Synopsis of Biological Data on Skipjack Tuna, *Katsuwonus pelamis*

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ABSTRACT

This synopsis of biological data on skipjack tuna, *Katsuwonus pelamis*, includes information on nomenclature, taxonomy, morphology, distribution, reproduction, nutrition, growth, behavior, physiology, population structure, exploitation, and management of the species. Over 600 of the more important published and unpublished reports up to 1980, including some published in 1981, were consulted.

INTRODUCTION

There has been a major expansion in the world's skipjack tuna, *Katsuwonus pelamis*, fisheries in the past decade or so with the catch increasing better than twofold, from 320,000 metric tons (t) in 1969 to 699,000 t in 1979. While catches increased in both the Atlantic and Pacific Oceans, the most striking increase has been in the western central Pacific, which includes the Japanese southern water fishery and the fisheries of Papua New Guinea and the Solomon Islands. In this area the catches have risen over sevenfold, from 41,500 t in 1969 to 316,000 t in 1979.

The catch of skipjack tuna can probably be increased over present levels, but by how much is uncertain. To deal with the rational utilization of this resource as it approaches the level of full exploitation, it is imperative to have in hand all information concerning the biology, physiology, and various other factors relating to the fish and fishery.

Synopses of biological and technical data and information on the skipjack tuna by oceans were first compiled by Waldron (1963) for the Pacific Ocean, Postel (1963) for the Atlantic Ocean and Mediterranean Sea, and Jones and Silas (1963) for the Indian Ocean, and were presented at the Food and Agriculture Organization of the United Nations (FAO)-sponsored World Scientific Meeting on the Biology of Tunas and Related Species, 2-14 July 1962, at La Jolla, Calif. Forsbergh (1980) completed a synopsis of the species for the Pacific Ocean.

This paper reports current knowledge of the species in all oceans and reviews and evaluates, wherever appropriate, the results of past and recent research on the skipjack tuna through 1980.

1 IDENTITY

1.1 Nomenclature

1.11 Valid name

Katsuwonus pelamis (Linnaeus 1758)

1.12 Objective synonymy

Scomber pelamis Linnaeus 1758 (original description); Osbeck 1765; Bonnaterre 1788; Gmelin 1788; Rafinesque 1810
Scomber pelamys Bloch and Schneider 1801; Risso 1810; Cuvier 1829; Valenciennes 1836
Scomber pelamides Lacépède 1802
Thynnus pelamis. Risso 1826; Steindachner 1868; Hoek 1904
Thynnus vagans Lesson 1828 (original description), 1830
Thynnus pelamys. Cuvier and Valenciennes 1831; Temminck and Schlegel 1842; Cantor 1850; Bleeker 1856; Günther 1860, 1876; Playfair and Günther 1866; Day 1878; Lütken 1880; Macleay 1881; Eigenmann and Eigenmann 1891; Richard 1905; Cunningham 1910; Parona 1919
Pelamys pelamys. Bleeker 1862, 1865
Orcynnus pelamys. Poey 1868; Goode and Bean 1879; Goode 1884
Euthynnus pelamys. Jordan and Gilbert 1882; Carus 1893; Joubin and Le Danois 1924
Gymnosarda pelamis. Dresslar and Fesler 1889; Jordan and Evermann 1898; Jenkins 1904; Snodgrass and Heller 1905; Evermann and Seale 1907; Jordan 1907; de Miranda Ribeiro 1915; Meek and Hildebrand 1923; Breder 1929; Hornell 1935; Palma 1941
Euthynnus pelamis. Smitt 1893; Starks 1910; Tanaka 1912; Jordan and Jordan 1922; Bigelow and Welch 1925; Fowler 1928, 1938; Herre 1932; Deraniyagala 1933; Nobre 1935; Smith 1949; de Beaufort and Chapman 1951; Bigelow and Schroeder 1953; Steinitz and Ben-Tuvia 1955; Fourmanoir 1957; Bailey et al. 1960, 1970; Collette and Gibbs 1963; I. Nakamura 1965; Robins et al. 1980
Katsuwonus pelamys. Kishinouye 1915; Frade and de Buen 1932; Le Gall 1934; Morrow 1957
Gymnosarda pelamys. Thompson 1918; Barnard 1925

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Katsuwonus pelamis. Kishinouye 1923; de Buen 1926, 1930, 1935, 1958; Jordan et al. 1930; Soldatov and Lindberg 1930; Ehrenbaum 1936; Seale 1940; Serventy 1941; Godsil and Byers 1944; Nichols and Murphy 1944; Fowler 1945; LaMonte 1945; Clemens and Wilby 1946; Hildebrand 1946; Brock 1949; Rivas 1949, 1951; Herre 1953; Belloc 1955; Munro 1955, 1958; Briggs 1960; Jones and Silas 1960, 1963, 1964; Schultz 1960; Postel 1963, 1964; Talbot 1964; Whitley 1964; Williams 1964; Collette 1978

Katsuwonus vagans. Jordan et al. 1930; Barnhart 1936; Okada and Matsubara 1938; Fowler 1949

Katsuwonis pelamis. Herre 1933 [typographical error?]

Euthynnus (*Katsuwonus*) *pelamis*. Fraser-Brunner 1950; Mendis 1954; Bini and Tortonese 1955; Williams 1956; Scaccini et al. 1975

1.2 Taxonomy

1.21 Affinities

Phylum Vertebrata
  Subphylum Craniata
    Superclass Gnathostomata
      Series Pisces
        Class Teleostomi
          Subclass Actinopterygii
            Order Perciformes
              Suborder Scombroidei
                Family Scombridae
                  Subfamily Scombrinae
                    Tribe Thunnini
                      Genus *Katsuwonus*
                        Species *pelamis*

The Family Scombridae was defined by Regan (1909) and further clarified by Starks (1910), who divided it into five subfamilies: Scombrinae, Scomberomorinae, Acanthocybinae, Sardinae, and Thunninae. Kishinouye (1915) divided Regan's Scombridae into three Families: Scombridae, Cybiidae, and Thunnidae. He subsequently (1917) split Thunnidae into two Families, Thunnidae and Katsuwonidae, and placed both into a newly erected Order Plecostei on the basis of their well-developed subcutaneous vascular system. Takahashi (1924), however, rejected Kishinouye's new order, pointing out that the subcutaneous vascular system was not unique to tunas, but was also found in swordfish, *Xiphias gladius*; dolphin, *Coryphaena hippurus*; stargazer, *Gnathagus elongatus*; goby, *Aprocryptes chinensis*; and puffer, *Sphoeroides rubriceps*. These two views have persisted to the present.

Berg (1940) followed Kishinouye in placing the tunas into a single Family Thunnidae and renamed the Order Thunniformes. He relegated Katsuwonidae to subfamily status as Auxidini. Some investigators retained the Family Thunnidae, while relegating Katsuwonidae to generic status (Fowler 1945; Herre 1953; Morrow 1954, 1957; Munro 1955). Zharov (1967) divided the Thunnidae into two subfamilies, Thunninae and Katsuwoninae, while others recognized the Families Thunnidae and Katsuwonidae (Jordan and Hubbs 1925; Barnhart 1936; Kamohara 1941; Morice 1953; Godsil 1954).

Most other investigators followed Regan and Stark's classification, maintaining the Family Scombridae as a natural unit (Barnard 1925; Fowler 1928; Hildebrand 1946; Schultz and Stearn 1948; Smith 1949; Fraser-Brunner 1950; de Beaufort and Chapman 1951; Rivas 1951; Jones and Silas 1960, 1963, 1964; Schultz 1960; Collette and Gibbs 1963; Waldron 1963; I. Nakamura 1965; Gibbs and Collette 1967; Collette and Chao 1975; Collette 1978). Fraser-Brunner (1950) recognized only the subfamilies Gasterochismatinae and Scombrinae. I. Nakamura (1965) added a third subfamily, Thunninae, but Collette and Chao (1975) reverted to two subfamilies, as proposed by Fraser-Brunner, and split the Scombrinae into two tribes, placing Scombrini (the more primitive mackerels) and Scomberomorini (the Spanish mackerels) in one group and Sardini (the bonitos) and Thunnini in the other (Fig. 1).

Opinion on the generic name also has differed over the years and the differences continue to this day. Jordan and Gilbert (1882) credit Lütken for establishing the genus *Euthynnus* and separating *alliteratus* and *pelamys* from the other tunas largely on the basis of an important osteological character, the trellis formed on a portion of the abdominal vertebrae. Kishinouye (1915) established the genus *Katsuwonus* and separated it from *Euthynnus* based on differences in internal characters. Since then many others have recognized *Katsuwonus* (de Buen 1930; Jordan et al. 1930; Herre 1932; Serventy 1941; Godsil and Byers 1944; Clemens and Wilby 1946; Hildebrand 1946; Rivas 1951; Godsil 1954; Belloc 1955; Munro 1955; Briggs 1960; Gosline and Brock 1960; Jones and Silas 1960; Schultz 1960; Postel 1964; Talbot 1964; Whitley 1964; Zharov 1967; Collette and Chao 1975; Collette 1978).

Fraser-Brunner (1950), in his attempt to maintain the Family Scombridae as a natural unit, synonymized *Katsuwonus* with *Euthynnus*, as did other investigators (de Beaufort and Chapman 1951; Bigelow and Schroeder 1953; Mendis 1954; Bini and Tortonese 1955; Williams 1956; Bailey et al.

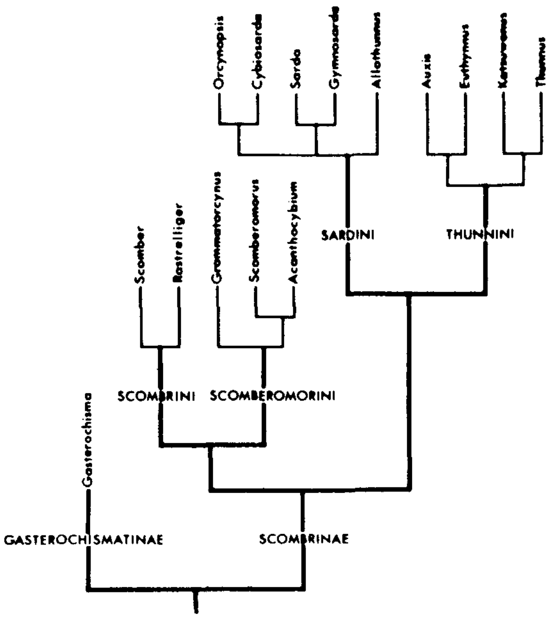

Figure 1.—The subfamilies, tribes, and genera of the Scombridae (from Collette and Chao 1975).

