Uchida, in press a) for newly established or developing fisheries. The Japanese catches in Table 14 are for the Japanese coastal and offshore fisheries while those in the Table are for the entire Japanese fishery in the northwest Pacific. Note that in 1971 the Japanese "southern water" fishery made up slightly more than half of the total catch in the northwest Pacific.

Fig. 1 The areal distribution of the catches shown in Tables 13, 14, and 15 can be seen graphically in Figure 1 (taken from Matsumoto 1974, and updated). The shaded area around various island areas has been exaggerated while subsistence, artisanal fisheries in the South Pacific and the small but developing fisheries off Australia, Mozambique, and New Zealand have not been indicated at all. If longline catches are any indication of skipjack tuna abundance, then the Indian Ocean must be very underdeveloped.

B. POPULATION STRUCTURE.

1. Sex Ratio.

Sex ratios given in the literature vary considerably but in general indicate that males are more common in the catch for all oceans. Batta (1972) presented data that shows males comprising 51% of the catch from sport fishing boats in 1964, 50% in 1965, and averaging 50% over the two years. In the Indian Ocean, Jones and Silas (1963) indicate that Raju (1962) found males predominating in most months, especially in larger size groups. For the Sulu and Celebes Sea and Sulu Archipelago area, Wade (1950)

presented data that showed males comprising 46% of the catch of troll caught skipjack tuna, although Wade discussed differences in sex ratio due to maturity. Data presented by Marr (1948) for the northern Marshall Islands indicated that males comprised from 58% to 67% of the catch for the years 1946 and 1947. For the Hawaiian area, Brock (1954) found that males predominated in the catch for most periods and averaged 54% over 1949 and 1950. Also, Tester and Nakamura (1957) reported that males comprised 61% of the catch from trolling in inshore waters. In the eastern tropical Pacific, Schaefer and Orange (1956) reported that males comprised only 40% of the catch.

Most of the sex ratio data seem to be byproducts of other research, for example maturity experiments, but surprisingly have not been used to study the affect of maturity on the sex ratio, variation with size of fish, or problems of availability or migration associated with attainment of maturity.

2. Age-Size Composition by Area

Age- or size-frequency distributions have been published for several reasons, among them to simply determine the composition of the catch, to detail seasonal changes in a fishery, to study migration through a fishery, to determine entry time-area strata for certain sized fish in the fishery, to investigate relationships between areas or fisheries, to set up a data base for further studies such as growth or cohort analysis, and to study gear selectivity. In the following

discussion, attention will be centered on relationship between areas or fisheries.

For the eastern tropical Pacific Ocean, Broadhead and Barrett (1964) provided charts of the length-frequency distributions for four areas in the northern areas of the skipjack tuna fishery (Figure 50). In general, these charts show that the four areas are remarkably similar in that the distributions are unimodal and are comprised mostly of small fish. Some area, for example the Gulf of California and the Mexican Coast tend to have larger fish, and the composition of fish around the Revillagigedo Islands is variable over years. For the Hawaiian Islands area, Brock (1954) published yearly length-frequency curves for 1946-51 (Figure 51), and Rothschild (1965) published monthly length-frequency curves for 1952-63 (Figure 52). The most striking characteristic of these distributions is their bi- or tri-modality. In the winter months, modal groups are generally found around 35, 50, and 70 cm while in the summer months modal groups are generally found around 45 and 70 cm. While Brock found a progression of modal groups over the years in his sample and developed a growth modal based on this progression of lengths, Rothschild found that progression of modal groups was irregular. In fact, some regression of modal lengths were observed, especially in the summer months. Rothschild (1965) compared the third quarter length-frequency distributions for Baja California (taken from Broadhead and Barrett 1964) with those from Hawaii and found a remarkable similarity for the small modal group in 1954 and 1960

Fig. 53 (Figure 53). For 1959, the length-frequency distributions of the two areas for fish differed considerably. It can be inferred from this figure and from other comments by Rothschild in his 1965 paper that the small fish in Hawaii and the eastern Pacific (at least Baja California) have a common origin and that origin is in the central equatorial Pacific Ocean. Rothschild and Uchida (1968) presented a length-frequency distribution that summarized results from exploratory fishing cruises in 1957-59 to the Marquesas Islands by vessels of the National Marine Fisheries Service, Honolulu Laboratory

Fig. 54 (Figure 54). This distribution is similar to those in Hawaii in that the distribution is multimodal, with modal lengths at approximately 47, 67, and 75 cm. Shomura and Murphy (1955) presented a length-

Fig. 55 frequency distribution for the equatorial central Pacific (Figure 55) that showed a wide range of sizes of skipjack tuna were available in the equatorial area; however, most of the fish caught were between 70 and 80 cm. It is well known that longline gear selects for large fish or at least large fish that are in oceanic waters, and catches from this gear probably are biased toward the larger individuals.

Further to the west, Murphy and Otsu (1954) showed that longline gear fished in the area of the Caroline and Marshall Islands also caught a wide range of sizes of skipjack tuna, but here the medium size (57 cm) fish dominated in the catch (Figure 56). In the Marshall

Fig. 56 Islands, Marr (1948) reported on trolling experiments carried out in 1946-47 (Figure 57). With modal lengths at 44 and 65 cm, the distribution differs considerably from that shown by longline gear in a similar area. Further westward, Higgins (1966) presented a length-

- frequency distribution for the live-bait fishery in the Palau Islands that showed a unimodal distribution in the summer and a tri-modal distribution in the fall (Figure 58). With a modal length of 52 cm in June 1965 and modal lengths of 50, 58, and 68 cm in October 1965, this distribution does not agree with that determined from longlining in the western equatorial Pacific (Murphy and Otsu 1954). Kasahara and Tanaka (1968) presented data from the "adjacent seas of Mariana and Palau Islands" (probably most of the data came from fish caught in the Mariana Islands) that is considerably more complex than those presented earlier for the western Pacific Ocean (Figure 59). In the summer months a dominant mode is usually found in the 40-cm range, similar to that found in Palau, but weaker modes of a larger size are also apparent. In the fall, the dominant mode is of a smaller length than that found in Palau; however, the winter distribution in this set of data looks much like the fall distribution in Palau. Generally, it seems that the length-frequency distributions are more consistent within fishing seasons than they are between seasons. Proceeding northward, Kawasaki (1964) presented data that shows a wide distribution of sizes available to the fishery in the fall and winter, but the larger sizes of skipjack tuna are not available as they are further to the south (Figure 60). In the summer months a single mode is present in the 40 cm range, and this mode seems to decrease in modal length from early spring to June followed by a slight increase in the late summer. Rothschild (1965) made a similar observation regarding the "progression" of modal groups in
- Fig. 58
- Fig. 59
- Fig. 60

the Hawaiian fishery. Further north in the northeastern offshore area fishery, Kawasaki (1964) presented evidence showing only smaller fish (40-50 cm) represented in the fishery (Figure 61). In addition, this modal group showed a steady increase in length through the season. A completely different ~~distribution~~ has been found in the Japanese southwestern area (southwestern Japan on into the Ryukyu Islands toward Taiwan). Kawasaki (1955) believes there is a local or nonmigratory group that resides in the archipelago as well as a migratory group that moves up toward Japan along a route much to the west of that group of fish that migrates up the Mariana, Bonin, and Izu Islands (Figure 62). Both southwestern area groups are bimodal, but the migratory groups is smaller in size with modes at 36 and 52 cm while the nonmigratory group has modes at 47 and 65 cm.

Length-frequency data from other areas is rather fragmentary. Wade (1950) presented data from catches in the Sulu Sea area adjacent to the Philippines (Figure 63). The data were grouped for an entire year and exhibits a single mode with mean length of about 50 cm. In the Indian Ocean, Jones and Silas (1963) present data that again showed a unimodal distribution in the summer months and a bimodal distribution in the winter months (Figure 64). For the Atlantic Ocean, Postel (1963) ~~showed~~ a unimodal distribution for skipjack tuna taken off Cape Vert (Figure 65). For the northwestern Atlantic, Batts (1972) presented a length-frequency distribution for skipjack tuna aged from dorsal spine samples (Figure 66). Up to five age groups were represented in these catches from charter fishing

boats off North Carolina, USA, and the representation of each age group varied considerably between locations and years.

C. SUBPOPULATIONS

[To be provided later.]

D. ABUNDANCE

1. Relative Indices of Abundance

Shimada and Schaefer (1956) produced the first quantitative assessment of the density of skipjack tuna in the eastern tropical Pacific. They set up classes of bait boat vessels according to fish carrying capacity, evaluated effort in terms of days absence and days fished, and set up the basic standardization procedure that is still used today. The relative index of abundance (catch per standardized-day's fished), catch of skipjack tuna, and calculated relative fishing intensity as determined by Shimada and Schaefer for 1934-54 are shown in Figure 67. The authors concluded from this figure that the fishery was having no measurable effect on the skipjack tuna stock. Calkins (1961) refined the computation of the index of relative abundance by eliminating areas lightly fished and by calculating weighted and unweighted indices of abundance (after Gulland 1956). They did not consider purse seiners in the standardization process since purse seiners landed only 13% of the skipjack tuna catch. Trends in the relative index of abundance calculated on a quarterly

Fig. 67

Fig. 68 basis for the years 1951-59 are given in Figure 68, and average
Fig. 69 seasonal trends are given in Figure 69. There is no indication
of a downward trend with time; in fact, the unweighted index of
abundance reached its highest value in 1959. Seasonally, skipjack
tuna are most abundant in the third quarter. By comparing the con-
centrations and density indices for skipjack tuna, yellowfin tuna,
and both species combined, Calkins concluded that there is no con-
sistent significant relationship between the two species. Joseph
and Calkins (1969) included both bait boats and purse seiners in the
standardization of effort for the period 1951-65 and developed a
more efficient method of eliminating areas of low effort, which
might bias the estimate of relative abundance. Again, no decline
Fig. 70 in the indices of relative abundance (Figure 70) for either the north-
ern, southern or the combined fisheries can be seen. It is also
apparent that there is little relationship between the northern and
Fig. 71 southern segments of the fishery. The monthly trends in Figure 71A,
B, and C show that there is as much variation between years within
each fishery as there is between the fisheries. From Figure 72A, B,
Fig. 72 and C it can be seen that there is a relationship between either
indices of relative abundance and fishing effort or catch and fishing
effort; hence, the fishery still cannot be shown to have a measurable
effect on the stock. Pella and Psaropulos (1975) have adjusted the
fishing effort statistics by stimulating the effect of greater vessel
speed, increased probability of capturing sighted tuna schools,
reduction of time spent in a set, and greater portions retained of

schools set upon successfully on the fishing power of vessels. Using a new standardized fishing effort statistic based on this simulation, they found a different history of stock abundance over the years of the fishery (Figure 73). There seems to be some indication of a decrease in abundance of skipjack on the northern grounds and a definite decrease on the southern grounds. It is not known at this time which index of abundance is the best descriptor of the stock(s).

Fig. 73

For the small skipjack tuna fishery in the Hawaiian Islands, several attempts have been made to determine a valid index of relative abundance and determine if the fishery has had an effect on the stock. Yamashita (1958) first collected catch records for Hawaii for the years 1900-53 and effort data for 1948-53. Using only a subsample of the total catch and effort data available, Yamashita calculated the catch per effective day's fishing for 1948-53, recognizing that only effective fishing trips were reported and assuming that each trip lasted for 1 day. This index of relative abundance generally followed the catch curve and showed no trend with time

Fig. 74

(Figure 74). Shippen (1961) determined from biweekly trends in catch and index of relative abundance that total catch was as useful an

Fig. 75

indicator of abundance as the index (Figure 75). He also determined through interviews that zero-catch trips were more frequent in winter months than in summer months. Uchida (1967) again used effort in terms of effective trips (assuming 1 day trips), but standardized using two vessel size classes according to baitwell capacity and

Fig. 76

inshore and offshore areas. His index of relative abundance (Figure 76) varied essentially as catch varied and showed no trend either upward or downward from 1952-62. Subsequently, Uchida (in press b) has used effort data that included zero-catch trips for the period 1965-70 to estimate indices of relative abundance and relative fishing intensity for the period 1965-70, and extending back to 1948 through statistical manipulation, to investigate trends in abundance

Fig. 77

(Figure 77). Total catch and the index of relative abundance were highly correlated, abundance showed no upward or downward trend over the history of the fishery, and no relationship existed between the index of relative abundance and relative fishing intensity. Hence, the fishery seems to have no measurable effect on the stock available to the Hawaiian fishery.

Fig. 78

For the western Pacific Ocean although there is a long history of commercial fishing, there are surprisingly few estimates of some index of relative abundance. Kawasaki (1964) standardized effort statistics by using the catch per trip for 100-200 GT vessels as the standard. The resultant trend in the index of relative abundance was plotted along with indices from Hawaii and the eastern Pacific Ocean (Figure 78). Kawasaki's interpretation was that the Japanese fishery was having no measurable effect on the western Pacific stock and that the indices from the three fisheries fluctuated in common. Using data from Kawasaki, none of the curves could be shown to be correlated. Also, Kawasaki (1964) presented data for a coastal region that again showed no apparent decline and probably

an increase in density of skipjack tuna available to the fishery
 (Table 16). Iwasaki (1970) using data for vessels larger than 150
 GT calculated indices of relative abundance for the Bonin-Mariana
 and Caroline Island areas (Figure 79). For the period 1958-69, the
 the density of skipjack tuna seemed to increase first in the Bonin-
 Mariana area (probably with increased area of exploitation) and
 then remained steady for the remainder of the time period. The trend
 in abundance of skipjack tuna in the Caroline Islands also seems to
 be holding steady. Thus, the Japanese fleet does not seem to be
 having a serious effect on the stock(s) in the area, if catch per
 vessel is a valid index of relative abundance. Kasahara (1971)
 presented evidence that the abundance of skipjack tuna in the Japanese
 coastal and offshore to the south and southwest of Japan has remained
 steady from 1957-69 (Figure 80). Kasahara also presented evidence
 that the relative abundance of skipjack tuna in some areas of the
 southern water fishery has been declining in recent years (Figure 81).
 Since the landings per vessel for the southern waters fishery has
 shown an increase (Figure 82), Kasahara concluded that the area of
 the fishery has been expanding. Kasahara also has shown (Table 17,
 Figure 83) that the relative abundance of skipjack tuna in specific
 areas in the southern water fishery have declined while others have
 remained steady over the years; however, the amount of effort
 expended in particular areas has changed drastically over the years.

In the Atlantic Ocean, most quantitative assessments of the skipjack tuna resource have been done in connection with the International Commission for the Conservation of Atlantic Tunas and cannot be cited in the literature. A comparison of indices of relative abundance of both skipjack and yellowfin tunas for the coastal fishery based in Angola has been published by de Campos Rosado (1971). The relative abundance of skipjack tuna has been increasing from about the 1959-60 season through the 1968-69 season (Figure 84). It was argued by de Campos Rosado that this trend followed a simple Volterra, two competing species model in reaction to overfishing of the yellowfin tuna stocks by foreign fleets. He did not discuss the possibility of changing availability or switching of target species by the local fleet.

Fig. 84

2. Estimates of Potential Yield

In the eastern Pacific Ocean, Joseph and Calkins (1969) have produced estimates of yield per recruitment, using the Ricker model, for both the northern and southern skipjack tuna fisheries (Figure 85A, B). Their models assumed that skipjack tuna make two passes through the fisheries; in addition, the models used growth models calculated for grouped and ungrouped data from capture-recapture experiments as well as mortality estimates derived in the same paper. From Figure 85A it can be seen that the yield per recruitment for the northern fishery can be increased only slightly by a doubling of the fishing effort (a multiplier equal to 1.00 represents the level of fishing mortality in 1963) while that for

Fig. 85

the southern fishery (Figure 85B) can be increased 1 to 1-1/2 times by increasing fishing effort 2 to 2-1/2 times.

Rothschild (1966) and Silliman (1966) both estimated the potential yield for the combined eastern Pacific stocks if they were harvested beyond the range of the existing fishery. Rothschild (1966) estimated the potential yield using the Beverton and Holt model of yield per recruitment, estimates of growth parameters (subsequently published by Rothschild 1967), and estimates of size at recruitment and Z , the total mortality coefficient, derived from information published by the Inter-American Tropical Tuna Commission. Using sojourn times (that is, time exposed to the existing coastal fishery) of 2 and 6 months (Figure 86), Rothschild estimated that the yield could be increased between 2 and 17 times the present catch. Silliman (1966) estimated the potential yield using a population simulation model (see Silliman 1969), estimates of Z derived from growth parameters subsequently published by Rothschild (1967), and ranges for natural mortality coefficient, M . The best fit to the data was obtained using a value of M equal to 0.3, and the maximum average sustainable yield of 225,000 metric tons was found at F equal 1.00 and M equal to 0.3 (Table 18). This estimate of potential yield was 2-3/4 times the yield of about 60,000 tons in 1954-61. If Rothschild's estimate of maximum length of skipjack tuna is conservative and if the escapement stock from the eastern Pacific fishery is only a segment of the total fish available in the central Pacific, then both Rothschild and Silliman underestimate the potential yield from the central Pacific.

Fig. 86

Table 18

While both Rothschild and Silliman have indicated a potential increase in yield by harvesting skipjack tuna after it has escaped from the coastal fishery and is, therefore, older, Joseph and Calkins (1969) observed that yield per recruitment in their study could be increased by harvesting fish younger than are presently available to the fleet.

Japanese workers have issued estimates of potential yield for skipjack tuna both in the western Pacific Ocean and also for other ocean areas. Kawasaki (1972) indicated that a document entitled "On the possibility of developing marine fishery resources" issued by the Fisheries Agency of Japan in June 1968 gave potential yield estimates of

Japanese coastal area	- Increase of 200,000-400,000 tons
Entire Pacific Ocean	- Increase to 1,000,000 tons
Indian Ocean	- 200,000-300,000 tons
North Atlantic Ocean	- 100,000 tons
South Atlantic Ocean	- 100,000-150,000 tons

Also Kawasaki (1972) quoted from remarks made by Akira Suda at the June 1971 conference of the Japan Fish Resources Convention Association. Suda indicated that since skipjack tuna larvae are 1.7 to 1.8 times more abundant than all other tunas in plankton catches and 5 to 10 times more abundant in the stomachs of predators, then skipjack tuna must be at least 2 times more abundant than all of the other tunas. Taking a catch of 400,000-500,000 tons for all other tunas, then the estimate of potential yield for skipjack tuna would be 800,000-1,000,000 tons for the Pacific Ocean. No rigorously derived

estimates of the yield potential of skipjack tuna in the western Pacific, Indian, or Atlantic Oceans have been published.