1960, 1970; Collette and Gibbs 1963; I. Nakamura 1965; Robins et al. 1980). Of those who relied heavily upon internal characters, I. Nakamura (1965) supported his choice on the basis that in both genera the atlas was not reduced in size and the alisphenoids did not meet ventrally at the median line. Robins et al. (1980), noting that the structure of the bony shelf that divides the anterior six vertebrae into dorsal and ventral portions is shared by *Auxis*, *Euthynnus*, and *Katsuwonus* only, suggested that the latter was more intimately related to *Euthynnus* than to *Thunnus*.

Because of the close relationship of these two genera, similarities in a number of characters such as noted above, are expected; however, the differences pointed out by Kishinouye (1923), Godsil and Byers (1944), Godsil (1954), and Collette (1978) seem large enough to justify their separation. These differences include the following:

1) The dorsal and ventral branches of the cutaneous artery in *Katsuwonus* are about equally developed, instead of having the ventral branch short and dendritic as in *Euthynnus*.
2) The trellis on the vertebral column moves the aorta ventrally a distance slightly less than the depth of a centrum in *Katsuwonus*; less than in *Auxis* and *Euthynnus*, but more than in *Thunnus*.
3) The liver in *Katsuwonus* resembles that of the yellowfin group of *Thunnus* more than *Euthynnus* and *Auxis* because the right lobe does not extend the length of the body cavity.
4) Hepatic veins are absent from the ventral surface of the liver in *Katsuwonus*, as opposed to *Auxis* and *Euthynnus*.
5) The prefontals are smaller in *Katsuwonus* and do not project into the dorsal outline in dorsal view.
6) The edge of the posterior orifice of the myodome in *Katsuwonus* is nearly vertical, whereas it is roughly spherical in *Euthynnus*.
7) The exoccipital condyle in *Euthynnus* projects beyond the transverse margin of the skull a distance approximately equal to the length of the first vertebra, whereas it is much shorter in *Katsuwonus* and equals roughly half the length of the first vertebra.
8) *Katsuwonus* has 41 vertebrae, whereas *Euthynnus* has 39 or fewer.

Attempts to determine generic relationships between *Katsuwonus* and *Euthynnus* by serological and immunogenetic techniques have also given mixed results. Electrophoretic analyses of hemoglobin (Sharp 1969, 1973) have indicated that *Katsuwonus* differs from *Euthynnus* and *Thunnus*. *Katsuwonus* has only two hemoglobin bands; *E. alletteratus* and *E. affinis* have three identical bands; and the four species of *Thunnus* examined (*albacares*, *alalunga*, *sibi*, and *thynnus*) have at least four bands. One of the bands in *Katsuwonus* and *Euthynnus* seems to be identical whereas none of the hemoglobins in *Katsuwonus* or *Euthynnus* is identical to any hemoglobin in the four species of *Thunnus* examined. Analyses of heart, red and white muscle tissues, and enzymes, on the other hand, have provided conflicting evidence. Sharp and Pirages (1978) found that *K. pelamis* and *E. affinis* were the most closely related of the non-*Thunnus* tunas, that both species were almost equally close to *T. albacares*, and that *E. lineatus* and *Auxis thazard* were about as close to each other as were *K. pelamis* to *E. affinis*, but somewhat more distantly related to *T. albacares*, and, therefore, to the *K. pelamis*-*E. affinis* group. The authors indicated that their results showed little reason for separating *Katsuwonus* from *Euthynnus*. While this seems to be true when considering only *E. affinis*, the distance between *affinis* and *lineatus* and the latter's close relationship with *A. thazard* suggests otherwise.

We thus agree with Collette's (1978) view that placing *Katsuwonus* in synonymy with *Euthynnus* would obscure the relationships of *Euthynnus* with *Auxis* and *Katsuwonus* with *Thunnus*.

1.22 Taxonomic status

The name *pelamis* was established by Linnaeus in 1758 and was accepted by workers throughout the remainder of the 18th century. Bloch and Schneider (1801) used the name *pelamys* and most workers also used this name in the 1800's and early 1900's. Some of these, notably Cuvier (1829), Valenciennes (1836), Temminck and Schlegel (1842), Cantor (1850), Bleeker (1856), and Günther (1860), although spelling the name *pelamys*, attributed the authorship to Linnaeus. Two other names, *pelamides* by Lacépède (1802) and *vagans* by Lesson (1828), were used briefly. Both names reflected differences in the geographic locality of capture. The name *pelamis* gained in acceptance between 1890 and 1935, and nearly all workers today use this name.

Existing morphological and meristic descriptions of the skipjack tuna, *Katsuwonus pelamis*, from all oceans (Jones and Silas 1963; Postel 1963; Waldron 1963) and biochemical genetic study by Fujino (1969) indicate that there is but one worldwide species—*Katsuwonus pelamis*.

1.23 Subspecies

No subspecies are recognized.

1.24 Standard common and vernacular names

The standard common and vernacular names of the skipjack tuna, obtained from various sources (Herre and Umali 1948; Rosa 1950; Herre 1953; Okada 1955; Van Pel 1960; Jones and Silas 1963; Postel 1963; Waldron 1963; Moreland 1967; Miyake and Hayasi 1972) are listed in Table 1.

1.3 Morphology

1.31 External morphology (and description)

Body robust, rounded in cross-section and full in outline; maxillary not concealed by preorbital; about 40 teeth on jaws, but absent on vomer and palatines; corselet is well defined with hardly any scales visible on rest of body; interspace between 1st and 2d dorsal fins hardly exceeding eye diameter; lateral line with a decided downward curve below 2d dorsal fin; margin of 1st dorsal fin strongly concave; pectoral fin short and triangular reaching posteriorly to the 9th or 10th dorsal spine most commonly, but to only the 8th or as far as the 11th spine in exceptional specimens (Fig. 2).

Table 1.—Common and vernacular names of skipjack tuna.

Country/locality	Standard common name	Vernacular name
Aden, Gulf of		AF muss; dabub; hargheiba
Albania	Palamida	
Angola	Bonito	
Australia	Striped tuna	Watermelon; skipjack
Brazil	Bonito de barriga listada	Bonito rajado
British Guiana	Oceanic bonito	White bonito
British West Indies	Oceanic bonito	White bonito; banjo; barriolet
Canada	Skipjack; thonine à ventre rayé	Skipjack tuna; oceanic bonito; striped bonito
Canary Is.	Bonito	
Chile	Atun	Cachurreta; cachureta; cachorreta; barrilete
Cuba	Atun	Merma
Denmark	Bugstribet bonit	
East Africa and Zanzibar	Skipjack	Sehewa (also refers to *Euthynnus* sp., *Auxis* spp.)
France	Listao; bonite; bonitou; bounicou	Bonite à ventre rayé
Germany	Echter bonito	Bauchstreifiger
Greece	Pelamys	Pelamis; tonina
India	Oceanic skipjack	Bonito; kali-phila-mas; varichoora; choora; metti
Indonesia	Cakalang	Tjakalang; tjakalang-lelaki; tjakalang-perempuan; tjakalang-merah; skipjack
Israel	Balamida	
Italy	Palometta	Paamia; paamitun; palametto; palamida; palamatu; palamia; tonina de dalmazia; nzirru; palamitu impiriali; tonnetto
Japan	Katsuo	Katuwo, katsuwo; magatsuwo; mandagatsuwo; mandara; hongatsuo
Korea	Ga-da-raeng-i	Ga-da-ri; yeo-da-raeng-i; gang-go-deung-so; so-young-chi; mog-maen-dung-i; da-raeng-i
Madagascar	Bonite	Bonite à ventre rayé; diodary; m'bassi
Madeira Is.	Gaiado	
Maldives	Kadumas (small); Godhaa (large)	Skipjack tuna
Mexico	Barrilete	
Monaco	Bonita	
Morocco	Listao	L'bakoura
New Guinea	Tjakalang	
New Zealand	Bonito	Striped bonito; striped tunny; skipjack; skipper
Norway	Bonit	
Peru	Barrilete	
Philippine Is.	Gulyasan	Striped tuna; skipjack; pundahan; bankulis; sobad; oceanic bonito; bonito; palawayan; puyan; tulingan
Poland	Bonite	
Polynesia (except Tahiti and Hawaii)	Atu	Bonito
Portugal	—	Gaiado; bonito de ventre raiado; bonito; listado; gayado; sarrajao, serra
Roumania	Palamida	Palamida lacherda
Senegal	Kiri-kiri	
South Africa	Skipjack	Skipjack tuna; oceanic bonito; lesser tunny; bonito; watermelon; katunkel
Spain	Listado	Skipjack; atun de altura; bonito de veintre rayado; bonito; palomida; bonitol; bonito de altura; lampo; llampua; bonito del sur; bonita
Sri Lanka	Bonito	Balaya; scorai
Sweden	Bonit	
Tahiti	Auhopu	
Taiwan	Theng chien	
Tunisia	Boussenna	Bonite
Union of Soviet Socialist Republics	—	Okeanskii bonito; katsuo; polosatyi tunets
United Kingdom	Striped bellied bonito	Striped bellied tunny; bonito
United States of America	Skipjack tuna	Skipjack; arctic bonito; oceanic skipjack; striped tuna; watermelon; victor fish; striped bonito; oceanic bonito; skippy; ocean bonito; mushmouth; aku (Hawaii); aku kinai (Hawaii)
Yugoslavia	Trup prugavac	Tunj prugavac

Body color in life is steel blue, tinged with lustrous violet along the dorsal surface 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; and a light grayish tinge on the underside of the mandible merges posteriorly with the whitish color on the lower half of the body. Four to six black longitudinal stripes are conspicuous below the lateral line on each side of the body. Matsumoto et al. (1969) described two specimens, one taken in Hawaiian waters, the other off Honduras, which lacked these stripes. They, however, represent extremely rare cases.

The counts of body parts for specimens from all oceans are given in Table 2. There seems to be no difference in the counts on fish from the Pacific and Indian Oceans and in at least two characters, first dorsal spines and gill rakers, on fish from all oceans.

Anatomical descriptions of the species may be found in Kishinouye (1923) and Godsil and Byers (1944). The vertebral column (Fig. 3) differs sufficiently from that of other fishes to be worthy of comment. Godsil and Byers (1944) wrote "The spinal column is extremely complex in this species. In the posterior half of the precaudal, and the anterior part of the caudal region, haemapophyses arise at both ends of each vertebra, with the anterior haemapophyses of one vertebra articulating with the posterior haemapophyses of the preceding vertebra. These haemapophyses project far below the spinal column and alternate with the longer haemal spines described below. An osseous bridge roughly parallel with the spinal column unites the anterior and posterior haemapophyses of each vertebra. Viewing the spinal column laterally, the bridge and the circular opening it forms may be easily seen. A branch arises from each bridge and extends downward to unite in the median line with its fellow from the opposite side. This forms the haemal arch from the tip of which a single haemal spine continues ventralward."