E. MIGRATION

Fink and Bayliff (1970) brought together tagging data from 1952-64 for the eastern tropical Pacific and summarized the results from these tagging experiments. During this time period, 90,412 tagged skipjack tuna were released and 4,381 were recaptured. Results from these experiments are summarized in Figure 87. Recruits to the northern fishery (west coast of Baja California, Gulf of California, and Revillagigedo Islands) first enter the fishery in the Revillagigedo Islands in April, migrate north to and along the Baja California coast during the spring and summer, and migrate south along that coast during the fall. Recruits to the southern fishery (Tres Marias Islands to northern Chile) enter the fishery in or near the Panama Bight and migrate both northwest to Central America and south to the Gulf of Guayaquil. Little interchange occurs between these two areas. Rothschild (1965) hypothesized that the fish recruited into the fishery in the eastern tropical Pacific are recruited from the central equatorial Pacific east of long. 130°W (Figure 88). While the warm water cell on the northern edge of Central America is not formed at a time that would cause the entering fish to split into a northern and southern segment as hypothesized by Rothschild (Williams 1972), the hypothesis has been accepted in general. The warm water cell could serve to keep the two groups isolated once they have been

Fig. 87

Fig. 88

Fig. 89

formed. Williams (1972) has extended the hypothesis by proposing three migration models for the recruitment of skipjack tuna into the eastern Pacific fisheries, the passive model (Figure 89A), the active model (Figure 89B), and the gyral model (Figure 89C). At the moment, there is little evidence to substantiate one model over the others. Seckel (1972) concerned himself with the problem of skipjack tuna migrating from the northern fishery back into the central Pacific spawning area. By using a numerical drift simulation model based on geostrophic and wind driven currents, Seckel determined that fish could drift from an area between lat. 10° and 20° N at long. 120° W to an area between lat. 19° and 22° N at long. 155° W in 21 to 23 months (Figure 90). This time interval is within the

Fig. 90

range of values for skipjack tuna tagged in the eastern Pacific and recaptured in Hawaii. Within the Hawaiian Islands, movement of tagged fish seems to be random. However, Shippen (1961) felt that large skipjack tuna entered the islands from the southwest in the spring, dispersed within the island chain in the summer, and exited to the southwest in the fall. His hypothesis was based on catch rates of large fish within the Hawaiian fishery.

In the western Pacific, Imamura (1949) and Kawasaki (1955a, 1955b, 1964, 1965) have hypothesized the existence of nonmigratory stocks of skipjack tuna in the southern water fishery and in the shoal area within the Japanese coastal fisheries. Kawasaki has hypothesized that most of the skipjack tuna entering the Japanese fishery are spawned to the south, migrate into the Japanese fishery at age 2

(age 1 as designated by western scientists), and return toward the equatorial region for spawning as they become older. The migrations into and out of the Japanese fishery have been summarized by Waldron (1963) and appear in Figure 91.

Fig. 91

Kawasaki (1964) has argued on the basis of similar sizes at recruitment and similar fluctuations in catches between the Japanese, Hawaiian, and eastern Pacific fisheries that all skipjack tuna originate from a common equatorial spawning stock. Fish migrate poleward up to the age of 2 when they are recruited into the traditional fisheries, and then return to the equator to spawn when they are 3 or 4 years old. Kasahara (1968) reproduced an unpublished chart by Naganuma (Figure 92) that seems to reflect a concept similar to Kawasaki's.

Fig. 92

Finally, Matsumoto (1974; in press) has postulated from an examination of longline statistics that there are several semiindependent stocks of skipjack tuna that all originate from different areas of the equatorial Pacific (Figure 93). In the North Pacific, the stocks follow a clockwise migration pattern from the equator, poleward, and back to the equatorial area, except for the stock in the eastern Pacific that follows a counterclockwise migration path. In the South Pacific, stocks follow a counterclockwise migration path.

Fig. 93

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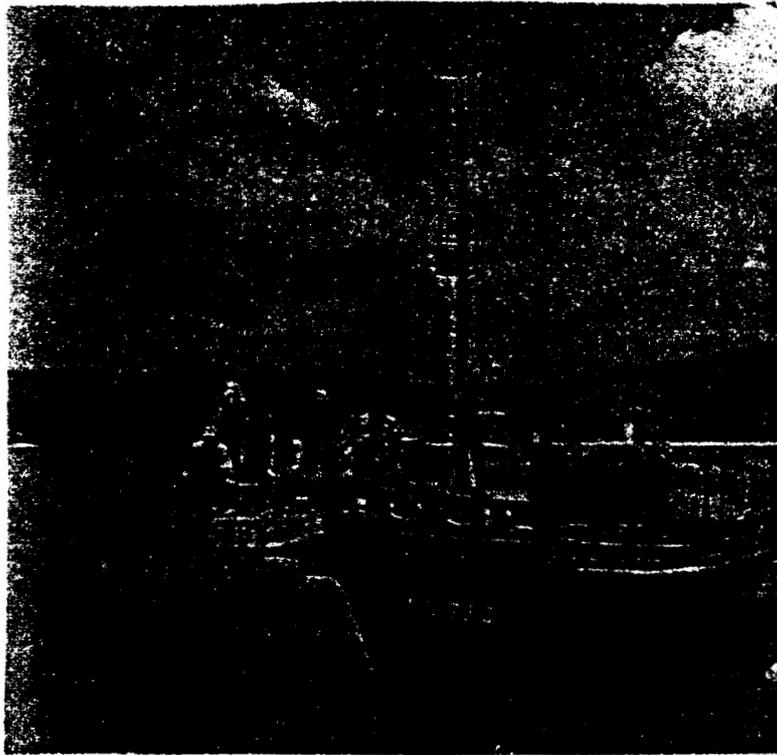
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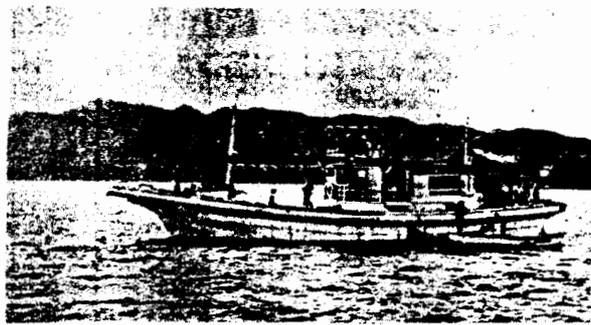
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Figure 44.-- Small Japanese style skipjack tuna bait boats: (a) operating out of Ambon in Maluku, Indonesia (taken from Australian Fisheries 34(2):10, 1975), (b) operating out of Palau, U.S. Trust Territory of the Pacific Islands (taken from Rothschild 1966:8), and (c) schematic drawing of a 150-gross ton vessel (taken from Yoshida 1966, who took it from Muramatsu 1960.)

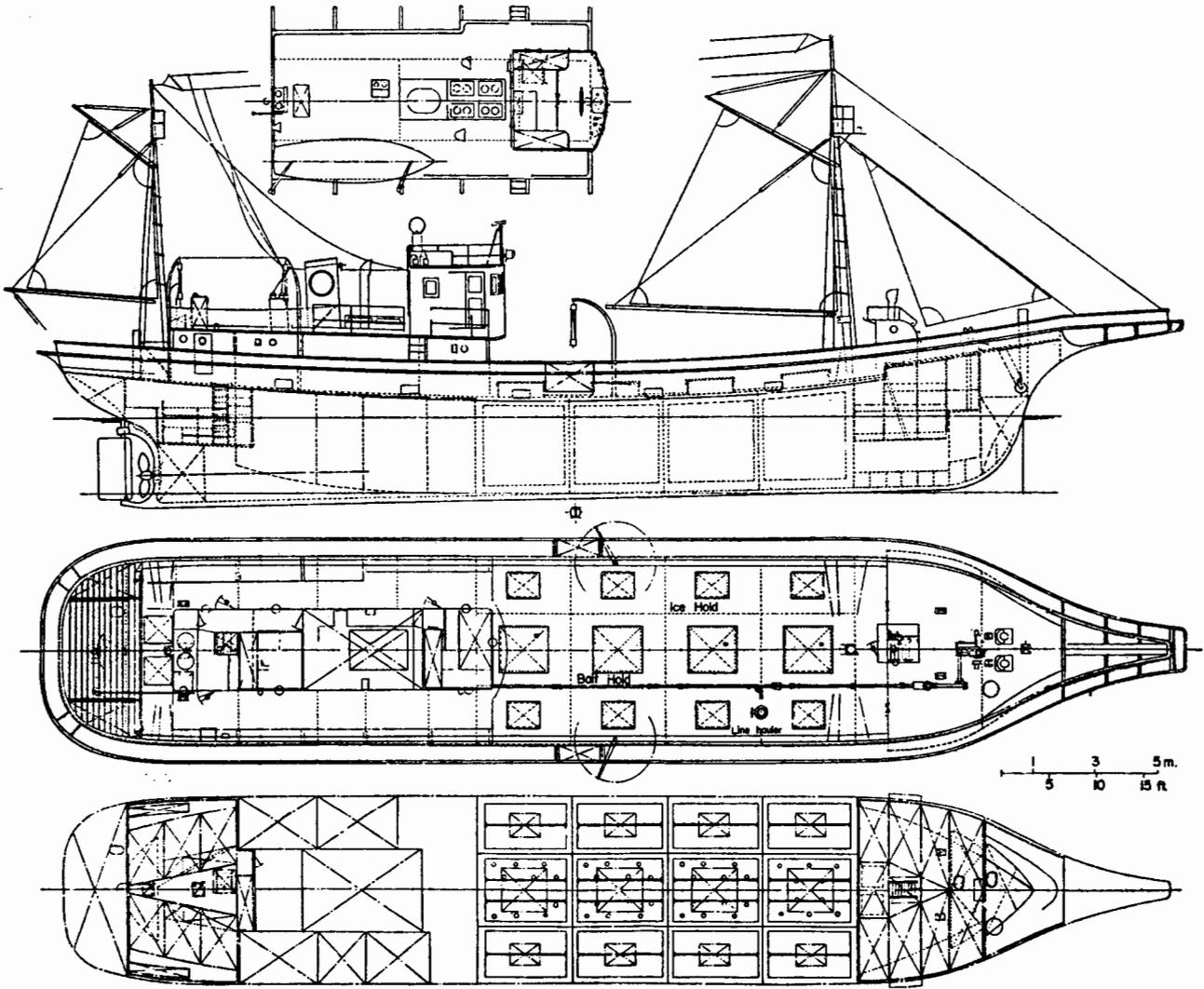


(a)



(b)

Fig. 2



(c)

Fig. 4-1

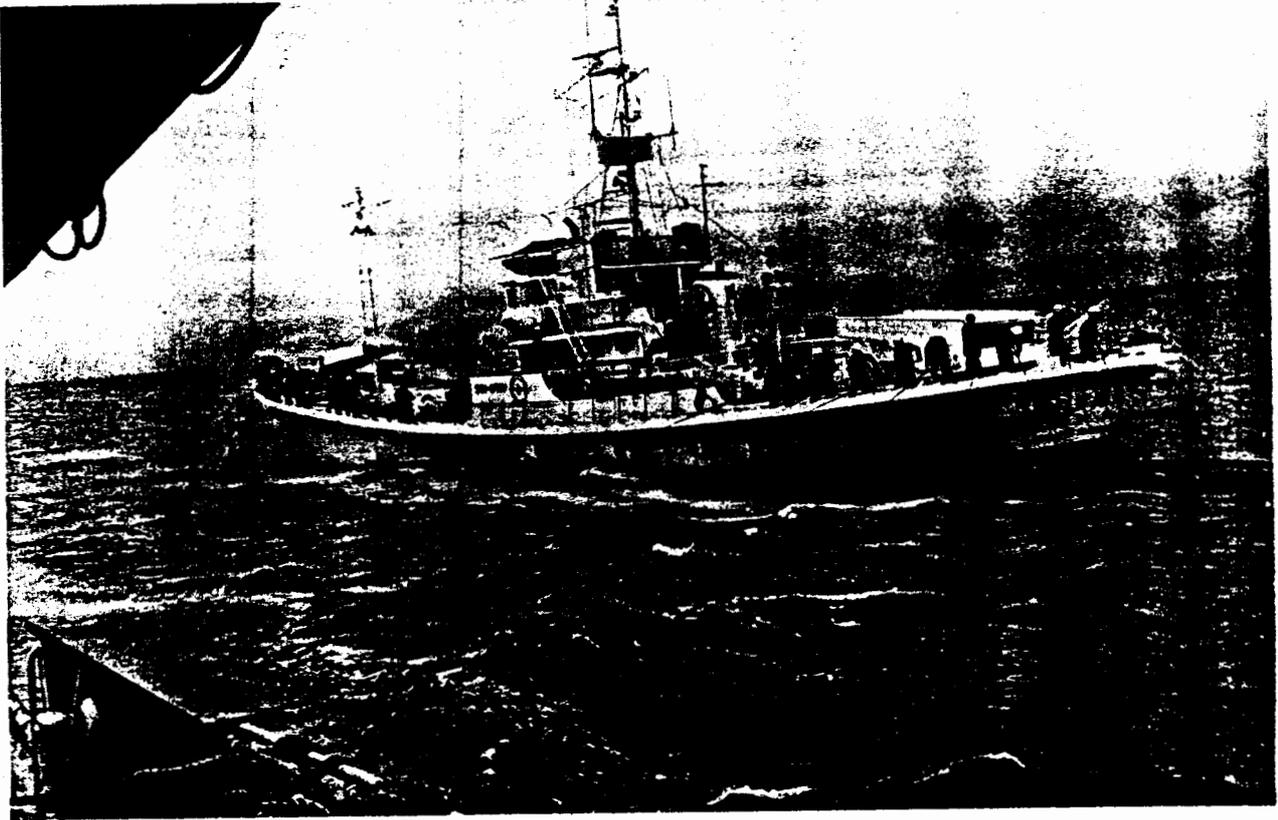


Figure 45.--No. 2 Fukukyu Maru of Yaizu in central northern Pacific skipjack tuna operation, July 1972. Photograph by Hiroyo Koami, Institute of Sea Sphere and Tsukiji Fish Market Company, Tokyo.
(From Kawasaki 1972.)

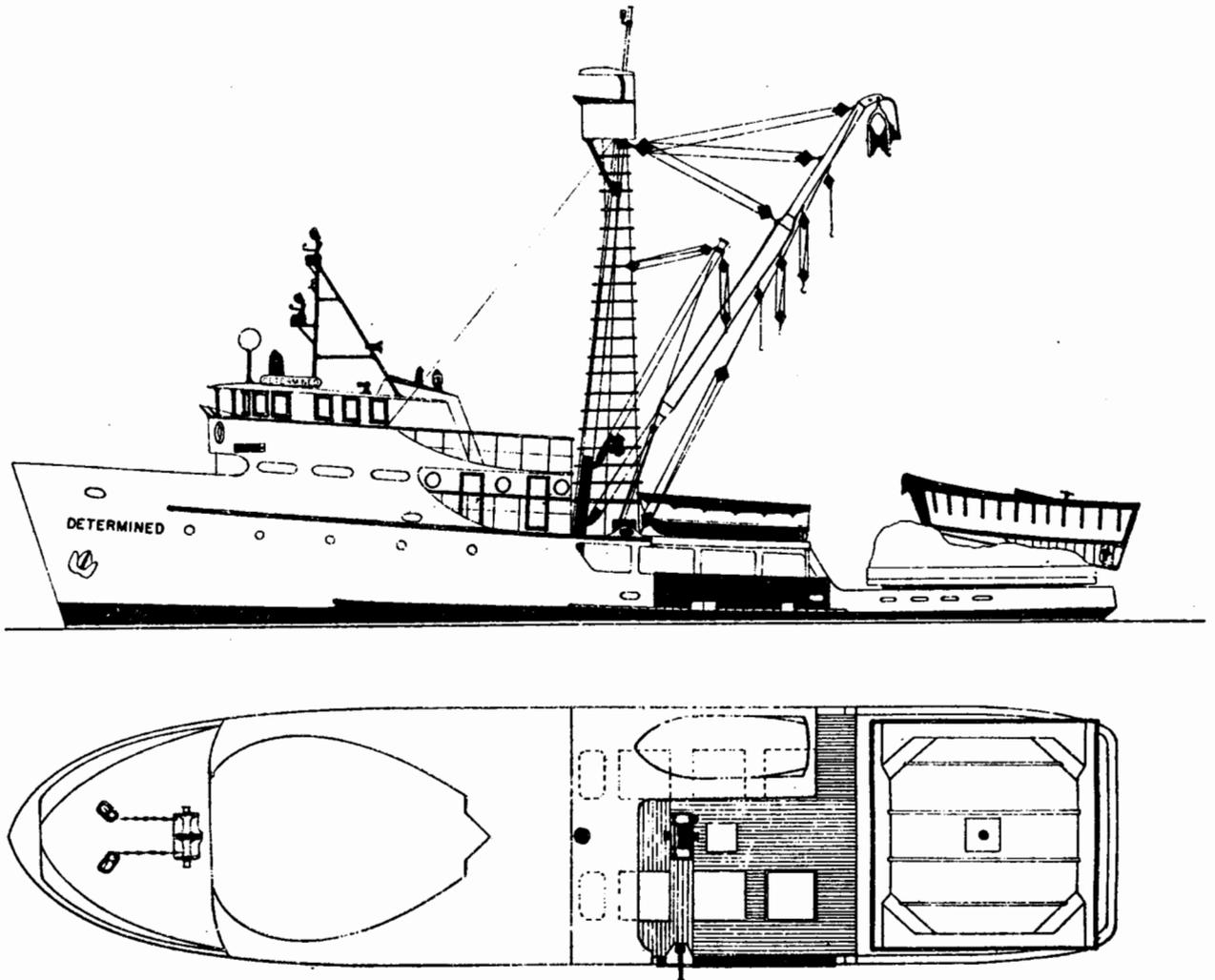


Figure 48.--Tuna clipper after conversion to purse seiner.

(From McNeely 1961.)

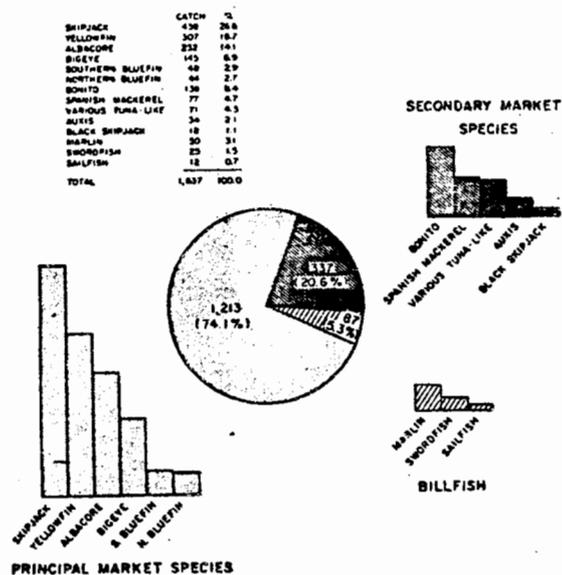


Figure X47.--The 1971 world catch of tunas and tunalike species (in thousands of metric tons). (From Joseph 1973.)