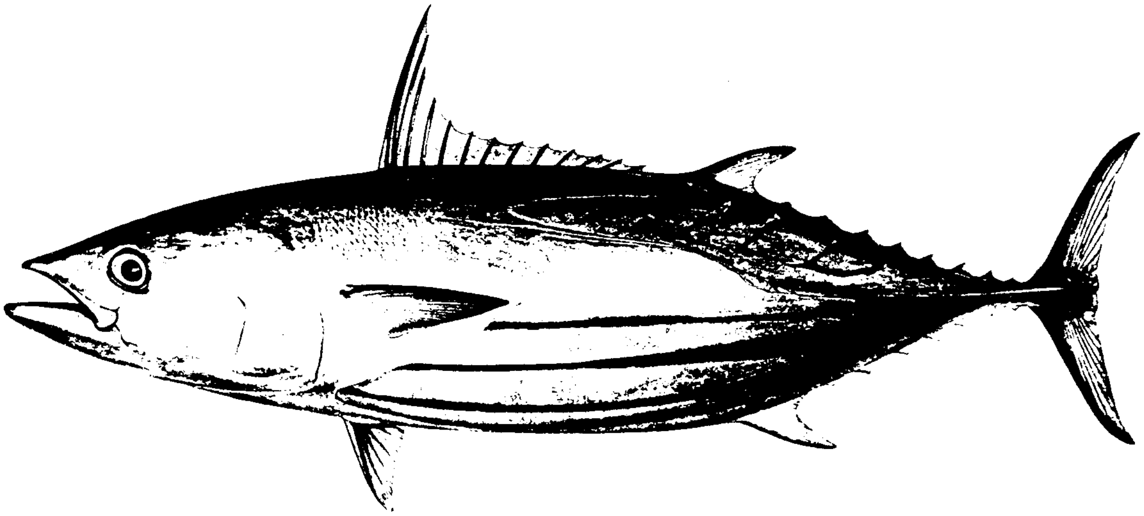

Figure 2.—The skipjack tuna, *Katsuwonus pelamis* (Linnaeus).

Table 2.—Counts of body parts for the skipjack tuna, *Katsuwonus pelamis*, from the Pacific, Indian, and Atlantic Oceans.

	Pacific Ocean	Indian Ocean	Atlantic Ocean		
Characters	Japan, Hawaii, E. Pacific (Waldron 1963)	E. Africa, Sri Lanka, Laccadive Is., Indonesia, Australia (Jones and Silas 1963)	Cape Vert (Postel 1963)	All oceans	(Mostly
1st dorsal spine	14-17	14-17	14-16	14-17	15-16)
2d dorsal rays	13-16	13-16	—	13-16	(14-15)
Dorsal finlets	7-10	7-9	—	7-10	(8)
Anal rays	13-16	13-17	—	13-17	(14-15)
Anal finlets	7-8	7-8	—	7-8	(7)
Pectoral rays	24-32	26-30	—	24-32	(26-30)
Gil rakers					
Upper	18-22 +	18-21 +	—	18-22 +	(18-20)
Lower	35-43	33-42	—	33-43	(38-41)
Total	53-63	50-63	51-62	50-63	(56-60)

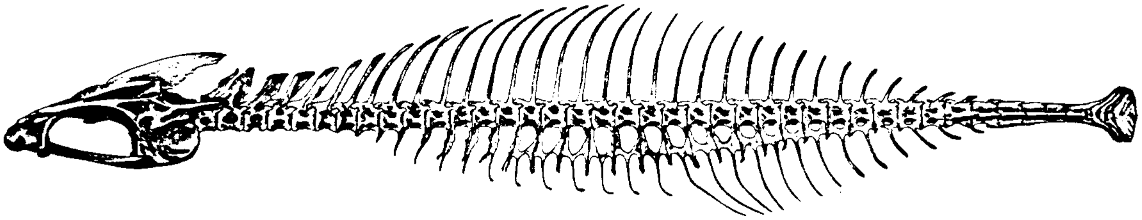

Figure 3.—Axial skeleton of an adult skipjack tuna (from Godsil and Byers 1944).

Such complex basketwork also occurs in the *Euthynnus* (Godsil 1954), but whereas the haemal arch in *K. pelamis* occurs adjacent to the vertebral column, that in *Euthynnus* is positioned away from the vertebral column (Fig. 4) at the tips of the haemapophyses. Viewing the vertebral column laterally, the inferior foramina in *Euthynnus* are elongate and about twice as long as those in *K. pelamis*.

The absence of consistent differences in both external and internal morphological characters of skipjack tuna from widely separated regions in the Pacific (Godsil and Byers 1944) indicates that there is but one species of skipjack tuna and that it is not possible to define subpopulations on the basis of these characters.

1.32 Cytomorphology

No information is available on chromosome number of skipjack tuna.

1.33 Protein specificity

The inability of standard morphometric analyses to resolve the problem of subpopulation or stock separation in skipjack tuna has led to the utilization of population genetic methodologies. Initial attempts involved the study of blood types through antigen-antibody reactions, and this was followed by some work on polymorphisms of the protein hemoglobin using starch-gel electrophoresis. As in other applications of population genetics, most work now involves the study of various serum and tissue enzymes, again using starch-gel electrophoresis. Sera are more commonly used because collecting the sample does not decrease the commercial value of the catch. Early isoenzyme studies involved samples collected from the central Pacific, then rather quickly from the eastern Pacific, Atlantic, western Pacific, and finally the Indian Ocean.

(1) Blood groups

Cushing (1956), who pioneered the application of blood typing for the study of tuna subpopulations, found two phenotypes on the basis of the agglutination of skipjack tuna erythrocytes in normal bovine serum. Subsequently, Sprague and Holloway (1962) named this system the C blood group apparently after Cushing. In the same paper, they published information on another blood group, B, and on blood factors A, D, and F which were not shown to belong to any inheritance system. Fujino (1967, 1969) found that the frequency of the K_1-positive phenotype of the B group was related to the size of skipjack tuna. Several papers were published after this purporting to have found or not to have found evidence of subpopulations from various areas in the Pacific Ocean (Sprague and Nakashima 1962; Sprague et al. 1963; Sprague 1963; Fujino 1969, 1970b, 1972). Neither the C nor B groups were shown to be amenable to Hardy-Weinberg analysis, and neither of these blood groups proved useful for population genetics studies.

Fujino and Kazama (1968) found another blood group, Y, which again did not prove useful in separating subpopulations, except when used together with other gene systems (Fujino 1969, 1970a). The Y group is made up of 15 phenotypes, coded by 6 codominant alleles; however, only 2 alleles, Y^{y} and Y^{so}, and the 3 resultant phenotypes are abundant enough to be useful in population studies. The system was shown to be amenable to Hardy-Weinberg analysis and independent of sex, size (age), and the C and B blood groups. Samples from various areas in the eastern, central, and western Pacific Ocean and the Atlantic Ocean failed to show heterogeneity of genotypic frequencies; however, the lower frequency of the Y^{y} allele found in the Atlantic Ocean indicates greater opportunity for divergence and, therefore, utility in subpopulation differentiation.

Fujino (1970a, 1971) described some preliminary results for an H blood group consisting of two phenotypes. While there was some evidence for the existence of subpopulations within the east-central Pacific Ocean (by testing phenotypes), the system was not shown to be amenable to Hardy-Weinberg analysis.

(2) Hemoglobins

Little work has been performed using hemoglobins because their instability requires preservation techniques that are hard to apply at sea and because they are not highly polymorphic.

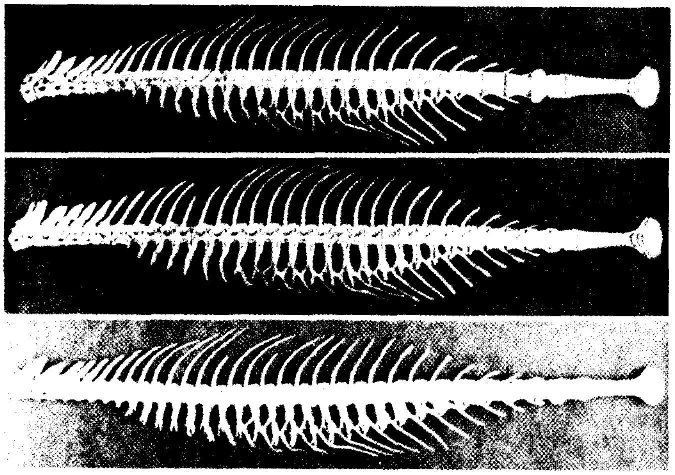

Figure 4.—Vertebral column of *Euthynnus*. Top to bottom: *lineatus*, *yaito* (= *affinis*), *alletteratus* (from Godsil 1954).

All samples examined by Sharp (1969, 1973) from off Baja California and Hawaii showed two phenotypic bands; therefore, the author made no inferences regarding subpopulation differentiation.

(3) Serum isoenzymes

While it is true that serum enzymes have provided the richest material for differentiating subpopulations of skipjack tuna, only esterase and transferrin, and recently guamine deaminase, have actually been found to be sufficiently polymorphic. In the mid-1960's while testing a series of tissues sampled from skipjack tuna collected off Hawaii, Sprague (1970) found six electrophoretic zones of esterases, one of which he interpreted as serum esterase. He hypothesized that the four observed phenotypes are coded by three alleles. Using blood serum, Fujino (1967) and Fujino and Kang (1968a) found three clear and three faint bands of serum esterase activity resulting in nine observed phenotypes and hypothesized, on the basis of the Hardy-Weinberg law, that they are coded by six codominant alleles. We follow the conventional allele numbering system based on relative mobility, hence the most abundant allele in the eastern and central Pacific is Est 2, rather than number 1 as in Fujino's papers (the reason for this difference is historical in that the now Est 1 is rare and was found after much work was already published). Because the faint bands are so rare, the system is usually treated as a six phenotype, three allele system for subpopulation study. The transferrin gene system was first described for skipjack tuna by Barrett and Tsuyuki (1967) from samples collected in the eastern tropical Pacific. They observed six phenotypes and hypothesized that they are coded by three codominant alleles. Researchers at the Australian National University (South Pacific Commission (SPC) 1981) have reportedly tested 42 gene loci (proteins) and found only 3 that were highly polymorphic. Glucose-phosphate isomerase, 6-phosphogluconate dehydrogenase (also reported by Sharp and Kane[3]), and apparently adenosine deaminase were variable but at low levels. Research on the esterase, transferrin, and guamine deaminase gene systems will be discussed in some detail below.

After the observed serum esterases were hypothesized to compose a single gene locus consisting of six codominant alleles, the locus was shown to be independent of sex, size, blood groups B, C, and Y, and serum transferrin (Fujino 1967, 1970a; Fujino and Kang 1968a, b). While these basic and essentially genetic factors were being established, the search for subpopulations, which was the real purpose of the studies, proceeded. Such population genetics studies involve testing individual sample lots for genetic equilibrium and testing for homogeneity both within and between sample lots from arbitrary areas. These tests are quite technical since they involve inheritance properties of the multinomial Hardy-Weinberg law, chi-square tests of homogeneity or, more recently, the *G*-test of Sokal and Rohlf (1969), and considerations of the effect of sample size on these tests. A great deal of controversy has surrounded the employment of these tests, i.e., the confidence to be placed on the results, and has led to three different approaches being followed by various scientists and organizations.

The first approach was advanced by Kazuo Fujino who was associated with the Honolulu Laboratory, National Marine Fisheries Service, and is now with the Kitasato University in Japan. Fujino (1970a) showed that the Hardy-Weinberg method is not very sensitive to deviations from expected proportions (genetic nonequilibrium) by employing a simple theoretical test. Taking the calculated allelic frequencies for the eastern-central and western subpopulations (to be described later) and constructing a one-to-one mixture of these subpopulations, lack of fit to Hardy-Weinberg proportions could not be shown with a sample size of 100 individuals (nor, we might add, would have been found if he had used a sample of 200 individuals). Later Fujino (1971) presented graphic evidence showing that a mixture of subpopulations could always be detected for a sample of 100 individuals from a one-to-one mixture of subpopulations having a difference > 0.443 in the frequency of the allele being tested, whereas a mixture could never be detected if the difference were < 0.328. For differences falling between 0.328 and 0.443, ability to detect a mixture depended on the absolute allelic frequencies. While an examination of the effect of sample size shows that it is, of course, easier to determine a mixture with larger sample sizes, Fujino's data indicate that the differences in the allelic frequencies between the hypothesized eastern-central and western subpopulations preclude the ability to consistently detect mixtures with a sample size of 100 (or as we said, even 200). From this result, Fujino seems to have concluded that a reasonable strategy would be to collect small samples (generally < 100 individuals) and to sample more schools. He has then proceeded to search for subpopulations by grouping sample lots (schools) from similar geographical areas, by testing for intra- and inter-area homogeneity, and by setting up statistical confidence regions for classifying individual school samples into separate subpopulations, without considering whether the individual schools represented mixtures of genetic units.

Fujino (1967) and Fujino and Kang (1968a) presented results from their initial examination of material from the Atlantic, Hawaiian Islands, the northeastern tropical Pacific, Palau Islands, and Japan. They found no evidence of heterogeneity of samples within these areas, nor between Hawaii and the eastern tropical Pacific or between Palau and Japan. However, their tests did show that samples from Hawaii were different from the combined samples from Palau and Japan; and Atlantic material was different from that collected in the eastern Pacific. Fujino (1969) used both the esterase system and the Y blood group in attempting to separate subpopulations. Using rejection ellipsoids for Y^y and Est 2, he found that the eastern-central Pacific samples overlapped with those from the western Pacific, and these, in turn, overlapped with samples from the Atlantic. Thus, while the Atlantic material was shown to be different from the eastern-central and western Pacific material, the employment of these two gene systems did not contribute to differentiating between eastern-central and western Pacific material. He also stated that there was no evidence of heterogeneity (for any of the five gene systems, including esterase and blood group Y) between the Caribbean Sea and Gulf of Guinea (three and five sample lots, respectively). Fujino (1970a) for the first time actually used the names eastern-central and western subpopulations

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[3] Sharp, G. D., and W. P. Kane. Biochemical genetic comparison and differentiation among some eastern Atlantic and Pacific Ocean tropical tunas. Manuscr. in prep. U.N., FAO, Fish. Dep., Via delle Terme di Caracalla, 00100 Rome, Italy.

and restated that he had found no evidence of heterogeneity of samples within these areas, even with the inclusion of new material such as those from Ecuador. Also for the first time, Fujino described the boundary between these two subpopulations, and he did this by assigning schools to either of the subpopulations based on rejection limits for Est 2. While the western subpopulation was shown to be present the entire year in inshore waters off the east coast of the main Japanese Islands and around the Ryukyu Islands, the Bonin-northern Mariana Islands chain, and Palau Islands, he stated that the boundary between the subpopulations shifts easterly in the summer and westerly in the fall and winter in the waters between the Bonin-northern Mariana chain and the international dateline. Then in the same year, Fujino (1970b) presented additional information on these subpopulations, namely, that there was no evidence for seasonal variation in the esterase gene frequency in either Hawaii or Palau, that new material from the Line Islands was not different from the historical Hawaiian material, that there was no evidence for heterogeneity within the western Pacific subpopulation based on samples from Japan, northern Mariana Islands, Ryukyu Islands, and Palau Islands, and further that the relatively low numbers of skipjack tuna larvae found in the area between long. 170°E and the international dateline in the Northern Hemisphere was supportive of the two subpopulation hypothesis. On the basis of new samples from schools in the western Pacific, which were assigned to either the eastern-central or western subpopulation based on rejection limits for Est 2, Fujino (1972) adjusted the boundary, indicating that the range of the western subpopulation extends out to long. 165°E (between the eastern Caroline Islands and the Marshall Islands/Gilbert Islands) without marked seasonal variation and hypothesized that the Izu-Bonin-northern Mariana Islands complex acts as a barrier to the eastern-central subpopulation. Using the estimated growth rate of skipjack tuna (based on Rothschild 1967), Fujino was able to separate the western subpopulation into A and B components associated with an apparent hatching time in the Northern Hemisphere summer and winter, respectively. Figure 5 depicts the hypothesized range of the western subpopulation, the overlap of northern summer and winter spawning areas, and the migration routes of the A and B units. Subsequently, Fujino (1976) reported some additional results from material collected from the southwestern Pacific. He classified all four schools sampled in New Zealand and one from Tasmania as belonging to the eastern-central subpopulation. From Australia, two schools were classified as belonging to the western subpopulation and one to the eastern-central. Likewise for the New Hebrides (7 schools) and southern Solomons (12 schools), both subpopulations were represented. All schools from New Caledonia (2) and Papua New Guinea (13) were classified as being western subpopulation. Finally, Fujino (1980) presented nonoverlapping Est 2 frequency ranges, namely 0.394-0.570 for the eastern-central and 0.578-0.758 for the western subpopulation. Using these values to classify schools, Fujino found that 40-50% of the schools off eastern Japan in May-June belonged to the western subpopulation and averaged 65% for the entire year. Fujino also indicated that he could subdivide the western subpopulation using a new esterase gene system (EstR) from red blood cells. Taking samples classified as western subpopulation and testing for this new esterase, Fujino found that the Satsunan-Tosa-Kishu group had an average EstR 1 gene frequency of 0.754 and the Bonin-Izu group had an average gene frequency of 0.083. The relationship of these new genetic subpopulations to the previously described A and B units was not stated. Three schools assigned to the eastern-central subpopulation had an average EstR 1 value of about 0.38, thus falling between the two hypothesized western subpopulations.

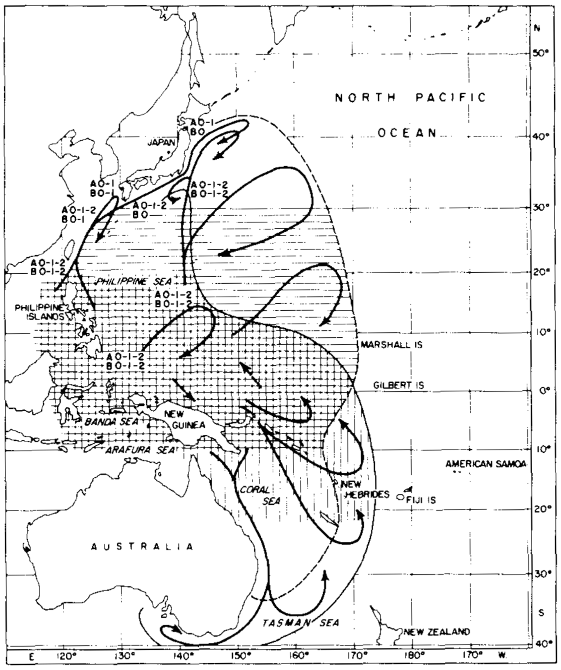

Figure 5.—Distribution and migration routes of the western Pacific skipjack tuna subpopulation proposed by Fujino (1972). Eastern limits of distribution during northern winter and summer are indicated by a solid line and a broken line, respectively. Intensive spawning grounds are shown by horizontal and vertical hatching and migration routes are indicated by curved lines with arrows.

The second approach of determining subpopulations was advanced by Gary D. Sharp who was associated with the Inter-American Tropical Tuna Commission (IATTC) and is now with FAO. Sharp (1978) pointed out that if replicate samples were collected from homogeneous units, one should expect a normal distribution of estimates about whatever parameter was being estimated. He stated, however, that this has not resulted for gene frequencies in the extensive, large-sized samples of both skipjack tuna and yellowfin tuna, *Thunnus albacares*, and argued that this was due to the genetic nonhomogeneity of the schools. As evidence that schools are genetic composites, he referred to his studies on shifts in gene frequency and the clumping of rare alleles in individual schools (Sharp[4]; Sharp and Kane footnote 3). While Sharp (footnote 4) was able to show significant differences between schools based on morphometric discriminant analysis, these differences seemed unrelated to genetic differences. Based on these considerations, Sharp recommended that sample sizes

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[4] Sharp, G. D. Studies of Pacific Ocean skipjack tuna (*Katsuwonus pelamis*) genetics through 1978. Manuscr. in prep. U.N., FAO, Fish. Dep., Via della Terme di Caracalla, 00100 Rome, Italy.

should be on the order of 200 individuals per school. In his study of subpopulations, Sharp placed greater emphasis on the lack of homogeneity of individual schools, compared the distribution of gene frequency estimates among geographical areas, and employed the usual statistical tests for both intra- and inter-area homogeneity.

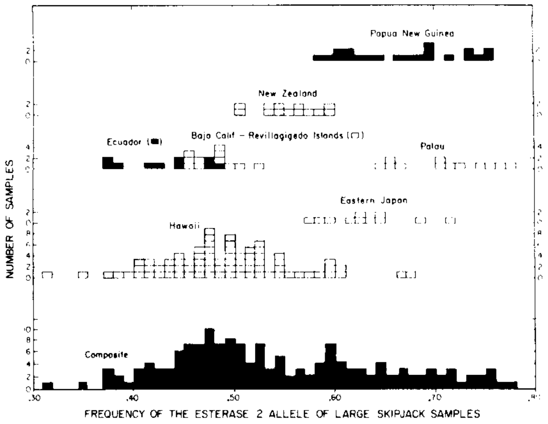

Figure 6.—Frequency distribution of Est 2 skipjack tuna allele for large samples from various sources (from Sharp text footnote 4).