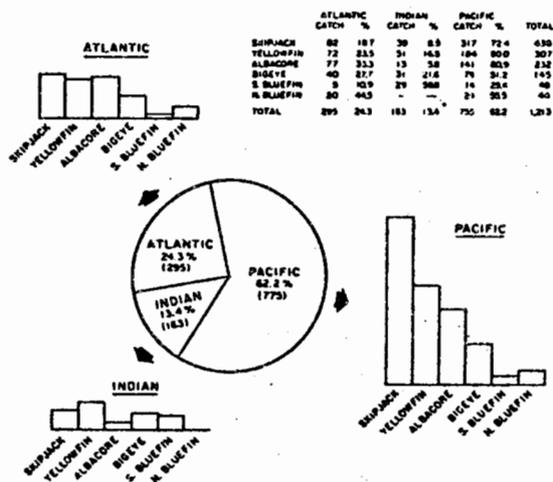


Figure X48.--The 1971 world catch of the principal market species of tunas by oceans (in thousands of metric tons). (From Joseph 1973.)

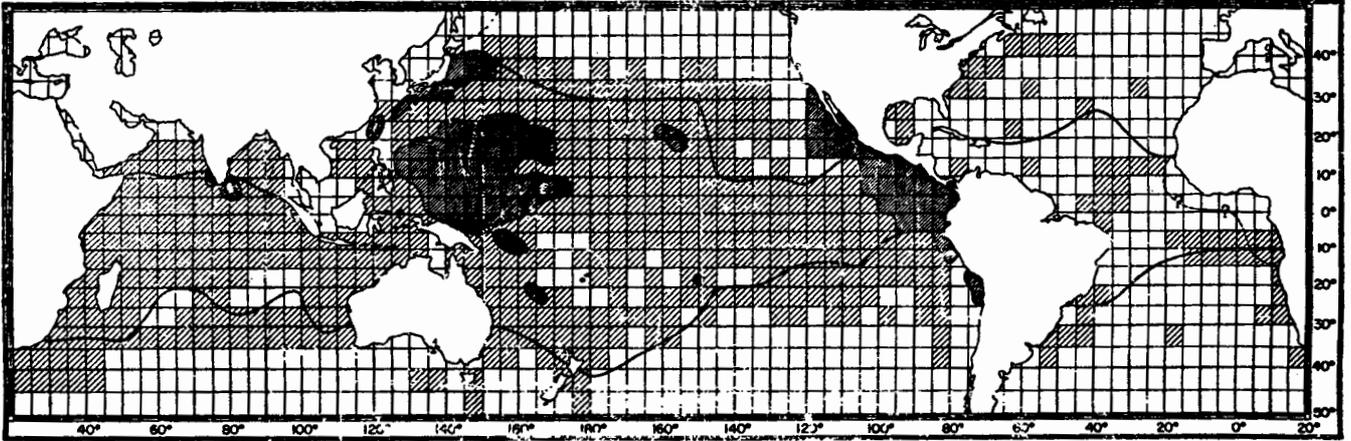


Figure 49.--Area of present skipjack tuna fisheries.

(From Matsumoto 1974.)

1974

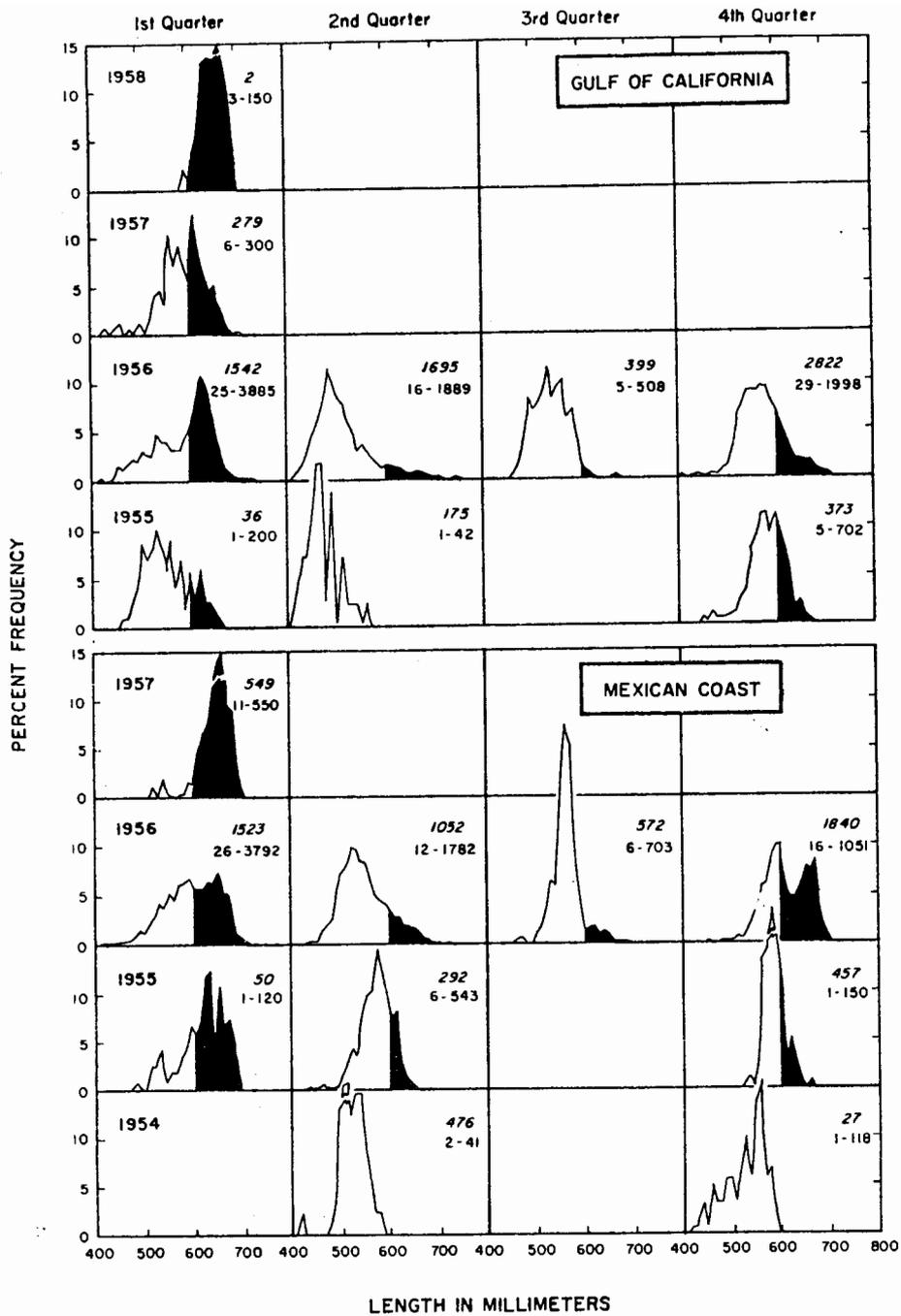


Figure 50.--Length distribution of skipjack tuna by quarter of the year for the Gulf of California, Mexican waters, the Revillagigedo Islands, and coastal areas of Baja California. (From Broadhead and Barrett 1964.)

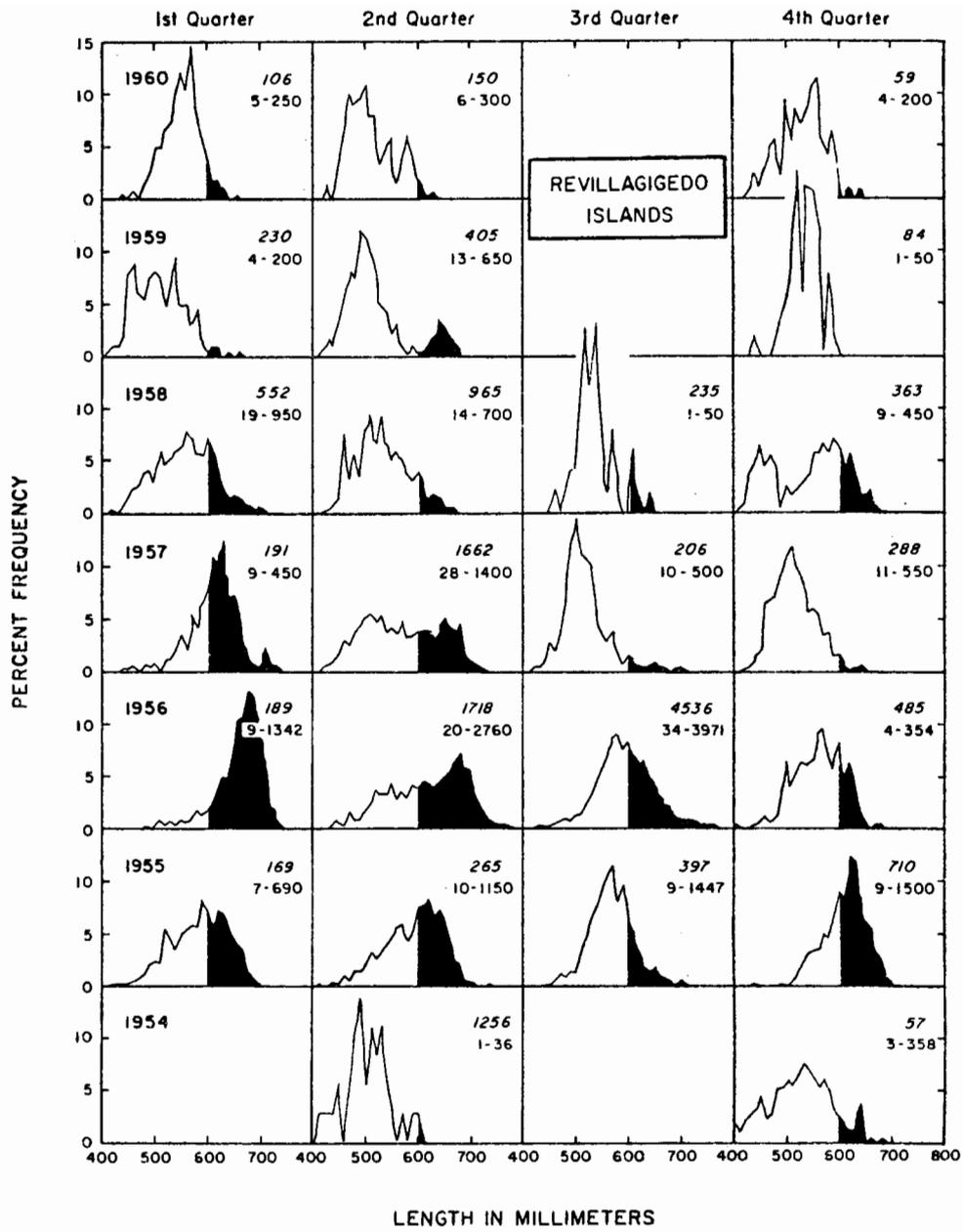


Figure 50.--Continued.

50.2

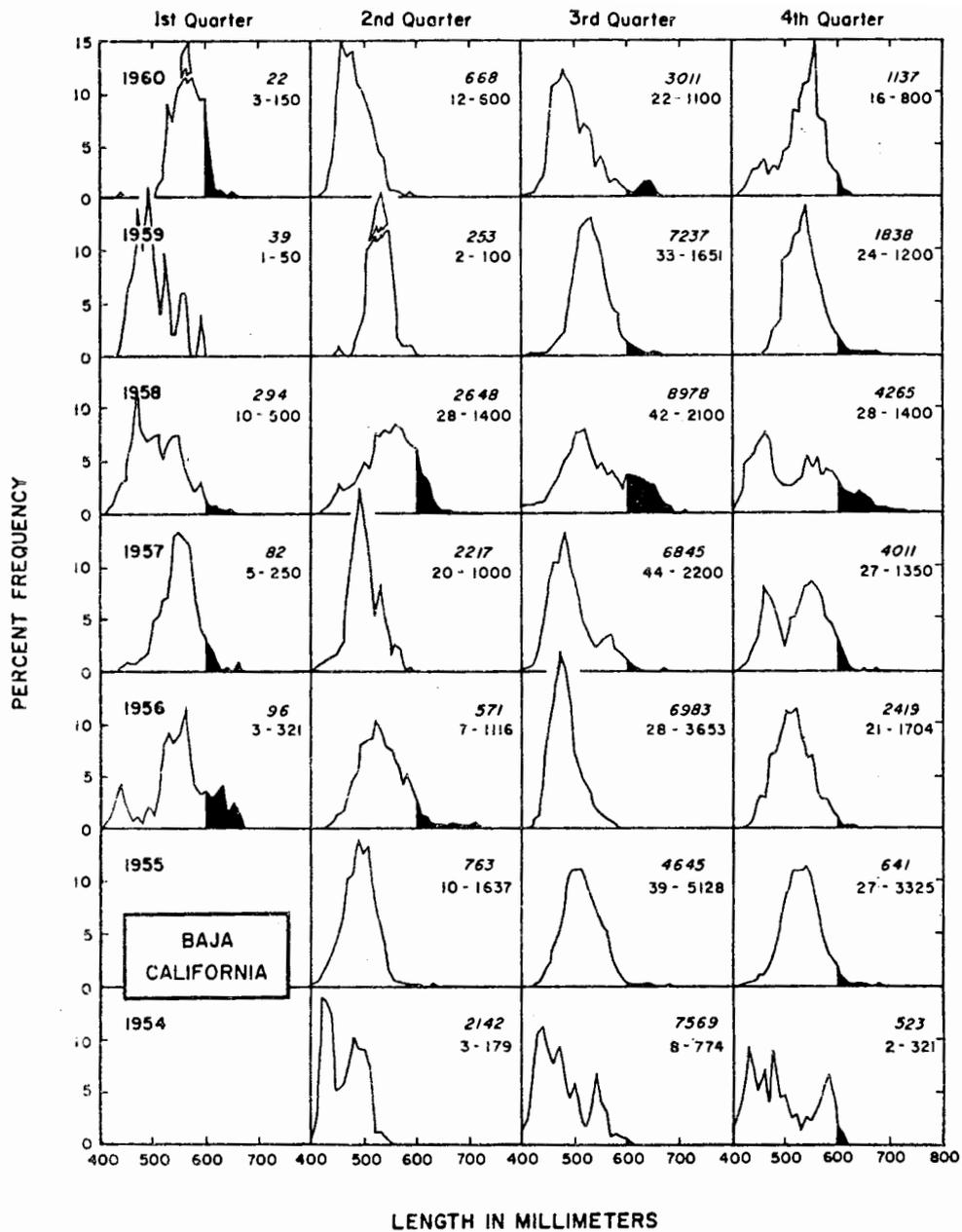


Figure 50.--Continued.

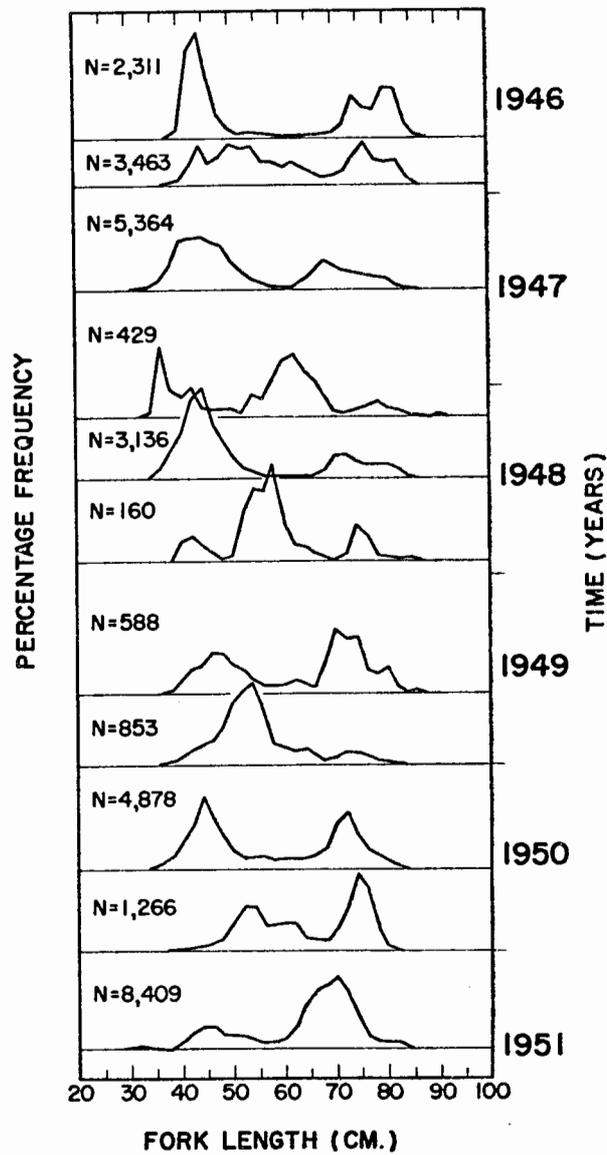


Figure 51.--Length-frequency distributions of Hawaiian skipjack tuna, grouped by time periods of approximately 6 months, 1946-51. (From Higgins 1966, who adapted it from Brock 1954.)

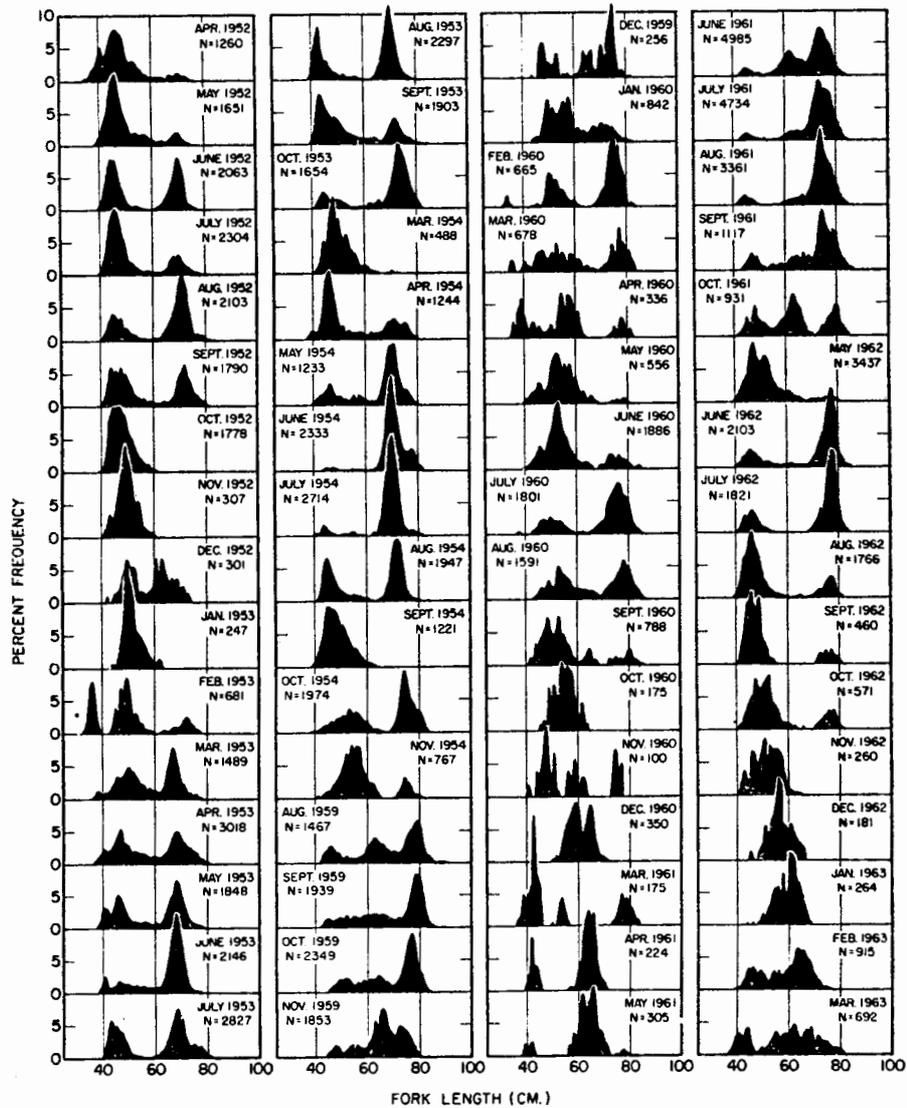


Figure 52.--Monthly length-frequency distributions of Hawaiian skipjack tuna, 1952-63. (From Rothschild 1965.)

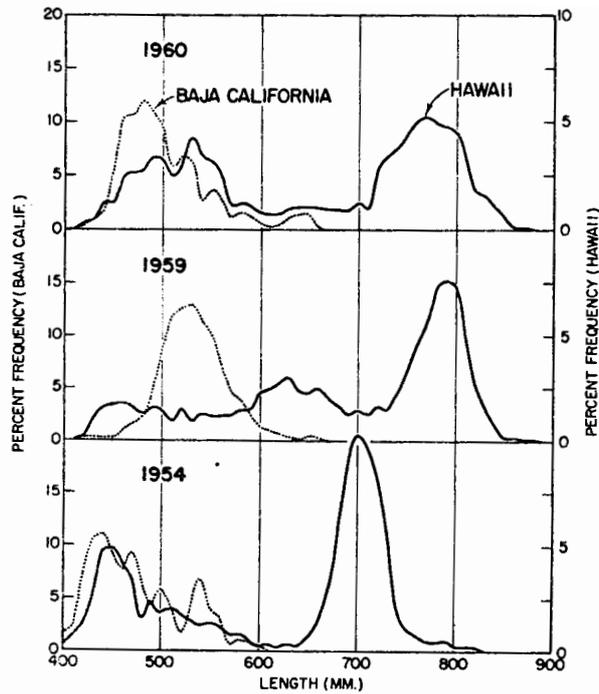


Figure 53.--Length-frequency distributions for skipjack tuna taken during the third quarter of the year from fisheries off Baja California and the Hawaiian Islands. (From Rothschild 1965.)

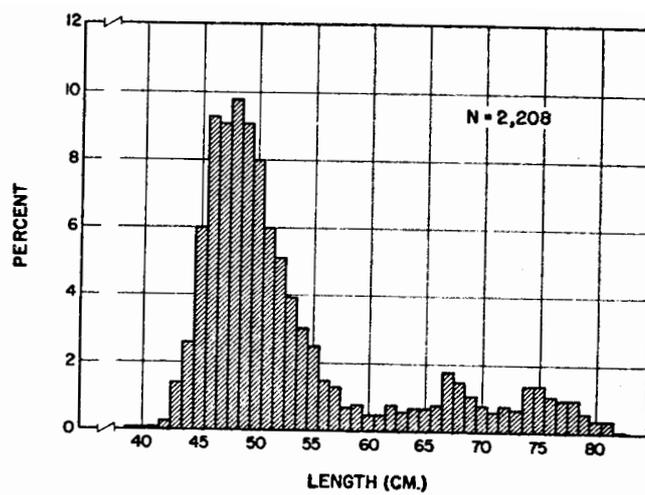


Figure 54.--Length-frequency distribution of skipjack tuna caught by live-bait fishing in the Marquesas Islands, 1957-59. (From Rothschild and Uchida 1968.)

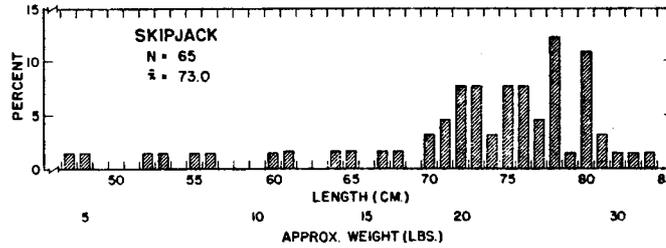


Figure 55.--Length-frequency distribution of skipjack tuna taken on experimental longline gear in the equatorial central Pacific Ocean by the National Marine Fisheries Service, Honolulu Laboratory, 1953. N = number measured, \bar{x} = average length. (From Shomura and Murphy 1955.)

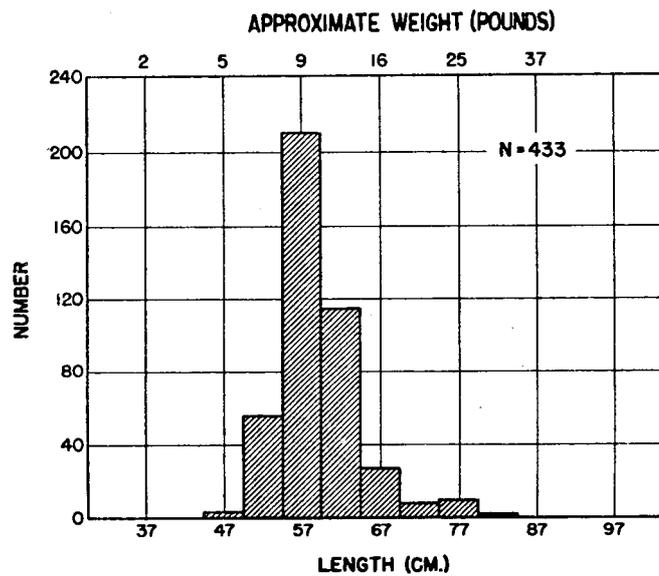


Figure 56.--Length-frequency distribution of skipjack tuna taken by longline gear during Japanese mother ship operations in the western equatorial Pacific, 1951. (From Murphy and Otsu 1954.)

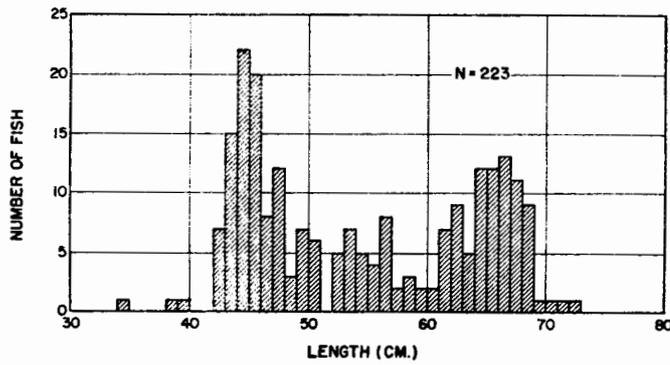


Figure 57.--Length-frequency distribution of skipjack tuna taken by trolling near the northern Marshall Islands, 1946-47. (From Higgins 1966, after Marr 1948.)

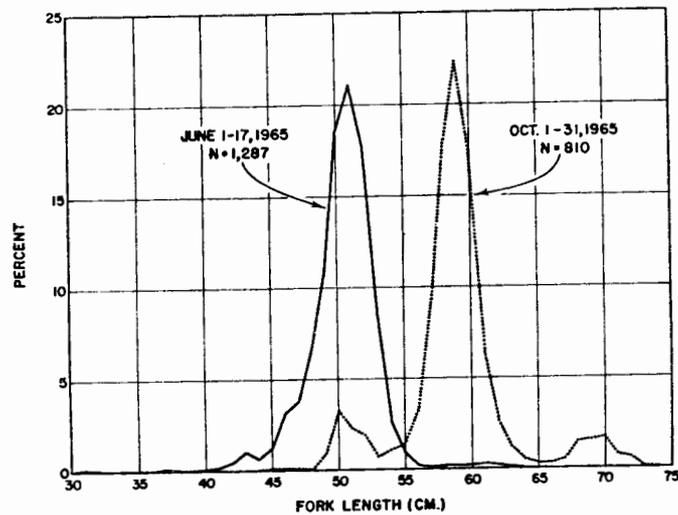


Figure 58.--Length-frequency distribution of skipjack tuna taken by the bait fishery in the Palau Islands, 1965. (From Higgins 1966.)

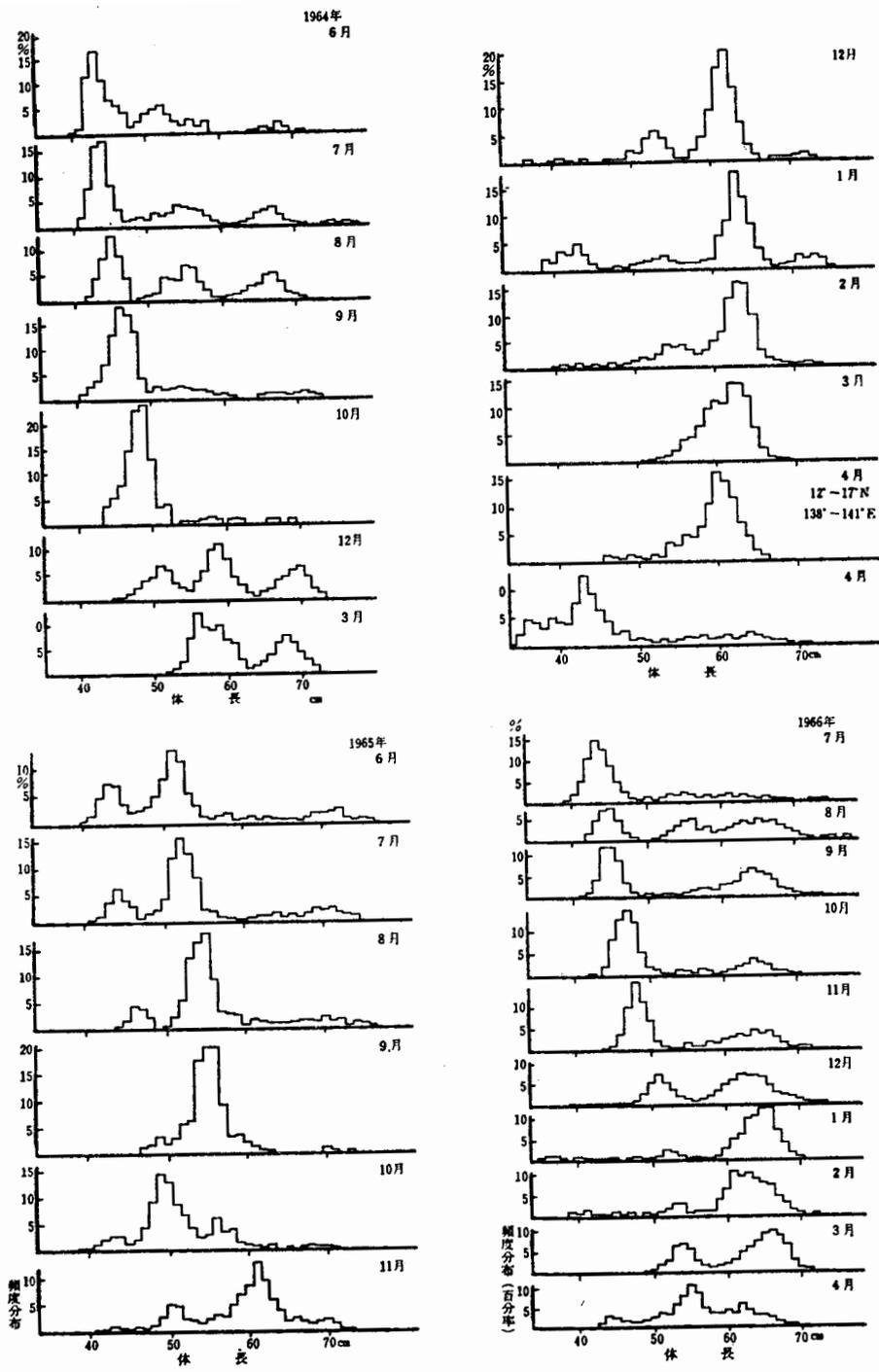


Figure 59.--Monthly length-frequency distribution of skipjack tuna caught by Japanese live-bait fishery in the adjacent seas of the Mariana and Palau Islands. (From Suda 1971, after Kasahara and Tanaka 1968.)

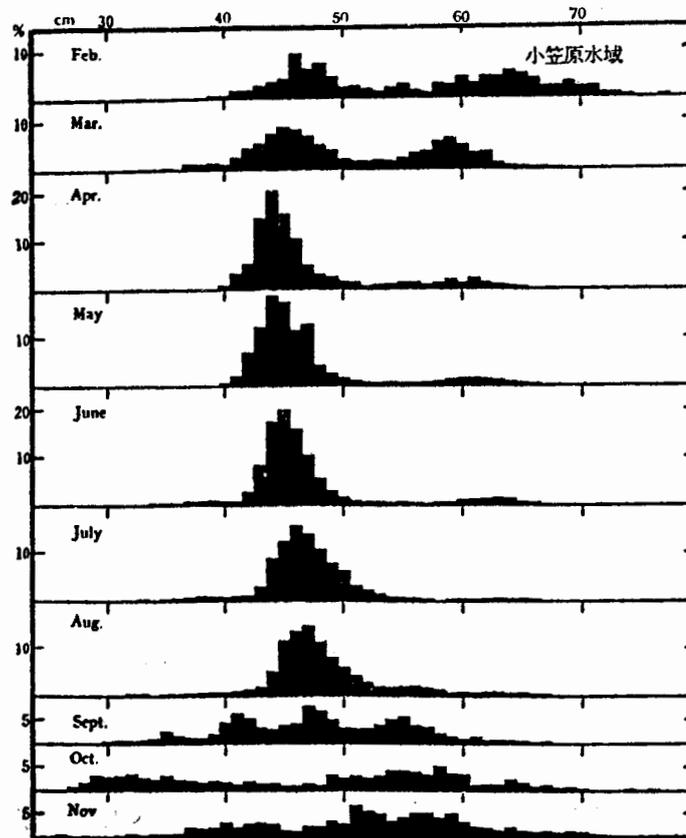


Figure 60.--Average monthly length-frequency distribution of skipjack tuna taken by the Japanese live-bait fishery adjacent to the Bonin Islands, 1951-55. (From Suda 1971, after Kawasaki 1964.)

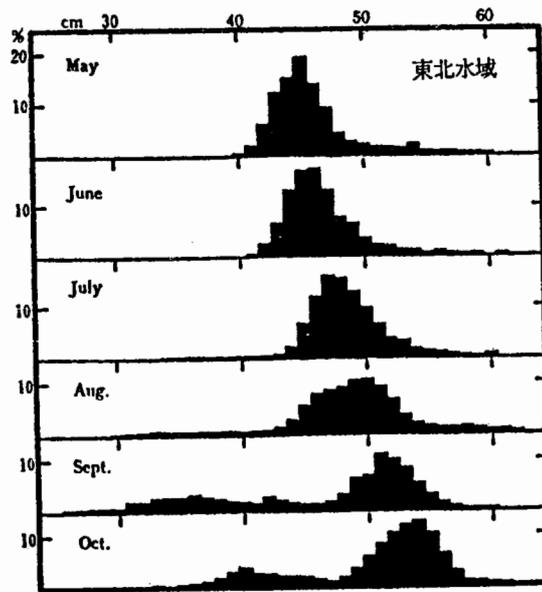


Figure 61.--Average monthly length-frequency distribution of skipjack tuna taken by Japanese live-bait fishery in the northeastern offshore area of Japan, 1951-55. (From Suda 1971, after Kawasaki 1964.)

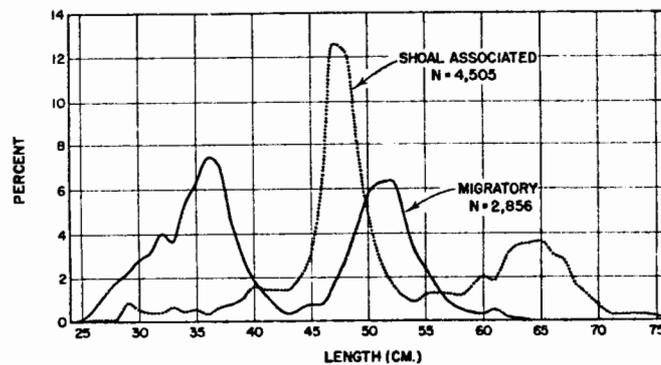


Figure 62.--Length-frequency distribution of skipjack tuna taken in the southwestern sea area of Japan, 1954, with nonmigratory (shoal associated) and migratory groups indicated. (From Higgins 1966, after Kawasaki 1955.)

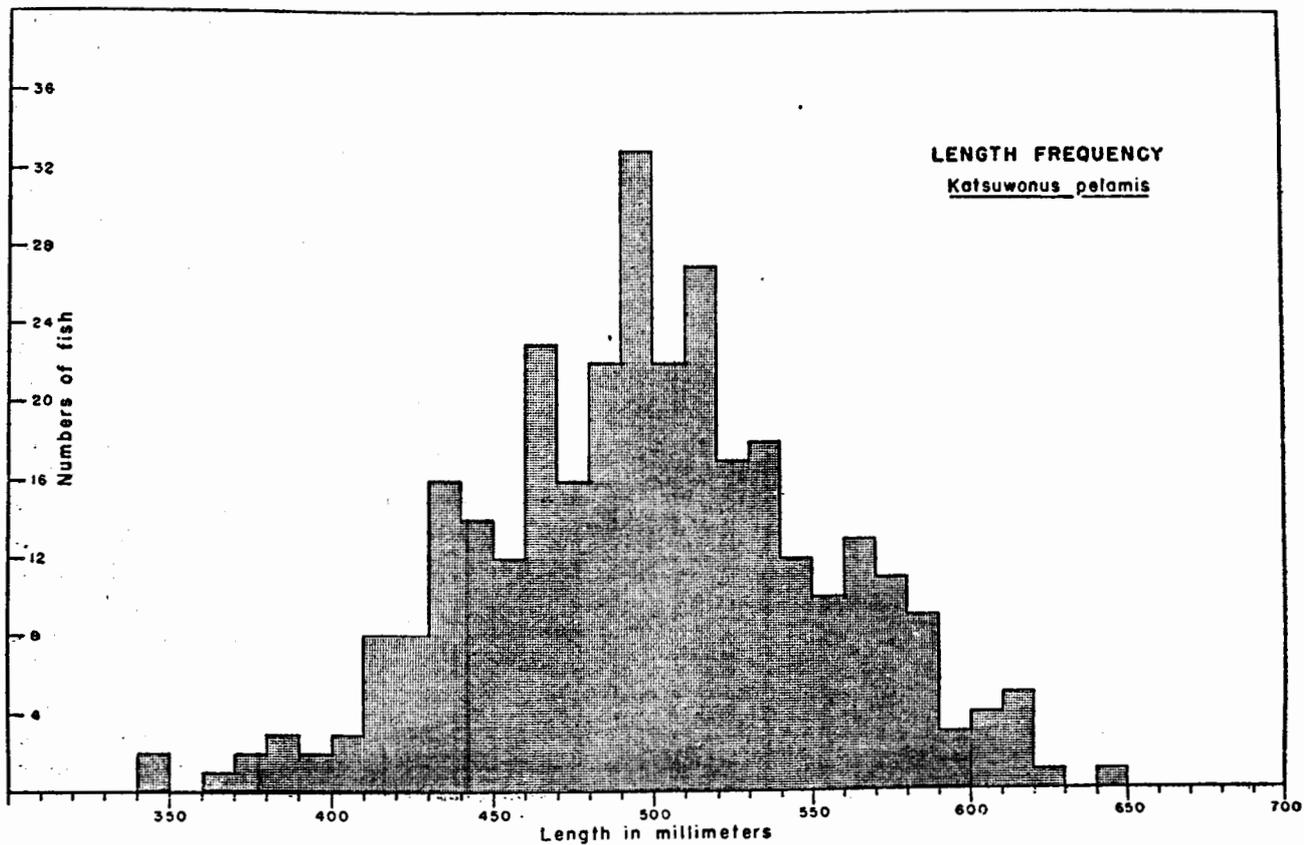


Figure 63.--Length-frequency distribution of skipjack tuna taken by trolling in the Sulu Sea area adjacent to the Philippines, 1947-48. (From Wade 1950.)