While he indicated that his large-sample data from the eastern tropical Pacific, Papua New Guinea, and New Zealand fit Hardy-Weinberg expectations in all but two cases (in the former site), Sharp (footnote 4) and Sharp and Kane (footnote 3) showed that nearly all sampled schools exhibited statistically improbable clumping of rare alleles or a shift in the estimated gene frequency midway in the length range of the samples, or both. These results indicate not only that the Hardy-Weinberg test is not sensitive to mixtures but that schools tend to be both mixtures of siblings as well as groups with differing gene frequencies. These results cast doubt on the utility of computing average gene frequencies for use in classifying schools to hypothesized subpopulations. Also in testing for homogeneity within geographical areas (eastern tropical Pacific, New Zealand, Papua New Guinea, Hawaii) using his own large samples and the larger sized samples of Fujino's, Sharp (1978, footnote 4) found significant heterogeneity in the esterase system (and in transferrin also, but to a lesser extent). Since tests among areas also show significant heterogeneity, Sharp's results are generally supportive of Fujino's results in that there is evidence for subpopulation differentiation between the eastern-central and western Pacific and within the western Pacific; however, they also indicate that subpopulation differentiation within the eastern-central subpopulation is likely. Sharp's approach then deviates from Fujino's by comparing the similarities of gene-frequency distributions among the various sample sites rather than assigning schools to hypothesized subpopulations based on rejection limits. Thus, Sharp (footnote 4) observed (Fig. 6) that the esterase gene-frequency distribution for Hawaiian samples seems to have components similar to those found in samples off eastern Japan, and other components similar to those in the northern areas of the eastern tropical Pacific and off Ecuador. Also, the typical gene frequency in the eastern tropical Pacific corresponds to the most common gene frequency in Hawaii. For both Palau and Papua New Guinea, there seem to be three groups showing much overlap between the areas. For New Zealand, Sharp says there is one group similar to the eastern Pacific and one unique group, but all of these distributions fall into the upper end of the Hawaiian distribution. The distribution for the northern area of the eastern tropical Pacific is similar to that for Hawaii and contains some components similar to those from Ecuador. The latter was said to have a unique component (with low gene frequency), but this again falls within the range of the Hawaiian samples. Based on all of these findings, Sharp (footnote 4) hypothesized the existence of six subpopulations in the Pacific (Fig. 7). Considerable overlapping of the subpopulation ranges occurs in the central and western equatorial areas.

The third approach was used by the SPC in association with their Skipjack Survey and Assessment Programme. Blood samples and various biological information have been collected fairly uniformly across the South Pacific and into the Northern Hemisphere in the western Pacific. With their

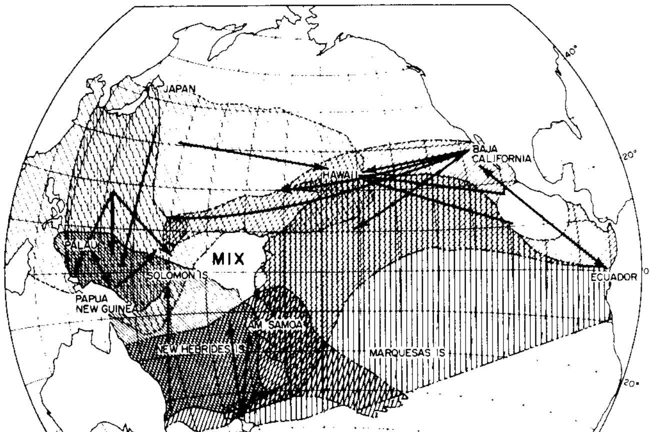

Figure 7.—Ranges of six skipjack tuna subpopulations (from Sharp text footnote 4), with examples of the movement of tagged fish.

interest in determining what effect, if any, population structuring would have on yield and fishery management in the SPC area, they have emphasized the analysis of longitudinal gene-frequency variations and of differences among western, central, and eastern segments (areas A, B, and C) of the SPC.

Having the benefit of much of the research described above, the SPC collected relatively large samples (100 individuals/school), integrated their genetic research with tagging and sampling for size composition, and examined the quantitative aspects of the population genetic methods employed. Thus, they performed certain basic statistical tests of their data before analyzing for subpopulations (South Pacific Commission 1980, 1981), which provided them with the following results. With a sample size of 100, gene frequency of the samples was estimated with a precision of 0.07 at the 95% confidence level. If two genetic populations differ in their gene frequencies by 0.1, they could be statistically separated with a sample size of 25 at a power of 90% (this seems in direct conflict with the results in Fujino 1971). And if over six sample lots (600 individuals) were combined within an arbitrary area, significant heterogeneity was usually found.

Regarding population genetic results, they found that samples from areas A (west of long. 170°E) and B (between long. 170° and 165°E) showed a higher degree of heterogeneity than area C (east of long. 165°E); however, this was based on 76, 32, and 11 sample lots, respectively. Most interestingly, they found a longitudinal cline of Est 2 (Fig. 8) from about long. 140°E (gene frequency of 0.71) to 130°W (gene frequency of 0.37). As would be expected from the results of the tests for heterogeneity for areas A, B, and C, the variance about the cline (regression line) decreased from west to east. To the east of long. 130°W, the cline appeared to cease or to level off. To the west, Lewis[5] felt that the cline continued into the Pacific and Indian Ocean waters of Indonesia, whereas the South Pacific Commission (1981) suggested that the cline may level off. More samples will be needed from the Indian Ocean to resolve this issue.

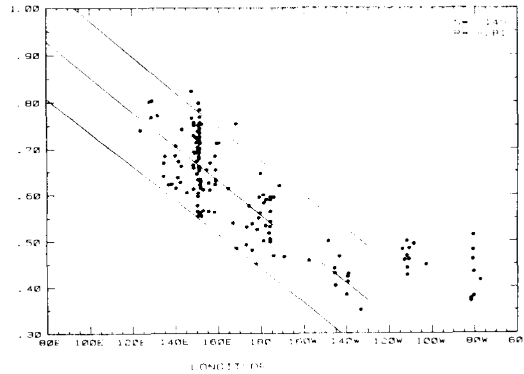

Figure 8.—Relation of esterase gene frequency and longitude. Regression line and 95% prediction limits indicated. Regression excludes samples from east of the SPC area (east of dotted line). N is number of samples; R is correlation coefficient (from South Pacific Commission 1981).

While tagged fish were continuing to be recaptured (and indeed long-term recaptures of many fish tagged in French Polynesia were just being reported), the South Pacific Commission (1980, 1981) attempted to integrate the tagging and genetic experiments. On the basis of the calculated gene frequency of the tagged school, the expected longitudinal range of recapture was estimated from the regression line of gene frequency on longitude. Of the 106 tag recoveries at large for at least 90 d, only 1, released in Kiribati, was recovered in an unexpected area (South Pacific Commission 1980). Then, regressing the net west-east movement of all tagged fish from each school for which gene frequency was estimated (29 schools) against the difference between calculated gene frequency of the school and the gene frequency estimated from the cline, they failed to find a significant relationship (South Pacific Commission 1981). A positive relationship would have indicated that fish tended to migrate to areas having schools with average gene frequencies more similar to that of schools in which they were at the time of tagging. While this second test may seem to be more critical, it may be biased because it includes short-term recaptures which tend to disperse very little and because fish tagged in the western perimeter of the Pacific basin may be restricted in their migration to the west.

Returning to serum transferrin, Fujino and Kang (1968b) stated that the system was independent of sex and, later, of the blood groups C, B, and Y (Fujino 1970a). They found no evidence for heterogeneity either within or among the central-eastern Pacific, Atlantic (also shown by Fujino 1969), and western Pacific areas. However, when they grouped the data by areas, the pooled data showed an excess of heterozygotes compared with Hardy-Weinberg expectations. They presented data purportedly showing that the frequency of certain alleles varied with size and hypothesized that differential mortality with size could maintain the balanced polymorphism. Subsequently, however, Sharp and Kane (footnote 3), using larger sample-size lots collected in the eastern tropical Pacific and off New Zealand, found that most samples fitted Hardy-Weinberg proportions. Reexamining Fujino's data, they showed that only one size group out of five deviated from Hardy-Weinberg proportions. Lewis (footnote 5) reported that samples collected from Pacific and Indian Ocean waters of Indonesia had transferrin frequencies falling within the normal range seen in all other historical samples. Presenting results from samples collected all across the South Pacific, as well as from certain sites in the western North Pacific, the South Pacific Commission (1980) found no variation of transferrin gene frequency with longitude. By plotting the variation of the frequency of the major transferrin allele against those for the major esterase allele, the variations were shown to be independent and the variation for transferrin was the smaller of the two by far. The gist of all of these studies is that transferrin has not proven useful in differentiating subpopulations of skipjack tuna.

(4) Tissue isoenzymes

Sprague (1970) found as many as 12 esterase activity bands in samples of dark and light skeletal muscle, heart muscle, kidney, liver, spleen, gonad, brain, and whole blood collected

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[5] Lewis, A. D. Undated. Report, Collection of biological material from skipjack (*Katsuwonus pelamis*) and other scombrids for genetic analysis, Indonesia, 9-23 December, 1979. Typescript, no pag. Australian National University, Department of Population Biology, Ministry of Agriculture, Forests, and Fisheries, Fisheries Division, Suva, Fiji.

from skipjack tuna in Hawaiian waters. These 12 bands appear to be arranged in 6 regions, but only 2 of the regions were hypothesized to compose a genetic system. The fourth region contained serum esterases as described in the previous section. Sprague contended that the esterases in region 5 were also usable for subpopulation studies, but insufficient data were available at the time to do so. He hypothesized that the three observed phenotypes in this region are coded by two alleles. McCabe and Dean (1970) also found innumerable bands of esterase activity in samples of liver and skeletal muscle taken from skipjack tuna in the Atlantic Ocean. They indicated that the esterases in only two activity regions, Est Ib and Est III, were stable and, therefore, usable for subpopulation studies carried out in the field. Region Est III seemed to be a dimer system made up of four phenotypes coded by four alleles. Since one of the alleles had a frequency of 0.964, this esterase system is, for practical purposes, monomorphic and not likely of much use in studying subpopulations in the Atlantic Ocean; however, the situation in the Indian and Pacific Oceans could prove to be different. In region Est Ib, they observed 15 phenotypes in 300 samples and hypothesized that the phenotypes were coded by 7 alleles. No specific data were given, nor was it shown that the system was amenable to Hardy-Weinberg analysis. Nonetheless, Est Ib may have potential for use in determining subspecific differentiation, since no single allele had a frequency > 0.4. Unfortunately, the phenotypes must be determined by a two-stage electrophoresis process, making the process more complicated and expensive than is the case with serum esterases.