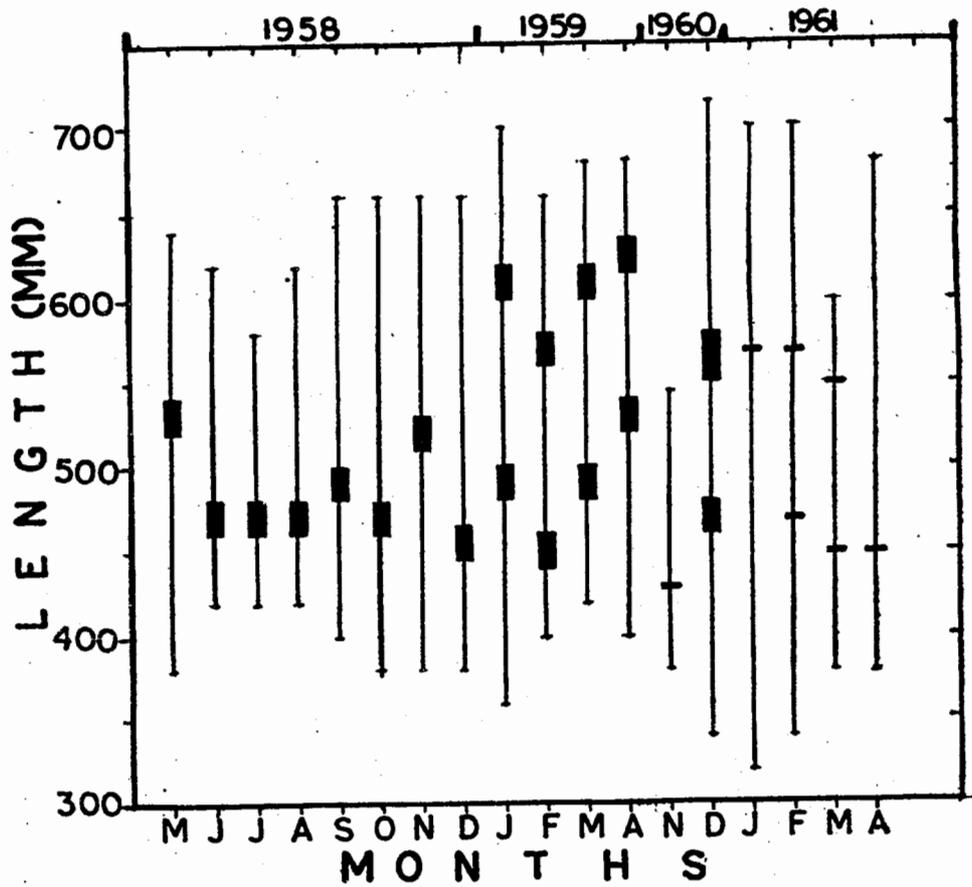


Figure 64.--Monthly length-composition of skipjack tuna landed at Minicoy, Indian Ocean, 1958-61. Horizontal black vertical position and bars indicate modes, and vertical thin lines indicate the size ranges for the months of observation. (From Jones and Silas 1963.)

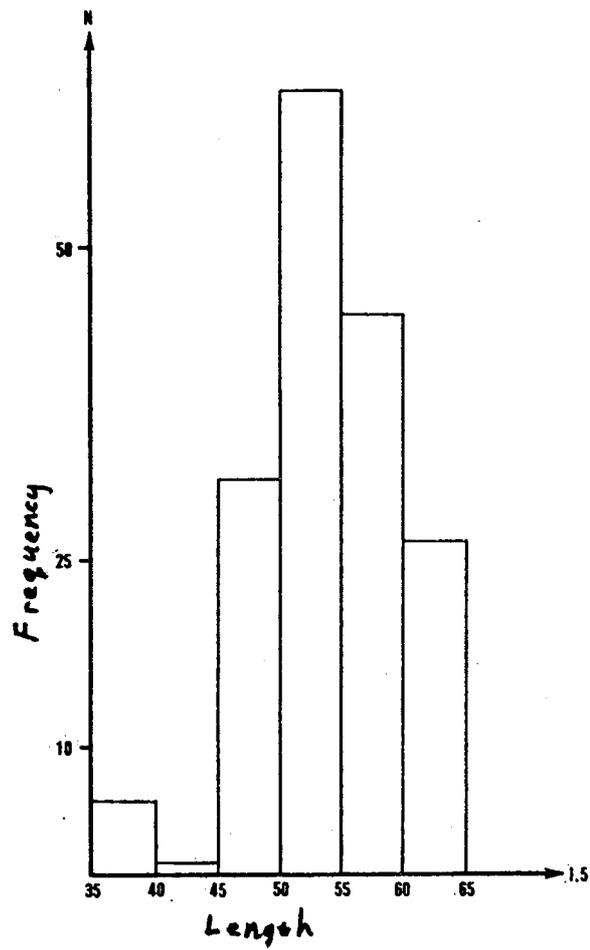


Figure 65.--Length-frequency distribution of skipjack tuna taken off Cape Vert. (From Postel 1963.)

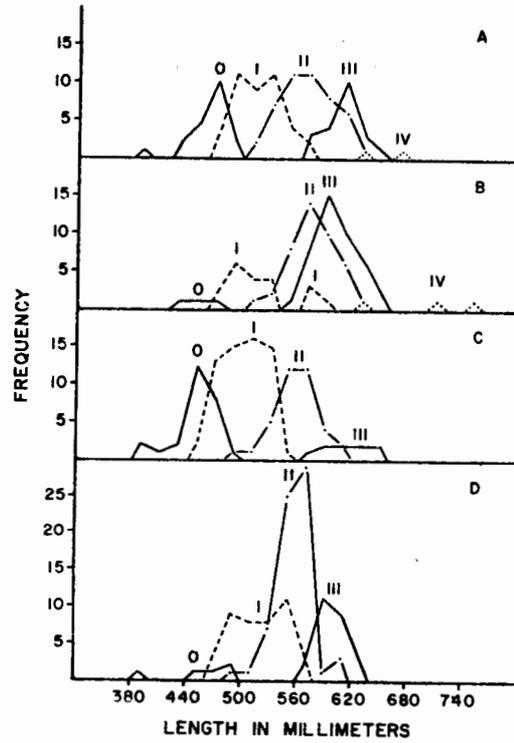


Figure 66.--Length-frequency distributions of aged skipjack tuna taken off North Carolina, USA, 1964-65. (From Batts 1972.)

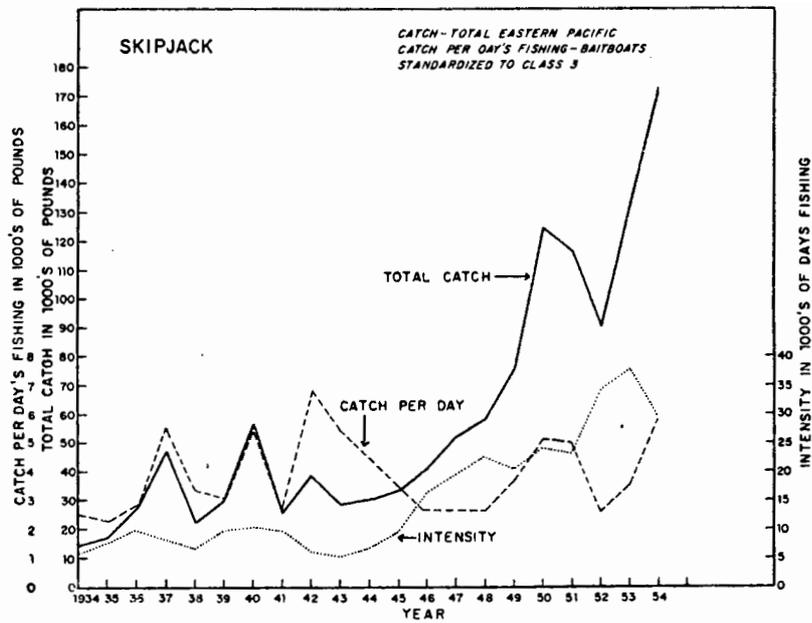


Figure 67.--Catch per standardized-day's fished, total catch, and calculated relative fishing intensity for skipjack tuna in the eastern Pacific Ocean, 1934-54. (From Shimada and Schaefer 1956.)

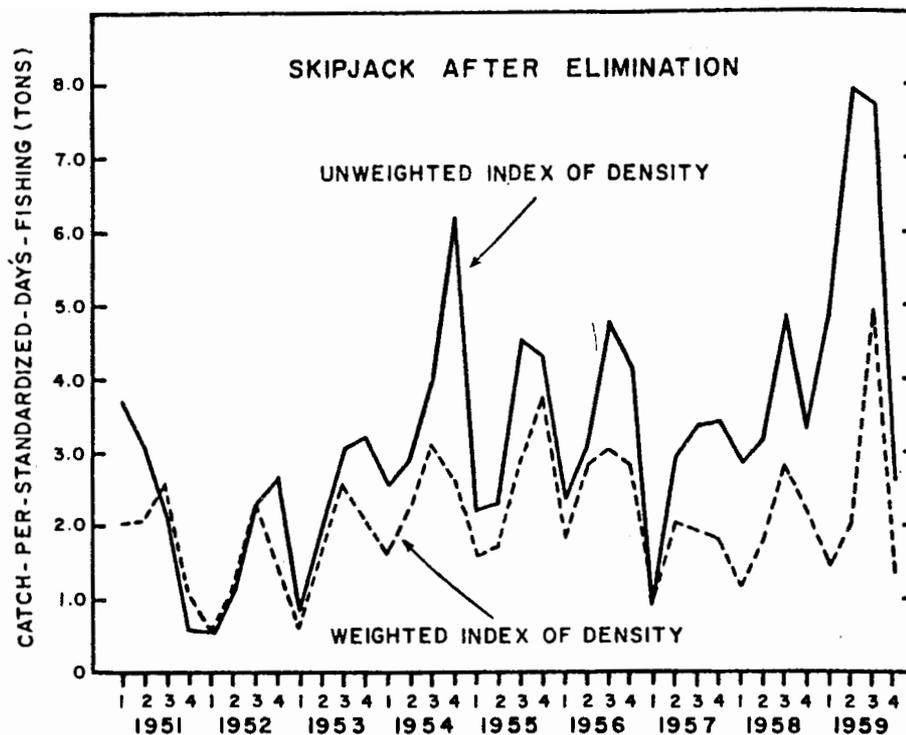


Figure 68.--Weighted and unweighted indices of abundance of skipjack tuna after elimination of lightly exploited areas in the eastern Pacific Ocean, by quarters, 1951-59. (From Calkins 1961.)

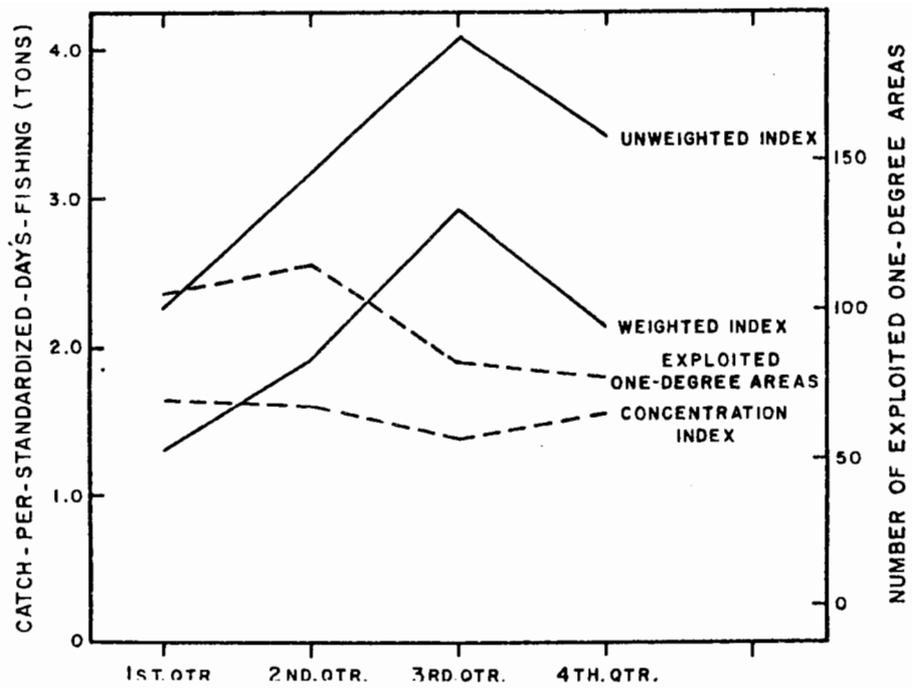


Figure 69.--Quarterly averages of indices of abundance and concentration and number of exploited one-degree areas, after elimination of lightly exploited areas, 1951-59. (From Calkins 1961.)

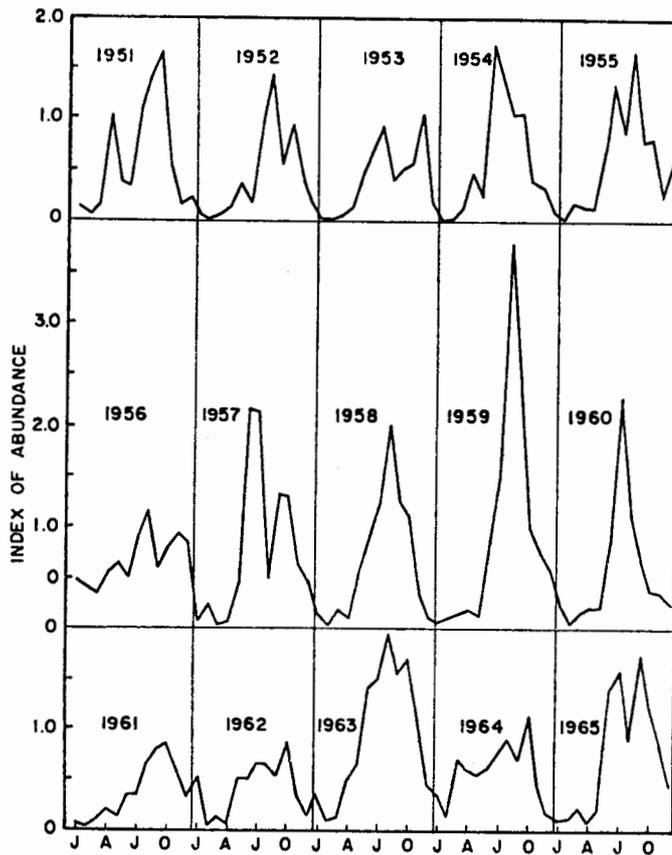


Figure 71A.--Monthly values of index of relative abundance for skipjack tuna in the northern fishery, eastern Pacific Ocean, 1951-65. (From Joseph and Calkins 1969.)

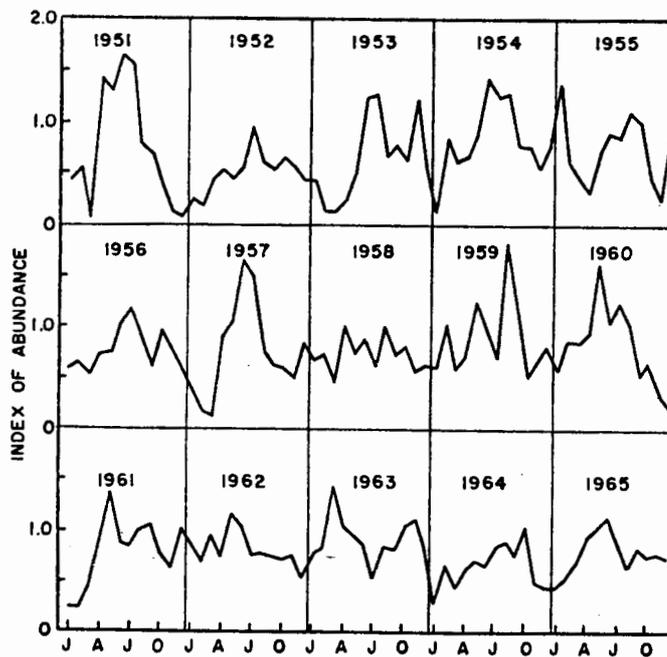


Figure 71C.--Monthly values of index of relative abundance for skipjack tuna in the combined fisheries, eastern Pacific Ocean, 1951-65. (From Joseph and Calkins 1969.)