McCabe et al. (1970) tested for dehydrogenase, acid phosphatase, and alkaline phosphatase activity in skeletal muscle sampled from skipjack tuna and reported finding polymorphisms of 6-phosphogluconate dehydrogenase (6-PGD) and alpha-glycerophosphate dehydrogenase (α-GPD) polymorphism in liver samples. The 6-PGD system was found to be a dimer with four phenotypes coded by four alleles, and the α-GPD system was found to consist of three phenotypes coded by three alleles. Since the frequency of PGD and α-GPD were both over 0.9, both systems are essentially monomorphic in the Atlantic and would probably not be useful for studying population differentiation in that ocean; however, the systems could prove to be useful in the Pacific and Indian Oceans.

Lewis (footnote 5) reported preliminary results from his investigation of 21 enzymes, encoded by 25 presumed gene loci, in liver tissues collected from skipjack tuna in north Queensland, Australia, and Padang, Indonesia. Only the adenosine deaminases ADA1 and ADA2 and guanine deaminase (GDA) were found to be sufficiently polymorphic (five, four, and three alleles, respectively) to encourage further research, whereas glucose phosphate isomerase (GPI), mannose phosphate isomerase (MPI), 6-PGD, isocitrate dehydrogenase (ICD), α-GPD, sorbitol dehydrogenase (SORD), glutamate oxaloacetate transaminase (GOT1 and GOT2), phosphoglucomutase (PGM1 and PGM2), peptidase 1 and 2, malic enzyme (ME1 and ME2), fumarate hydratase (FH), malic dehydrogenase (MDH), lactic dehydrogenase (LDH), pyruvate kinase (PK), glutamate pyruvate transaminase (GPT), 6-phosphofructokinase (PFK), phosphoglycerate kinase (PGK), and superoxide dismutase (SOD) were found to be absolutely or essentially monomorphic. No large differences were evident between the Australian and Indonesian material for ADA or GDA, but the samples from Indonesia seemed to be homogeneous and had a lower gene frequency than the samples to the east. The South Pacific Commission (1981) found a decreasing cline in gene frequency for the GDA_1 allele from west to east (Fig. 9).

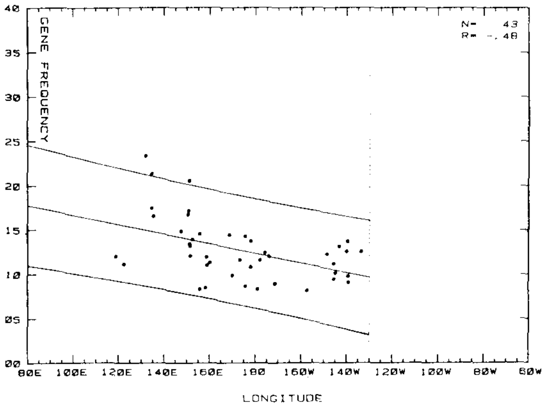


Figure 9.—Relation of guanine deaminase gene frequency and longitude. Regression line and 95% prediction limits indicated. Regression excludes samples from east of the SPC area (east of dotted line). N is number of samples; R is correlation coefficient (from South Pacific Commission 1981).

2 DISTRIBUTION

2.1 Total area

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 pole-and-line fisheries were constrained by distance to areas within easy access of bait supplies and purse seine fisheries were confined to those areas with a relatively shallow mixed layer, a characteristic of the purse seine fishery in 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; Marcille and Suzuki 1974; Matsumoto 1974, 1975) have utilized the Japanese tuna longline data to determine the distribution of skipjack tuna in midoceanic areas. Although the catches made by the longline gear were small, they constituted proof of the presence of skipjack tuna and the information thus obtained has expanded our knowledge about the distribution of the species.

The distribution of skipjack tuna (Fig. 10) was derived from atlases of the Japanese tuna longline catch data for various years from 1964 to 1979 ([Japan.] Fisheries Agency 1967a, b, 1968, 1969, 1971, 1972, 1973, 1979a, 1980a, 1981), the Japanese southern water fishery for various years from

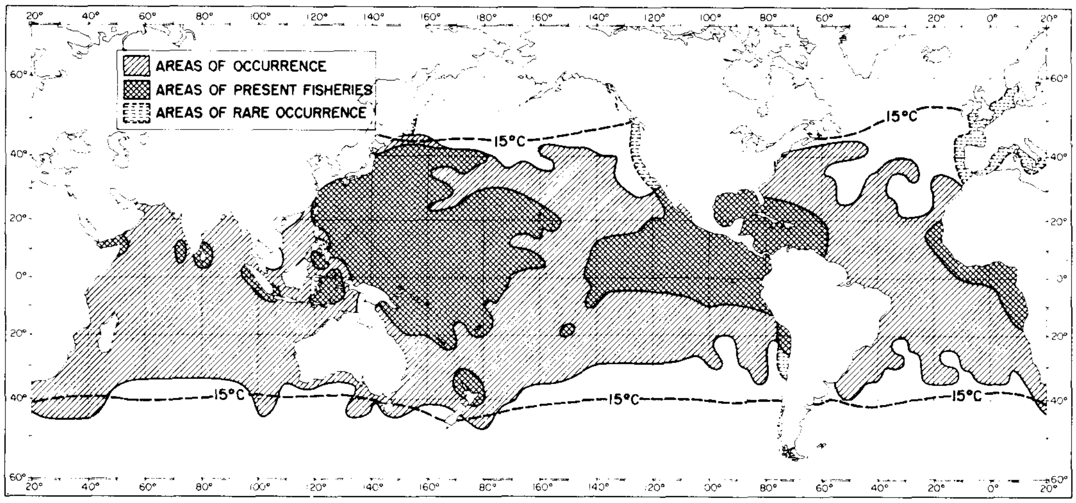


Figure 10.—Skipjack tuna distribution and fisheries in the major oceans. The mean 15 °C isotherms represent maximum late summer poleward displacement (data from various sources).

1964 to 1979 (Tanaka undated a, b, c, 1978, 1979, 1980; Tohoku Regional Fisheries Research Laboratory (Tohoku RFRL) undated a, b, c, d) the Japanese skipjack tuna bait boat fishery catch data for 1977 and 1978 ([Japan.] Fisheries Agency 1979b, 1980b), and other sources (Wade 1950; Robins 1952; Brock 1959; Roux 1961; Jones and Silas 1963; Postel 1963; Sakagawa 1974; Calkins 1975; Sakagawa and Murphy 1976; Santos 1978; Kikawa and Higashi 1979; Habib et al. 1980a, b, c; Blackburn and Serventy 1981). The species occurs continuously from east to west across all oceans, and over a wide latitudinal range from about lat. 45 °N to south of 45 °S in the western Pacific and from about lat. 30 °N to 30 °S in the eastern Pacific. In the Atlantic Ocean, skipjack tuna have been caught from about lat. 45 °N to 40 °S in the western side and from lat. 35 °N to south of 40 °S in the eastern side. Rare captures off Vancouver Island (Clemens and Wilby 1946) in the Pacific Ocean and off the British Isles, Scandinavia, and Denmark (Postel 1963) in the Atlantic Ocean extend the limits of occurrence northward to lat. 49 °N in the eastern Pacific and beyond lat. 55 °N in the eastern Atlantic. Skipjack tuna have been taken as far south as lat. 40° to 45 °S in the western Indian Ocean and south of Australia, and, although not indicated in Figure 10, in the eastern part of the Persian Gulf on rare occasions. The species occurs also in the Mediterranean Sea, from Gibraltar to Italy, but not in large concentrations as in the Atlantic Ocean (Belloc 1955).

2.2 Differential distribution

2.21 Spawn, larvae, and juveniles

Larvae of skipjack tuna have been found over a wide area in all the major oceans, including the Gulf of Mexico and throughout the Indo-Pacific Archipelago (Fig. 11). The known distribution of skipjack tuna larvae in the western and cen-

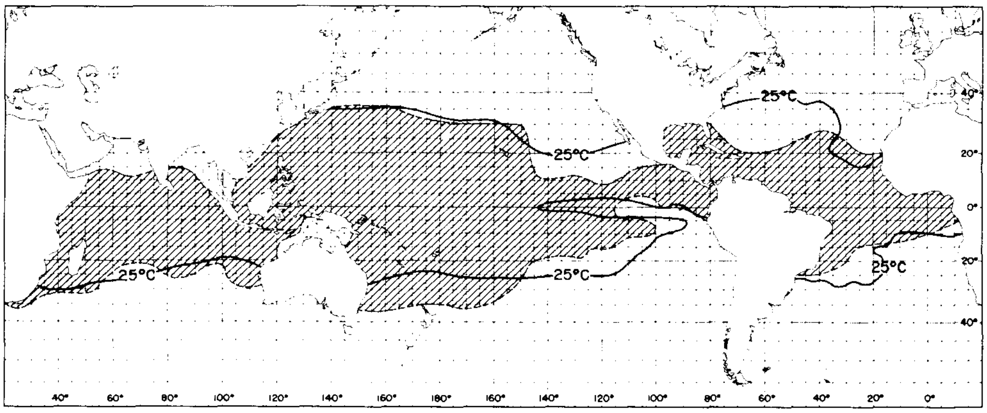


Figure 11.—Distribution of skipjack tuna larvae, 1952-75 (data from various sources).

tral Pacific extends from near lat. 35°N off Japan to as far south as lat. 37°S, off the southeastern part of Australia (Matsumoto 1958; Nakamura and Matsumoto 1967; Ueyanagi 1969, 1970; Mori 1970; Seckel 1972; Chen and Tan 1973; Nishikawa et al. 1978), and in the eastern Pacific from lat. 15°N to 5°S (Klawe 1963; Love 1970, 1971, 1972, 1974). The distribution in the Pacific is broad latitudinally in the west but narrow in the east due to the constriction of warm water favorable for spawning by cold currents flowing toward the Equator in both hemispheres. Both northern and southern boundaries shown may well represent the limits of distribution of skipjack tuna larvae in that ocean.

In the Indian Ocean, the distribution of larvae extends southward to the southern tip of Africa, to about lat. 36°S, and unlike that in the Pacific Ocean, larvae have been taken in the eastern part of the ocean from as far south as lat. 30°S (Ueyanagi 1969). The northern boundary is limited to lat. 11° to 15°N by the Asian Continent (Jones 1959; Gorbunova 1963, 1965a; Jones and Kumaran 1963; Ueyanagi 1969).