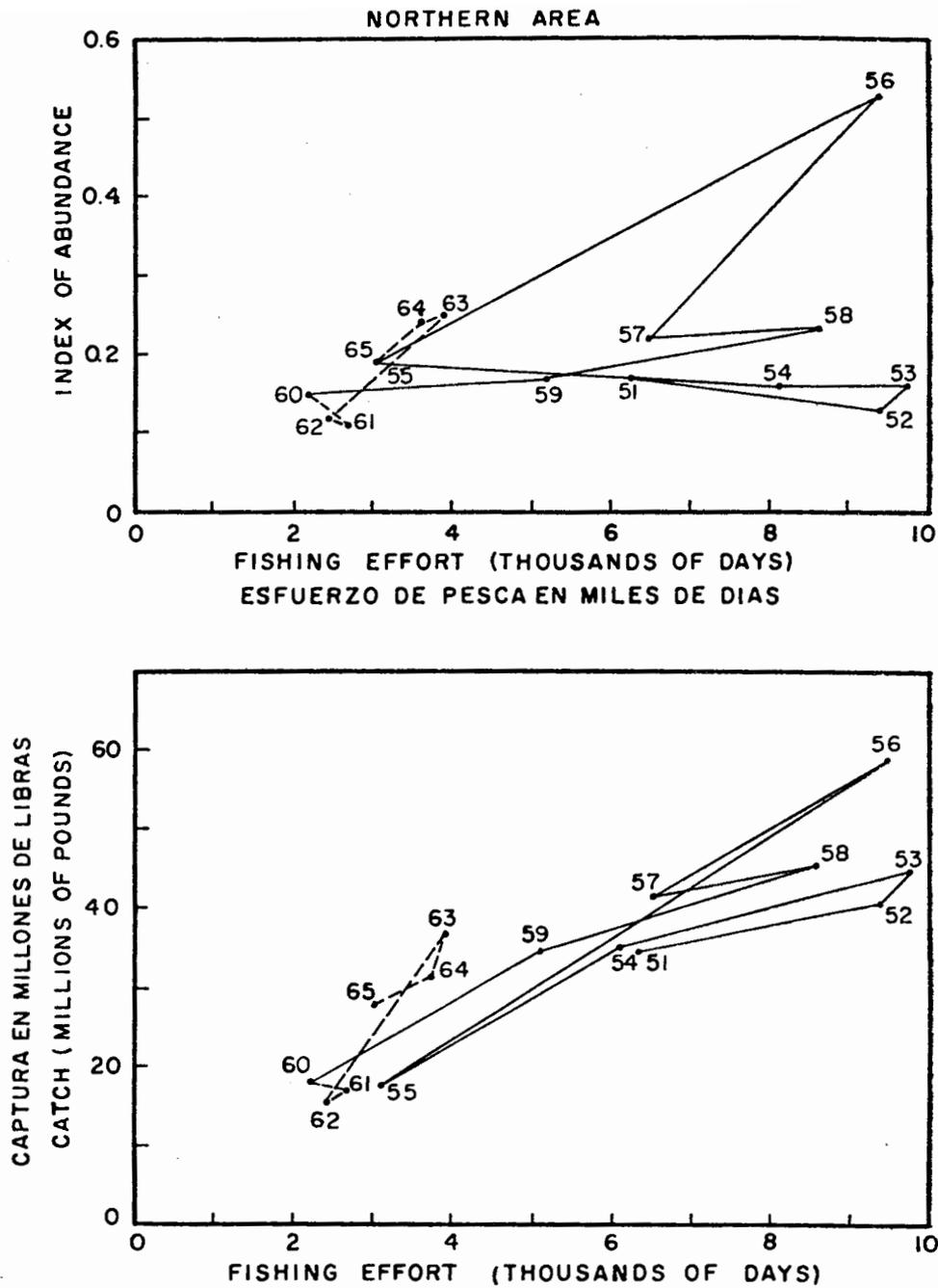


Figure 72A.--Index of relative abundance (upper panel) and total catch (lower panel) plotted against estimated total effort, 1951-65, for the northern fishery, eastern Pacific Ocean. (From Joseph and Calkins 1969.)

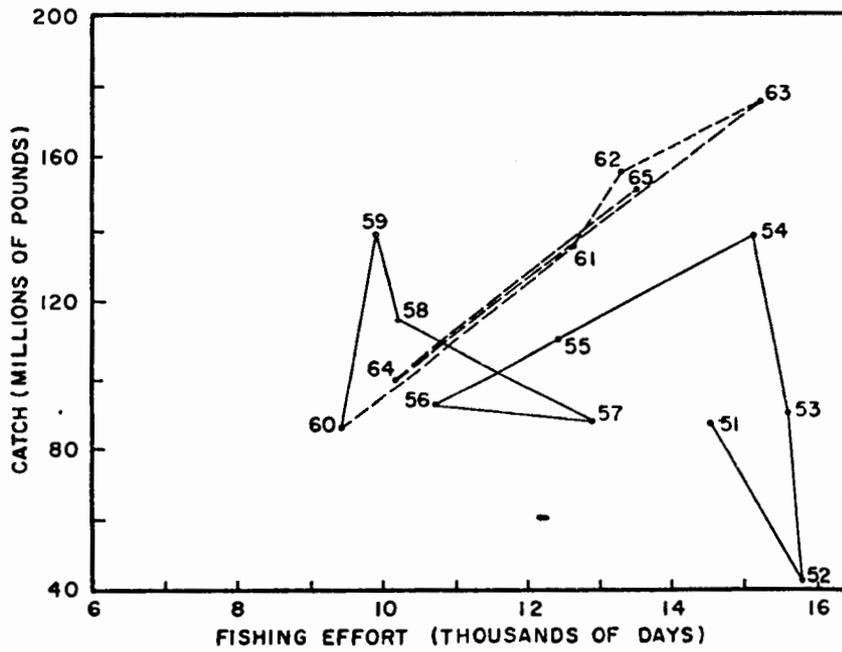
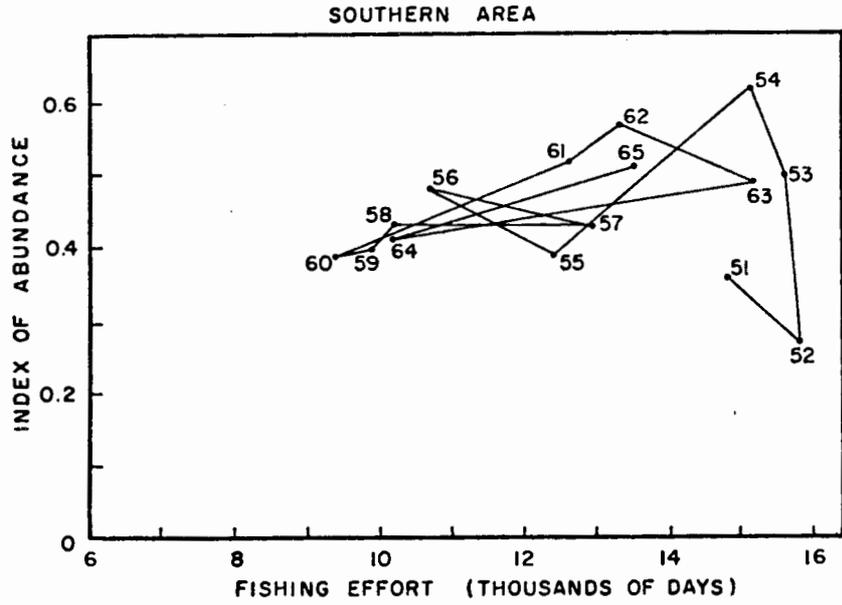


Figure 72B.--Index of relative abundance (upper panel) and total catch (lower panel) plotted against estimated total effort, 1951-65, for the southern fishery, eastern Pacific Ocean. (From Joseph and Calkins 1969.)

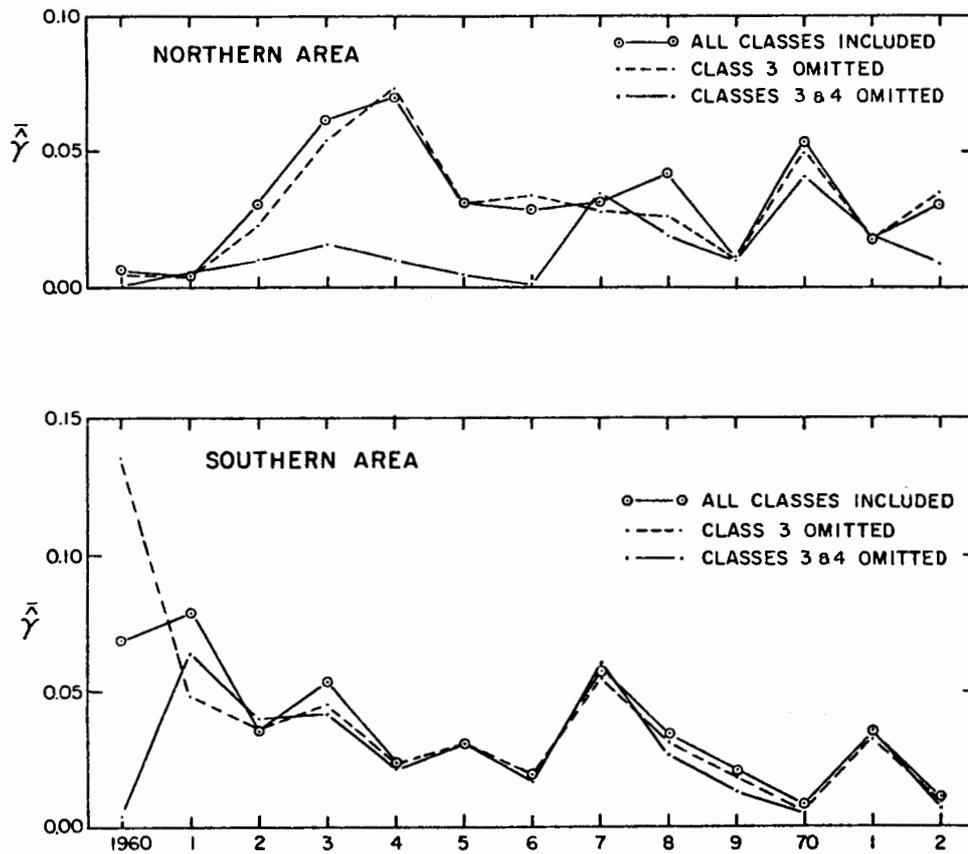


Figure 73.--Annual biomass indices of skipjack tuna in the traditional fishing areas of the eastern Pacific Ocean using different combinations of vessel classes, 1960-72. (From Pella and Psaropoulos 1975.)

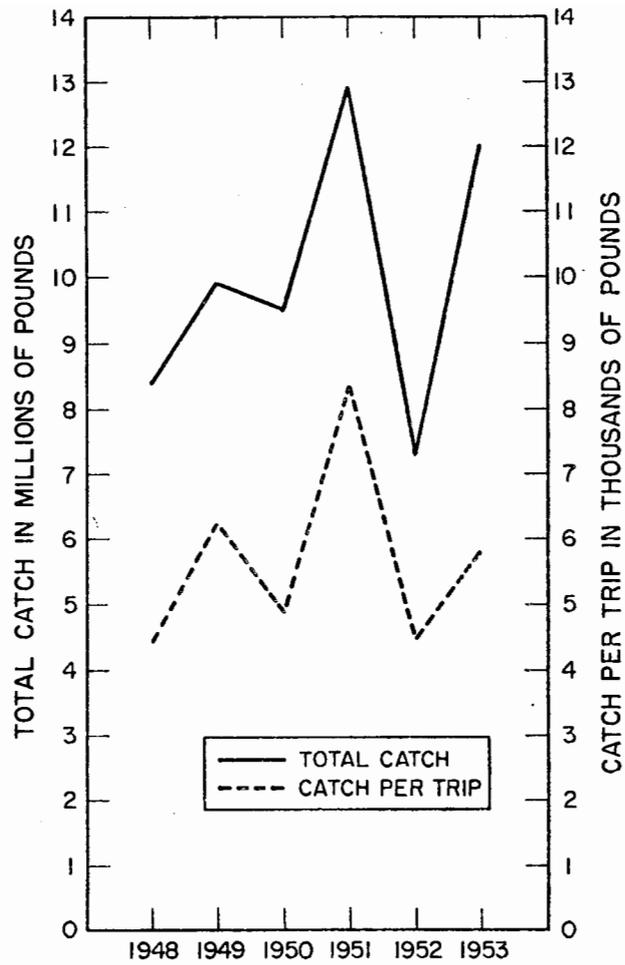


Figure 74.--Comparison between total annual catch and index of relative abundance of skipjack tuna in the Hawaiian fishery, 1948-53. (From Yamashita 1958.)

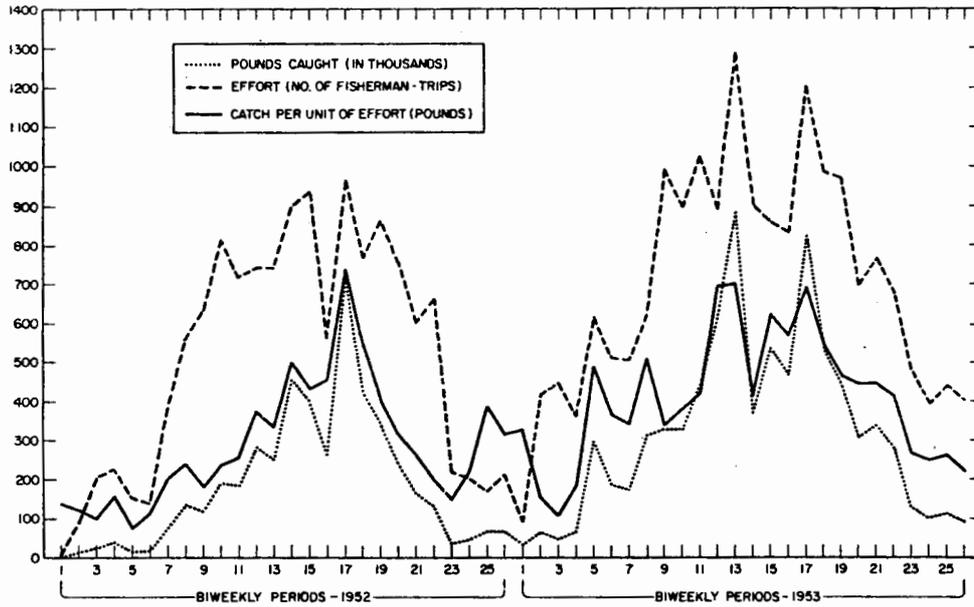


Figure 75.--Biweekly total catch, effort in effective day's fished, and index of relative abundance for skipjack tuna in the Hawaiian fishery, 1952-53. (From Shippen 1961.)

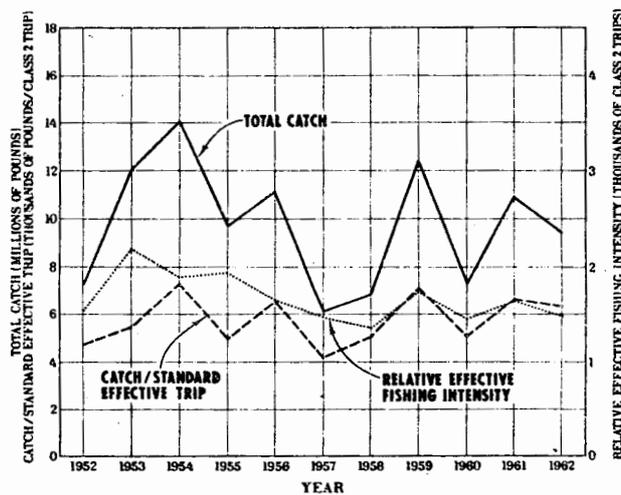


Figure 76.--Total catch, catch per standard effective trip, and the relative effective fishing intensity of skipjack tuna taken in the Hawaiian fishery, 1952-62. (From Uchida 1967.)

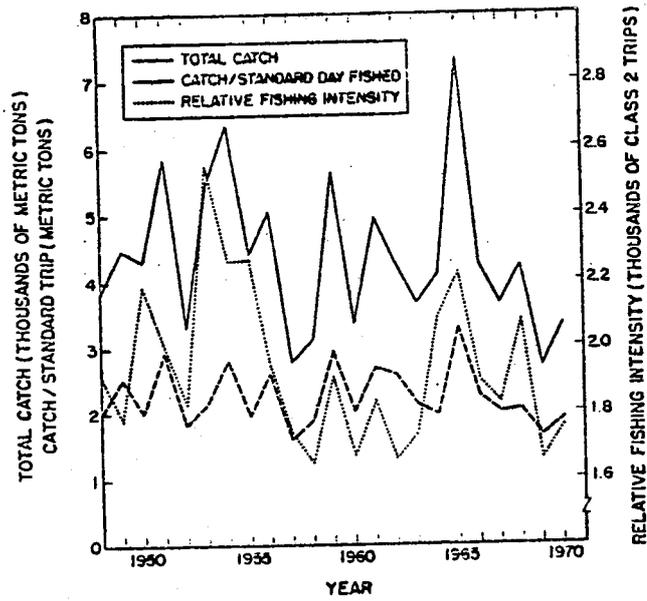


Figure 77.--Total catch, catch per standard day fished, and the relative fishing intensity of skipjack tuna taken in the Hawaiian fishery, 1948-70. (From Uchida, in press b.)

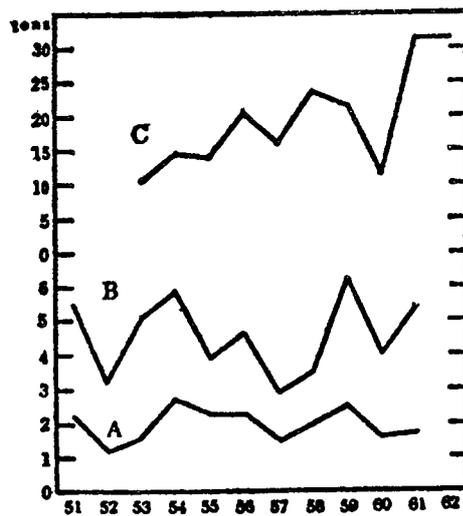


Figure 78.--Yearly indices of relative abundance in the Hawaiian fishery (A), the eastern Pacific fishery (B), and the Japanese north-eastern area fishery (C), 1951-62. (From Kawasaki 1965.)

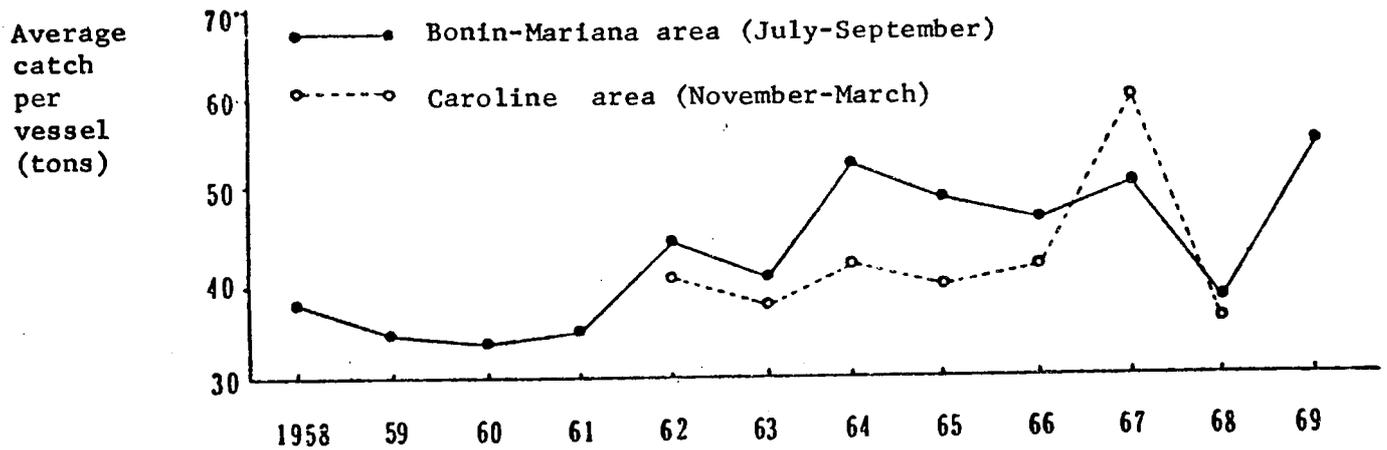


Figure 79.--Yearly indices of relative abundance of skipjack tuna for the Japanese southern water fishery, 1958-69. (From Iwasaki 1970.)

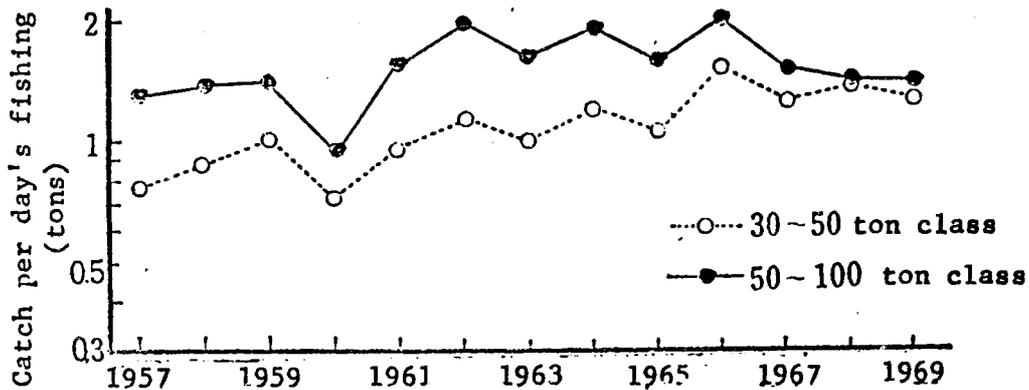


Figure 80.--Yearly indices of relative abundance of skipjack tuna in the Japanese coastal and offshore fisheries to the south and southwest of Japan, 1957-69. (From Kasahara 1971.)

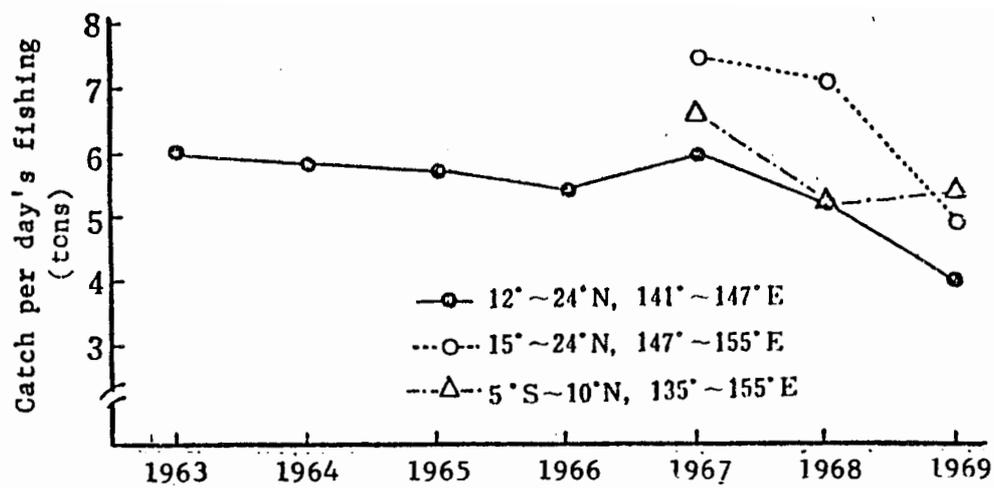


Figure 81.--Indices of relative abundance for the fishing season May-October of skipjack tuna in the Japanese southern water fishery, 1963-69. (From Kasahara 1971.)

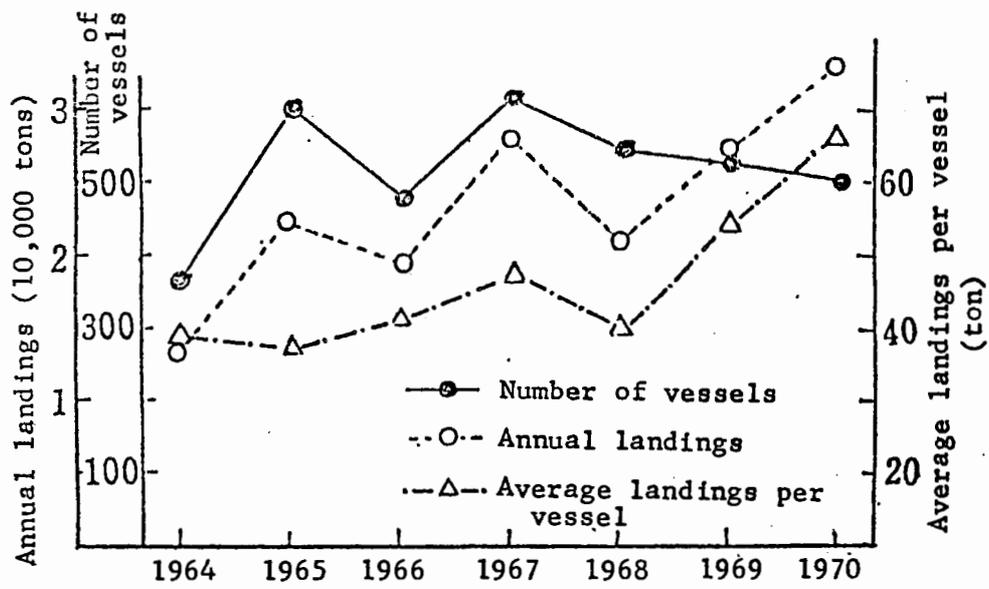


Figure 82.--The member of vessels, annual landings, and landings per vessel of skipjack vessels returning to Yaizu Port from the southern waters fishery, 1964-70. (From Kasahara 1971.)

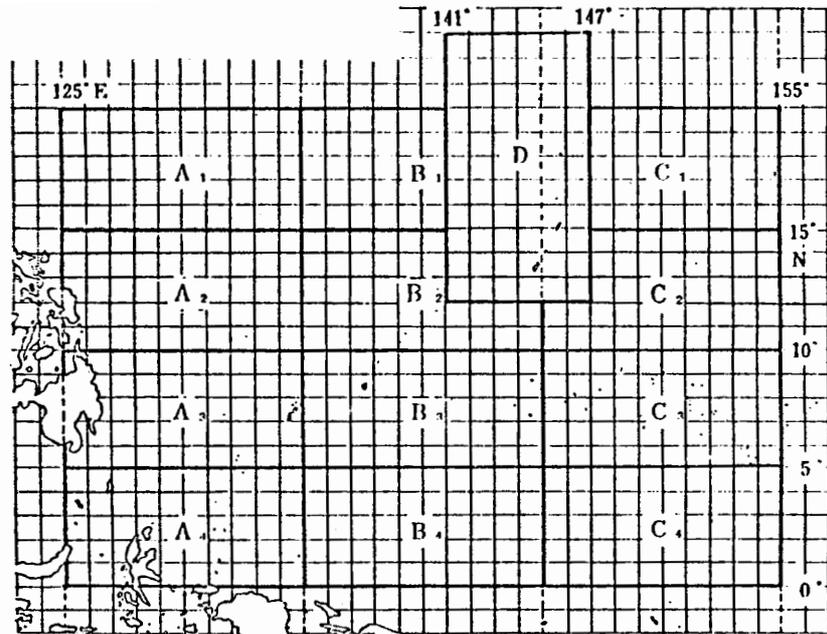


Figure 83.--The subdivisions of the principal fishing area in the southern waters from November-April. (From Kasahara 1971.)

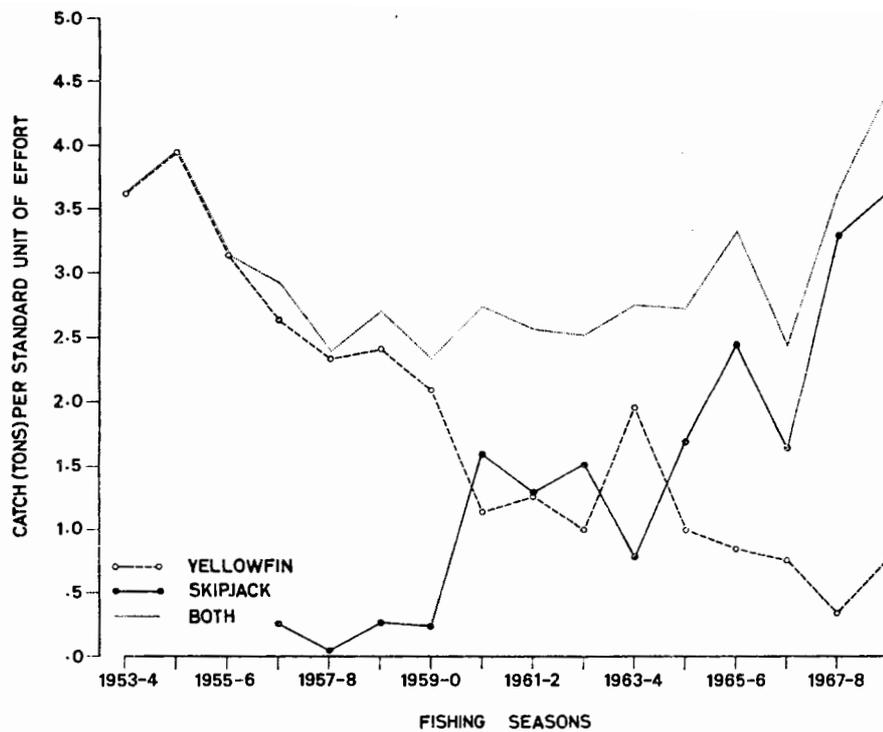


Figure 84.--Catch (tons) per standard day's landing of yellowfin and skipjack tunas and both species combined for the fishery off Benguela, Angola, 1953-54 through 1968-69 seasons. (From de Campos Rosado 1971.)

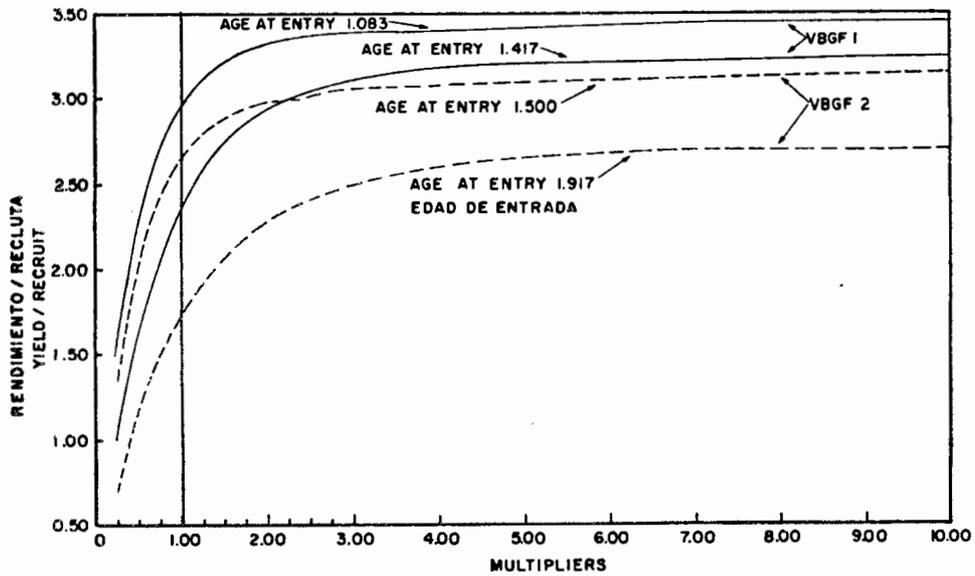


Figure 85A.--Yield per recruitment of skipjack tuna entering ages in the northern fishery, eastern Pacific Ocean, using growth parameters from ungrouped data (VBGF 1) and grouped data (VBGF 2) (From Joseph and Calkins 1969).

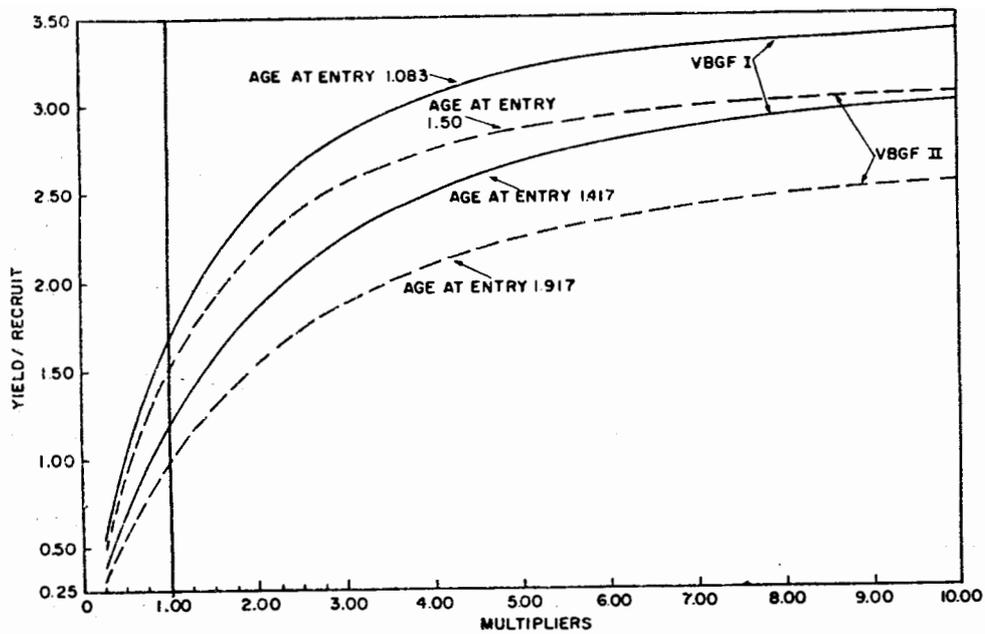


Figure 85B.--Yield per recruitment of skipjack tuna entering ages in the southern fishery, eastern Pacific Ocean, using growth parameters from ungrouped data (VBGF 1) and grouped data (VBGF 2) (From Joseph and Calkins 1969).

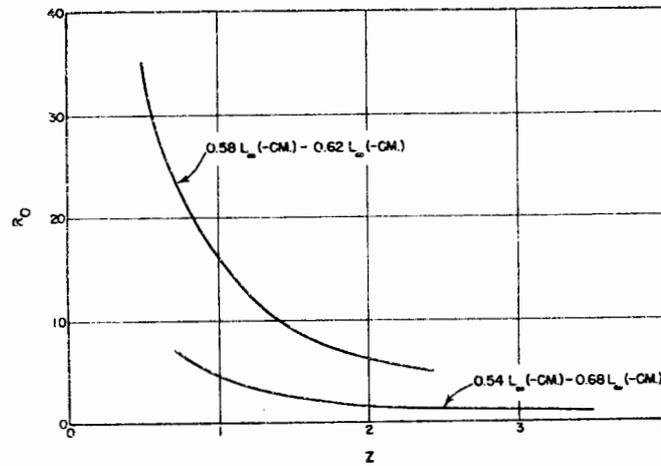


Figure 86.--Values of R_0 (ratio of yields under whole-life exploitation to yield under limited-life exploitation) for skipjack tuna, as a function of Z between 1 and 2. Upper curve in for assumed sojourn time of 2 months, lower curve for 6 months. (From Rothschild 1966.)

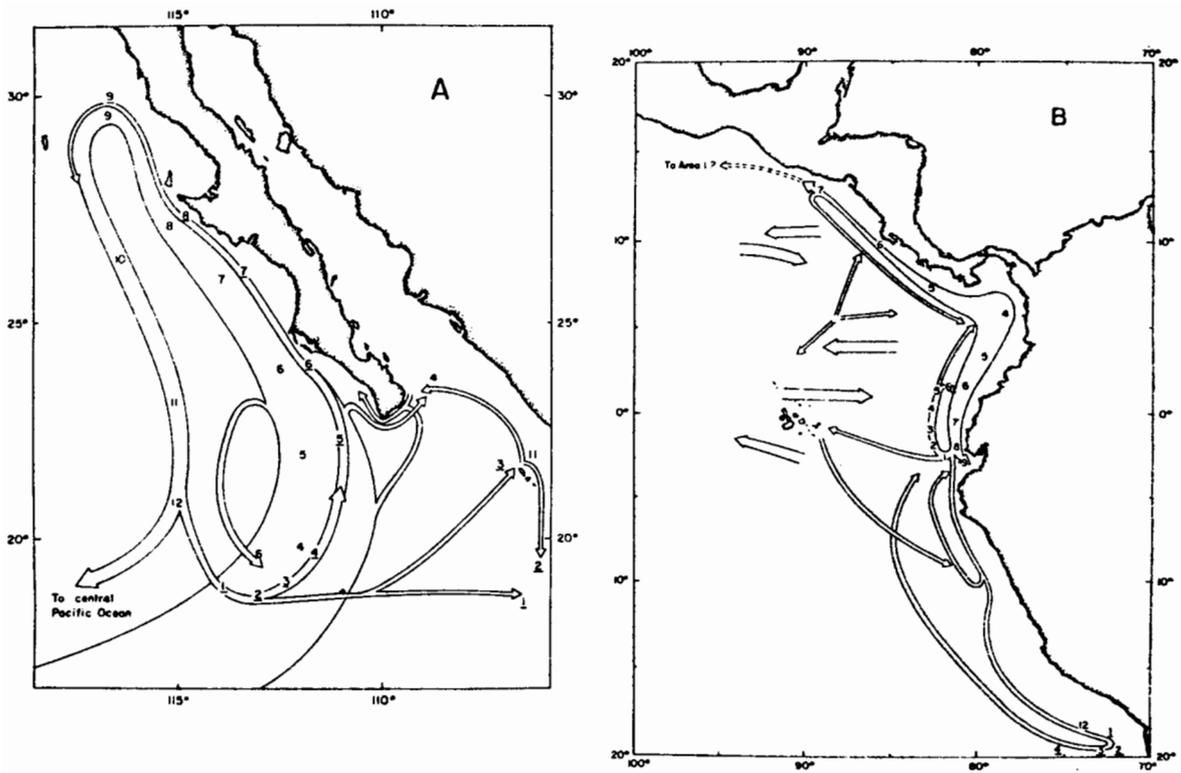


Figure 87.--Inshore migration of skipjack of the (A) northern fishery group (from Fink and Bayliff, 1970, Figure 89) and (B) southern fishery group (from Fink and Bayliff, 1970, Figure 90) based on tagging data; numbers refer to months. (From Williams 1972.)