The distribution in the Atlantic Ocean differs somewhat from that in the Pacific Ocean. Although the distribution is wider in the western side, the southern boundary does not reach much beyond lat. 25°S and the northern boundary does not extend beyond lat. 30°N (Klawe 1960; Suarez-Caabro and Duarte-Bello 1961; Gorbunova and Salabarria 1967; Richards 1969; Zhudova 1969; Richards and Simmons 1971; Ueyanagi 1971; Juarez 1974; Nishikawa et al. 1978). The large dip in the northern boundary in the region of the Sargasso Sea may be due to infrequent sampling. The distribution of larvae in the eastern sector of the ocean differs from that in the Pacific Ocean. Whereas the distribution narrows and the concentration of larvae diminishes greatly in the eastern Pacific (Klawe 1963), the distribution is broader and the abundance of larvae is much greater (Richards and Simmons 1971) in the eastern Atlantic Ocean.

Within the vast range over which the larvae are distributed, certain areas of high abundance can be recognized. Kawasaki (1965a) suggested that the center of abundance of skipjack tuna larvae in the Pacific Ocean was in the area bounded by lat. 5°N and 4°S and long. 160°E and 140°W. He later (1972) revised his western boundary to long. 120°E, on the basis of Ueyanagi's (1969) data, which showed a peak in larval abundance at long. 120°-150°E along a band of water from lat. 10°N to the Equator. Matsumoto (1975), after adjusting the catches of larvae made with different sized nets and different towing methods in a band of water from lat. 10°S to 20°N (Table 3; Fig. 12), reported that the center of larval skipjack tuna abundance was between long. 160°E and 140°W (similar to Kawasaki's first estimate), that the abundance was moderate between long. 100° and 140°W and between long. 120° and 160°E, and low in the eastern Pacific east of long. 100°W.

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 with a 1 m net during the spawning season averaged 4.1 larvae/tow (data from Seckel 1972) and waters to the south of Japan between lat. 25° and 30°N, where the catches in subsurface tows (20-30 m) with a 2 m net averaged nearly 4.0 larvae/tow (Ueyanagi 1969, fig. 22, Area A).

In the Atlantic Ocean, larvae are apparently more abundant in the eastern half of the ocean between lat. 10°N and

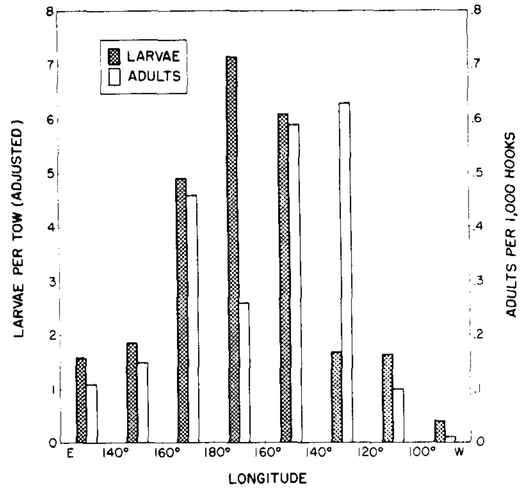


Figure 12.—Catch rates of skipjack tuna larvae and adults by longitude in the Pacific Ocean between lat. 10°S and 20°N (from Matsumoto 1975).

Table 3.—Catch rates of larval skipjack tuna in night surface tows from the Pacific Ocean (from Matsumoto 1975).

Longitude	Latitude	Quarter sampled	Net diameter (m)	Duration of tow (min)	Number of tows	Total larvae (no.)	Conversion factor[1]	Adjusted catch	Adjusted larvae per tow
80°-100°W	4°-15°N	I, II	1	30	33	7	[2]1.836	12.85	0.39
100°-120°W	10°-15°N	II	1	30	10	11	[2]1.836	20.20	1.63
100°-120°W	0°-7°S	I	1	30	12	19	[3]0.827	15.71	
120°-140°W	10°S-10°N	I, IV	1	30	21	42	[3]0.827	34.73	1.65
140°-160°W	10°S-20°N	I, III	1	30	32	239	[3]0.827	195.18	6.10
160°W-180°	10°S-20°N	I, II, III	1	30	45	389	[3]0.827	321.70	7.15
160°E-180°	10°S-20°N	I, III	1	30	6	45	[3]0.827	37.22	4.94
160°E-180°	10°S-20°N	II, IV	2	20	44	560	[4]0.375	210.00	
140°-160°E	10°S-20°N	II, III, IV	2	20	112	562	[4]0.375	210.75	1.88
120°-140°E	0°-20°N	II, IV	2	20	141	581	[4]0.375	217.88	1.54

[1] Conversion factor is the ratio of standard to average volume of water strained. Standard volume used was 1,454 m^3, the volume strained by a 1 m net towed at 2.0 kn for 30 min.

[2] Computed from average volume of 79 m^3 from 62 tows. Data from Klawe (1963).

[3] Computed from average volume of 1,759 m^3 from 289 tows. Data from NMFS Honolulu Laboratory files and Strasburg (1960).

[4] Computed from estimated volume of 3,878 m^3 at constant towing speeds of 2 kn. Catch data from Ueyanagi (1969).

10°S (Richards 1969). There are no other reports from the Atlantic or the Indian Oceans providing measures of abundance.

Juvenile skipjack tuna are rarely seen at sea and are extremely difficult to capture. They have been collected in various types of trawl and plankton nets, by dip netting at night under light, and from stomach contents regurgitated by seabirds, but the greatest number have come from stomachs of tunas and billfishes.

The relatively small number of recorded captures attest to the difficulty in capturing the juveniles. Higgins (1967) compiled all records of 512 juveniles, 1.2 to 30 cm in length, taken from the Pacific for the period 1916-66. Yoshida (1971) obtained 1,742 juveniles, 1.6 to 40 cm in length, from the stomachs of billfishes from Hawaiian and central South Pacific waters in the period 1962-66. Higgins (1970) examined 578 "juveniles," 7 mm to 4.7 cm in length, taken in midwater trawls in Hawaiian waters. Roughly 40% of the latter catch consisted of skipjack tuna larvae < 1.2 cm in length. Simmons (1969) compiled records of 163 juveniles, 13 to 15 cm in length, taken by various methods, including samples from stomach contents regurgitated by seabirds, from the Atlantic Ocean. Mori (1972) examined 5,851 juveniles and young, 3 to 35 cm in length including some adults to 70 cm, from stomachs of tunas and billfishes taken from the Pacific, Indian, and Atlantic Oceans during the period 1949-69. Of this number, 4,104 were juveniles < 35 cm in length: 3,778 from the Pacific Ocean, 202 from the Indian Ocean, and 124 from the Atlantic Ocean. Thus, the total juvenile skipjack tuna collected from 1916 through 1969 is < 7,000, of which roughly 300 were from the Atlantic Ocean, 200 from the Indian Ocean, and the remainder from the Pacific Ocean. Despite the small numbers of juveniles collected from the Indian and Atlantic Oceans, the dispersion of the capture sites presents a fair coverage of the two oceans.

The above data show that juvenile skipjack tuna are widely distributed in the tropical and subtropical waters of all oceans (Fig. 13). In the Indian Ocean the distribution extends from lat. 15°N to 35°S. In the Pacific Ocean the distribution extends generally from lat. 35°N to 35°S in the west and narrows to lat. 10°N and 5°S in the east. In the Atlantic Ocean the distribution extends from lat. 40°N in the west to lat. 30°S in the east. In all oceans the pattern of distribution resembles that of the larvae. From information acquired recently about the extremely rapid growth of skipjack tuna and other tunas reared from artificially fertilized eggs through the juvenile stages (Harada et al. 1971; Mori et al. 1971; Harada, Murata, and Furutani 1973; Harada, Murata, and Miyashita 1973; Ueyanagi et al. 1973), it would be expected that juveniles of skipjack tuna occur in all localities where larvae have been found.

In certain localities, i.e., North and South Atlantic, central Indian, and northwest and southeast Pacific, the distribution of juveniles is shown to extend beyond the range indicated for the larvae. This could be due to juveniles leaving the immediate spawning area as they grew larger and became more mobile. Mori (1972) suggested that this could occur when the juveniles attain the length of 30 cm.

2.22 Adults

Excluding those areas from which only rare captures have been reported, the distribution of skipjack tuna shown in Figure 10 (medium shaded areas) shows the maximum northward and southward limits. Both boundaries vary seasonally and annually as the skipjack tuna respond to seasonal changes in the environment. The boundaries generally shift poleward in the summer and fall as seasonal warming of the water occurs in higher latitudes and recede toward the Equator in winter and spring as the water cools. However, the northern and southern boundaries do not appear to shift in unison with each other and the north-south shifting of the boundaries does not occur simultaneously across the ocean, due to the varying effects of warm and cold currents in different parts of the oceans.

Matsumoto (1975) has shown that in the Pacific Ocean the northern boundary moves poleward in the third and fourth quarters and recedes toward the Equator in the first and second quarters (Fig. 14). The shift occurs at about the same time in both the western and eastern halves of the ocean. In

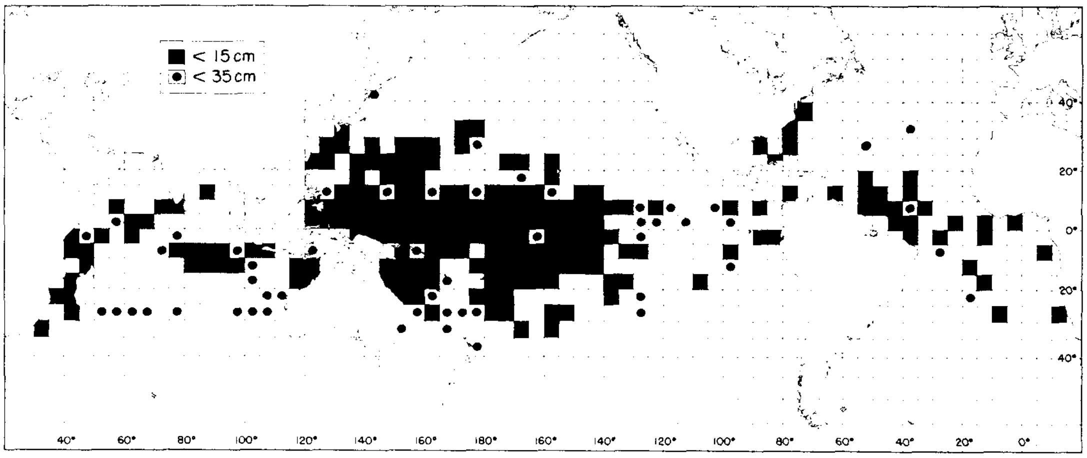


Figure 13.—Locations of known captures of juvenile skipjack tuna in the major oceans from 1916 through 1969 (data from various sources).