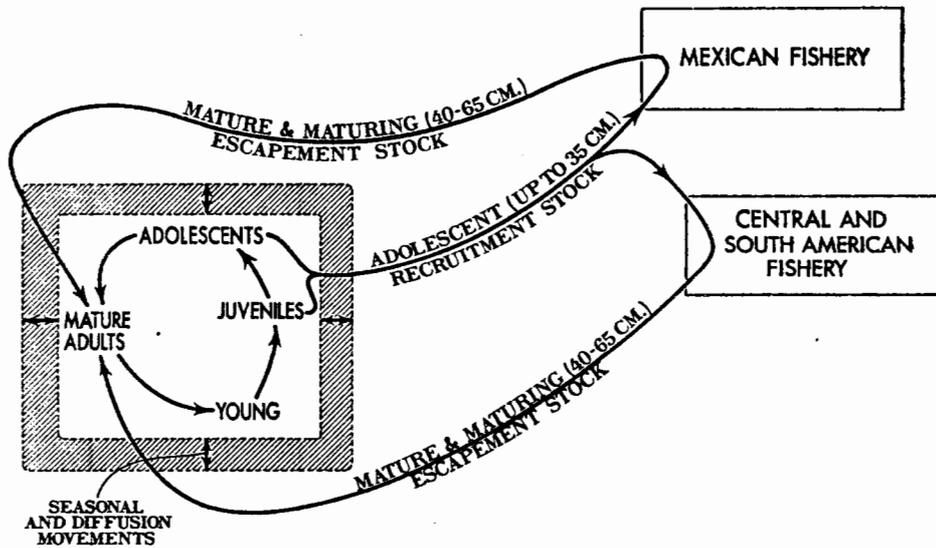


Figure 88.--Hypothesized origin and migration of skipjack tuna between the central Equatorial Pacific and the northern (Mexican) and southern (Central and South America) fisheries of the eastern Pacific Ocean. (From Rothschild 1965.)

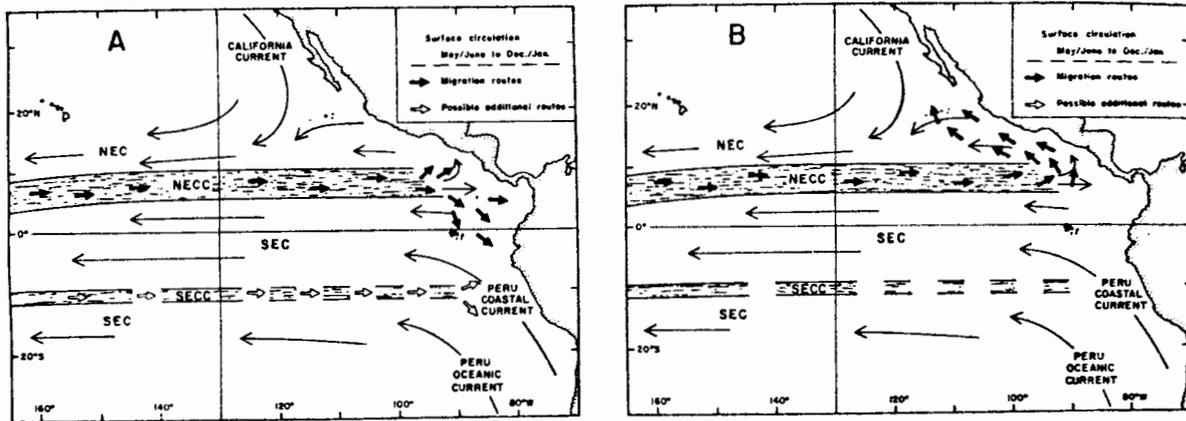


Figure 89A.--Passive migration model: (A) routes of young skipjack tuna into the southern fishery and (B) routes of young skipjack tuna into the northern fishery. NEC = North Equatorial Current; NECC = North Equatorial Countercurrent; SEC = South Equatorial Current; SECC = South Equatorial Countercurrent. (From Williams 1972.)

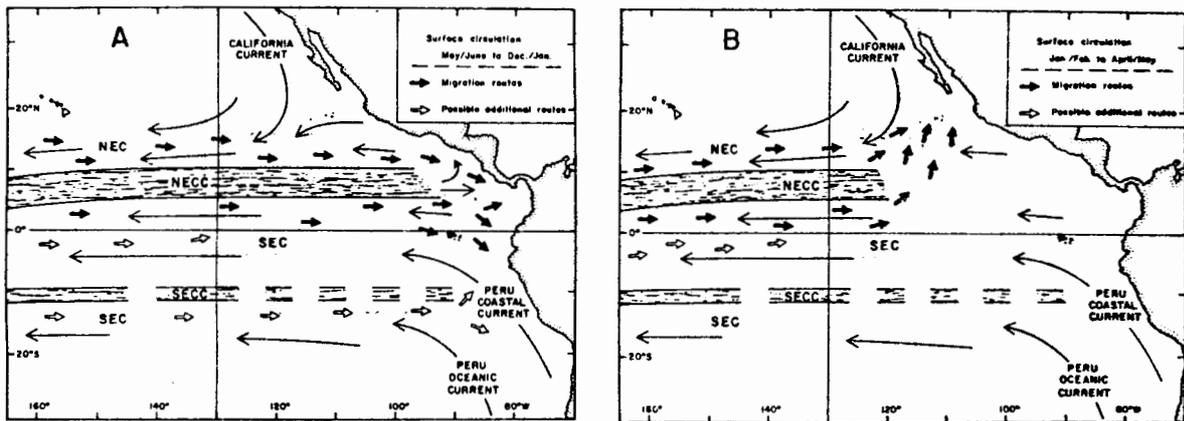


Figure 89B.--Active migration model: (A) routes of young skipjack tuna into the southern fishery and (B) routes of young skipjack tuna into the northern fishery. (From Williams 1972.)

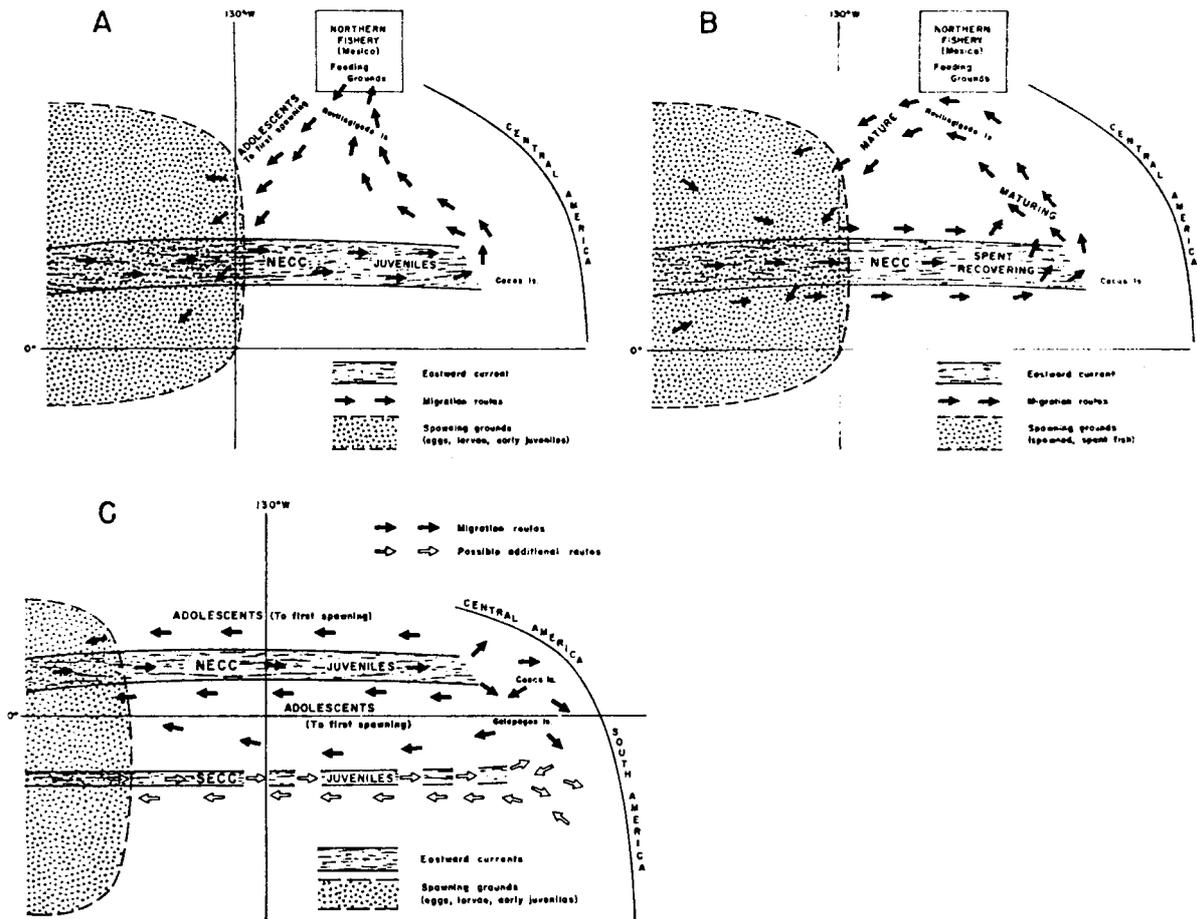


Figure 89C.--Schematic representation of gyral migration model: (A) routes of young skipjack tuna into the northern fishery, (B) routes of adult skipjack tuna of northern fishery, and (C) routes of young skipjack tuna into the southern fishery. (From Williams 1972.)

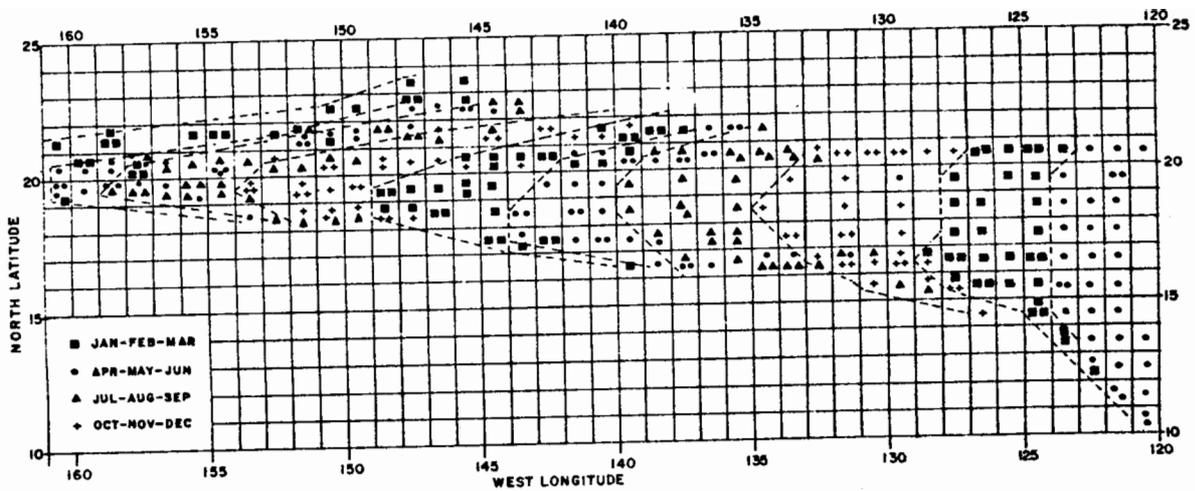


Figure 90.--Locations of drifting objects in June of the third model year that were introduced in each of the previous 30 months at long. 120°W. Dashed lines indicate most westerly location reached by objects introduced every quarter. (From Seckel 1972.)

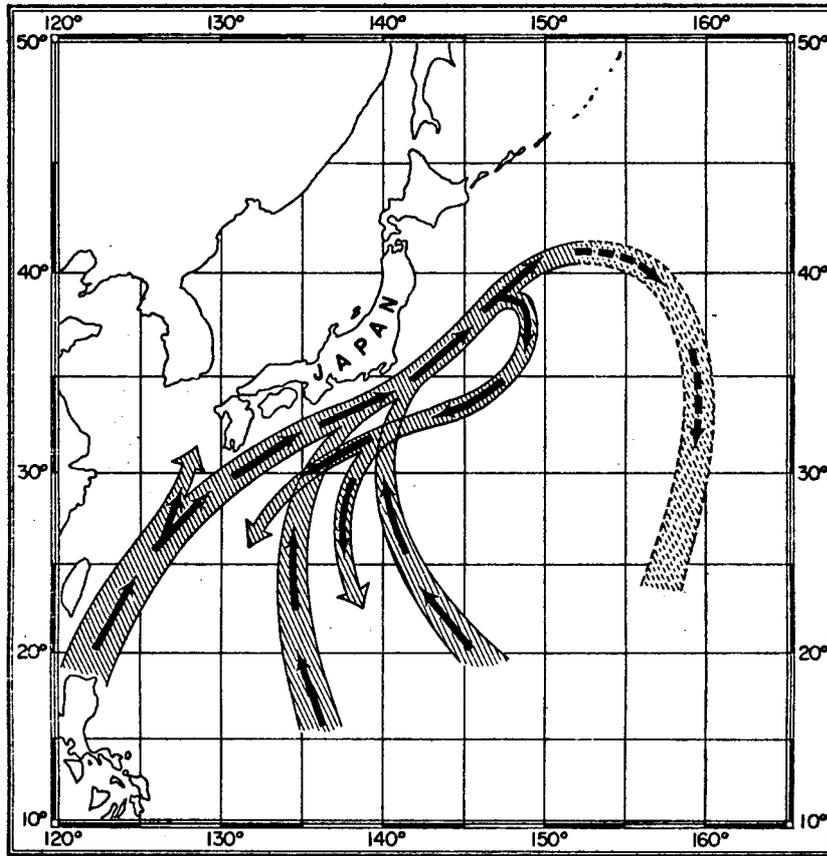


Figure 91.--Migration of skipjack tuna into the Japanese fisheries. (From Waldron 1963.)

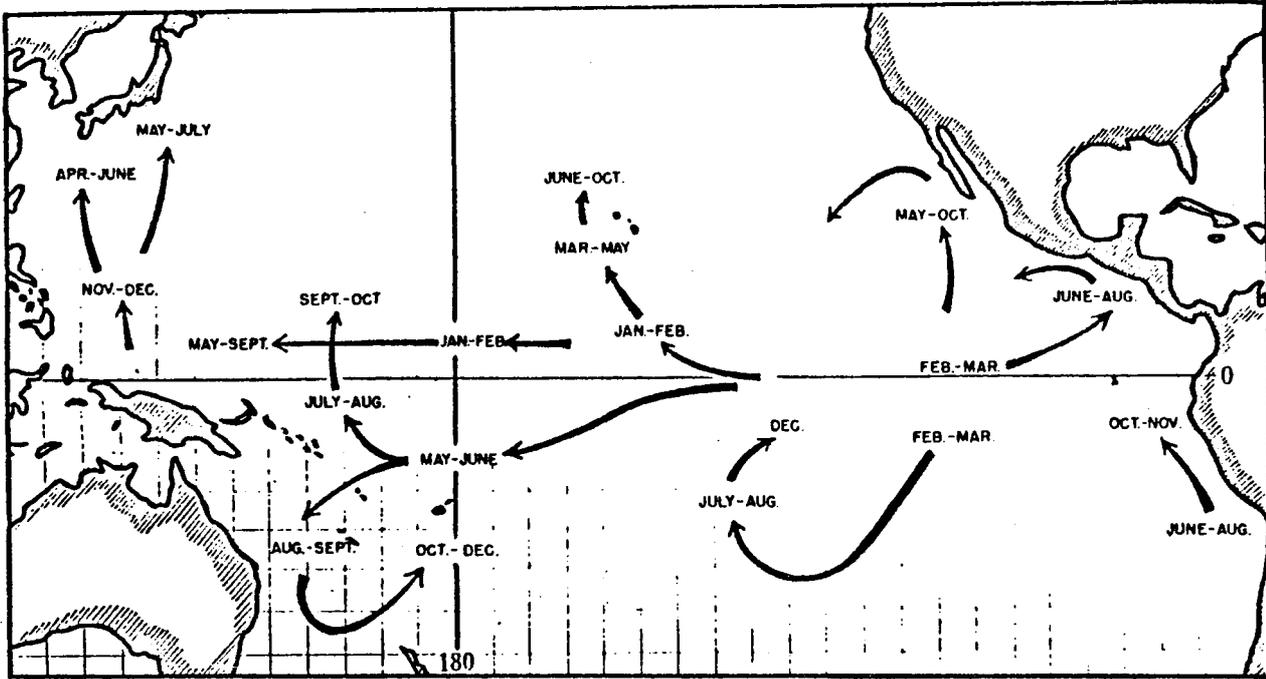


Figure 92.--Origin of and migration routes of skipjack tuna as postulated from tuna longline data. (From Kasahara 1968.)

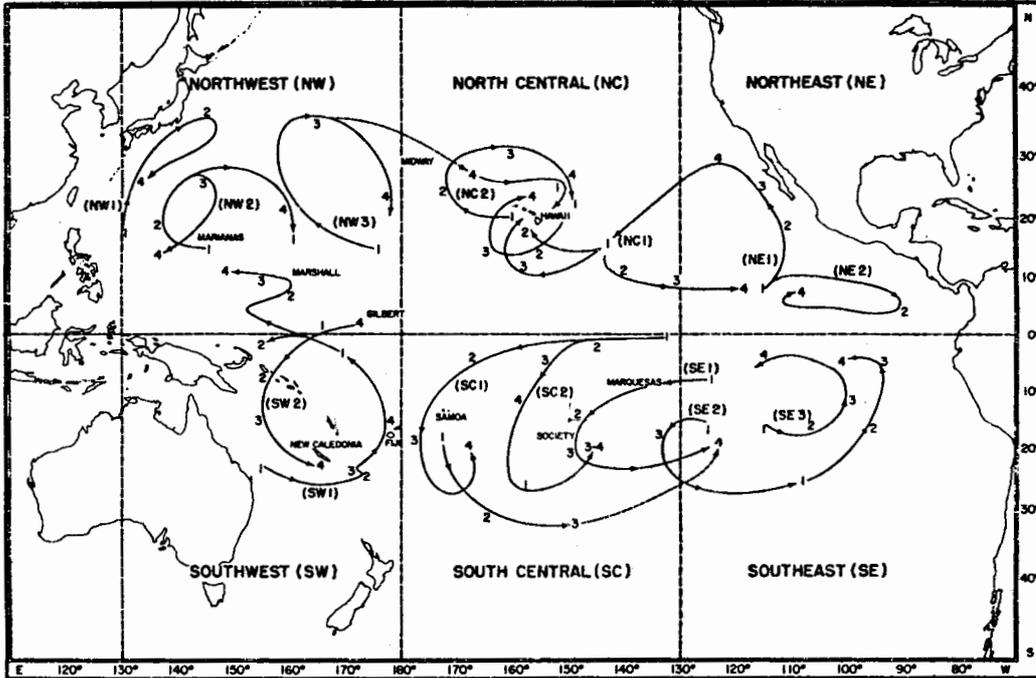


Figure 93.--Assumed movement of the various stocks of skipjack tuna in the Pacific Ocean. The numerals along the migratory routes represent quarters and locations of high catch-per-effort cells of skipjack tuna taken by the Japanese longline fishery, 1964-67. Stock designations are shown in parentheses. (From Matsumoto 1974.)