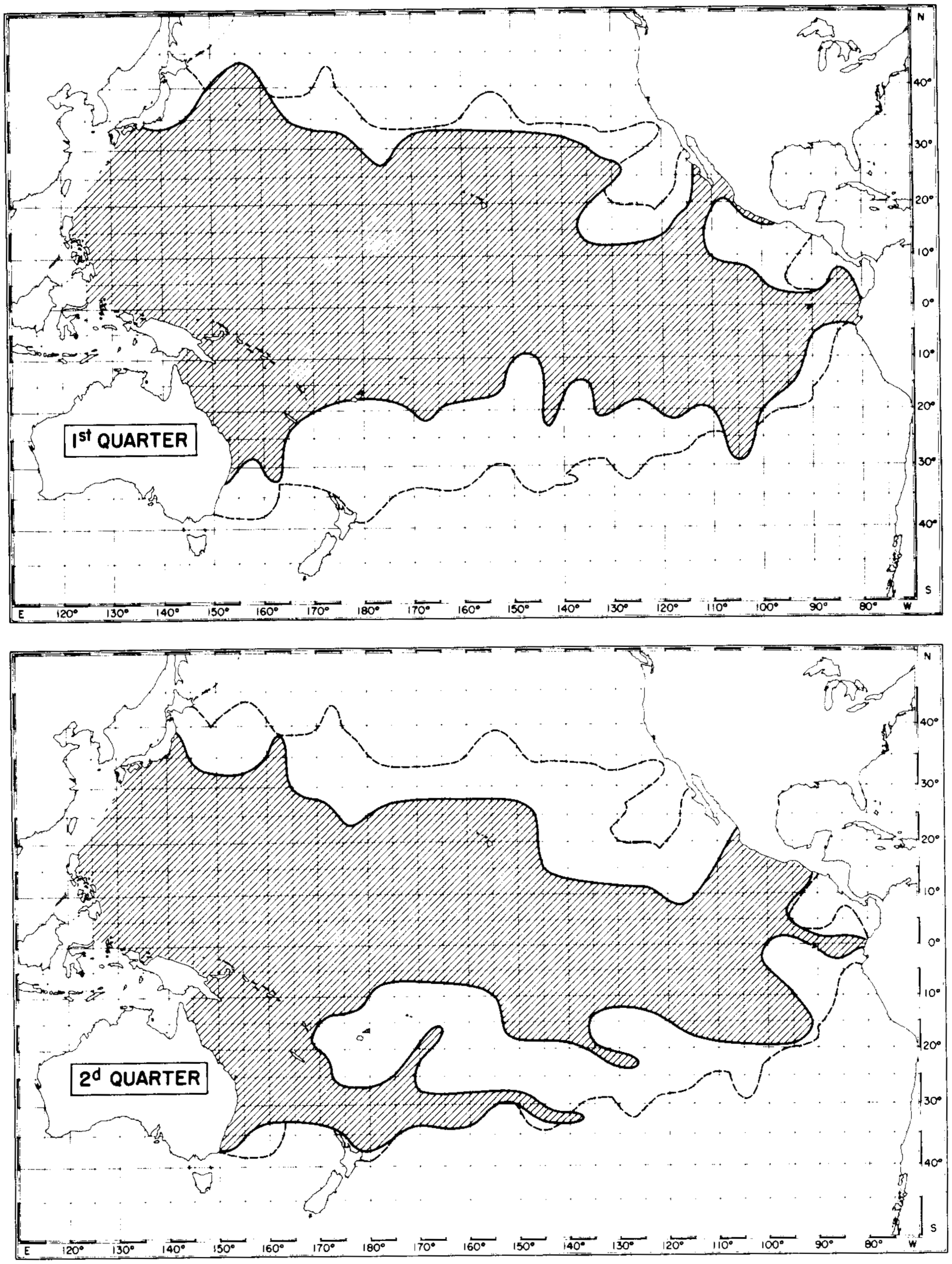
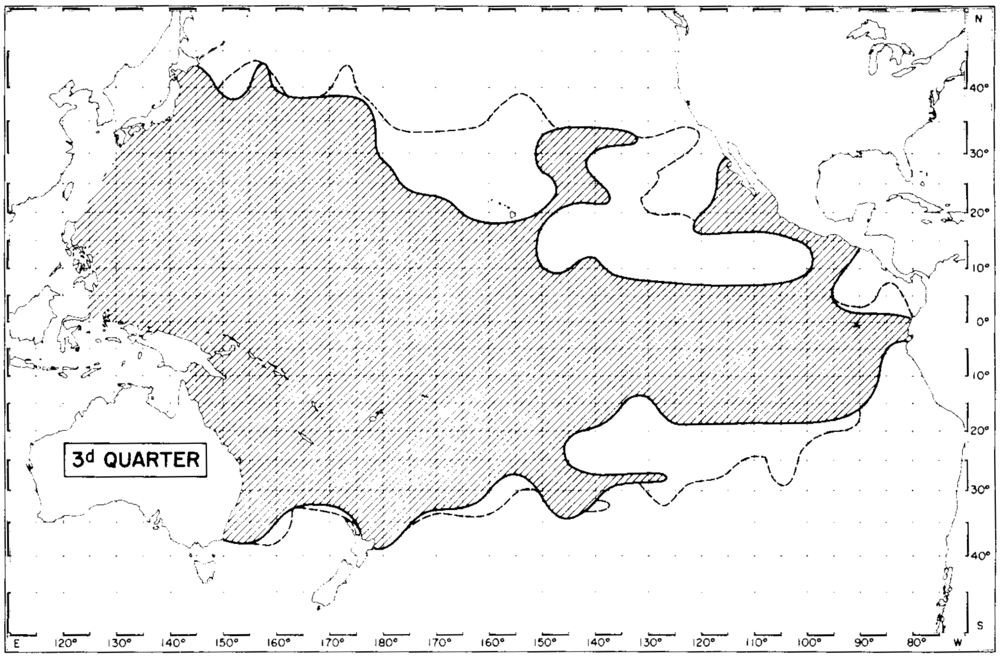


Figure 14.—Outlines of the northern and southern boundaries of skipjack tuna caught in the Japanese tuna longline fishery, 1964-67, by yearly quarters (shaded area). The broken lines denote the maximum range for all four quarters (from Matsumoto 1975).



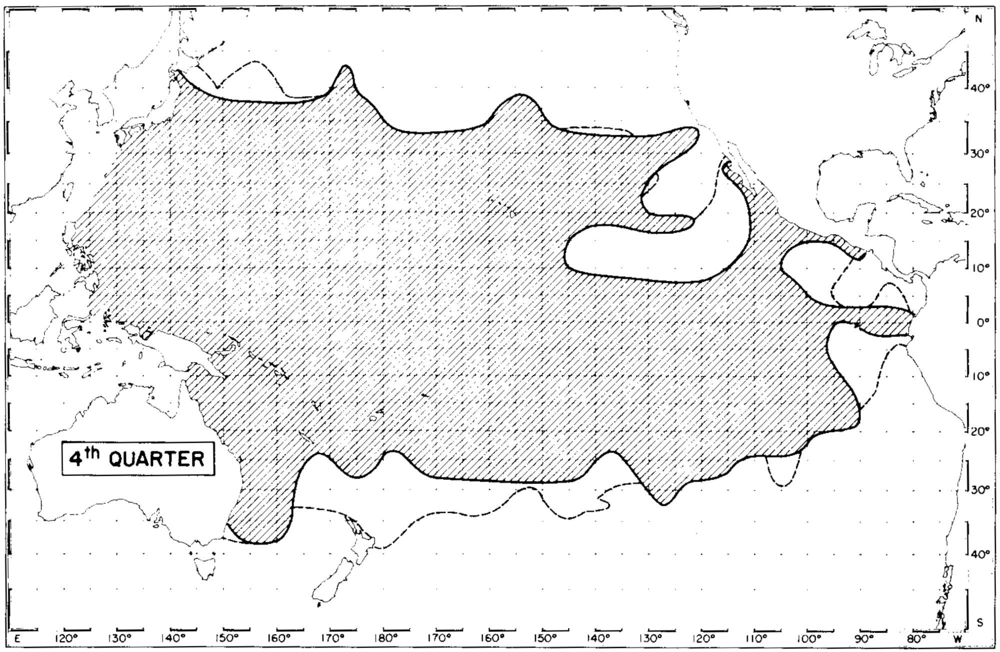


Figure 14.—*Continued.*

the Southern Hemisphere, however, the western half of the boundary moves poleward in the second and third quarters and toward the Equator in the fourth and first quarters, whereas in the eastern half, the shifting of the boundary occurs about 3 mo later. Although similar studies have not been made in other oceans, we believe that the boundaries of skipjack tuna distribution in those oceans also undergo similar changes.

Within this wide distributional range, adult skipjack tuna occur in varying densities in different parts of the oceans, with areas of moderate to high densities quite often being defined by the existence of a fishery (darkly shaded areas, Fig. 10). In the Indian Ocean, skipjack tuna fisheries occur in the Gulf of Aden and the vicinity of Laccadive Islands, Maldive Islands, and Sri Lanka, and sporadically along the coastlines of countries bordering the ocean from Australia across the Indian subcontinent to South Africa. In the western Pacific Ocean skipjack tuna fisheries occur in the vicinity of Japan, Ryukyu Islands, Taiwan, Philippines, Bonin Islands, Mariana Islands, Caroline Islands, Palau Islands, Papua New Guinea, Solomon Islands, New Caledonia, Australia, and New Zealand. In the north along lat. 40° to 45°N, the fishery extends eastward to long. 176°W. In the Equatorial Countercurrent and North Equatorial Current the fishery extends eastward to long. 154°W. In the central Pacific Ocean, fisheries occur around the Hawaiian Islands and French Polynesia. In the eastern Pacific Ocean, fisheries occur off Baja California, the Revillagigedo Islands, Clipperton Island, Central America, Cocos Island, the Galapagos Islands, and northern South America. The fisheries extend westward along the equatorial currents to long. 140°W. In the Atlantic Ocean, fisheries occur in the Gulf of Mexico, the Caribbean Sea, around Cuba, and off Africa between lat. 20°N and 15°S.

2.3 Determinants of distribution changes

2.31 Larvae and juveniles

Surface currents influence the distribution of skipjack tuna larvae indirectly by modifying the distribution of sea-surface temperatures (Brock 1959; Blackburn 1965). In both the Atlantic and Pacific Oceans the warm North and South Equatorial Currents flow westward and are deflected poleward as they reach the continents. Cold currents at high latitudes flow eastward and are deflected toward the Equator upon reaching the western shores of the continents (Fig. 15). This results in the expansion of the warm water area favorable for spawning in the west and the restriction of similar area in the east, as shown by the 25°C isotherm in Figure 11. A similar situation exists in the Indian Ocean, except that it applies only to the Southern Hemisphere.

Currents can directly influence the distribution of skipjack tuna larvae by transporting the eggs during the incubation period and early growth stages of the larvae. However, such influence is localized and not easily discernible because it is overshadowed by the extensiveness of the spawning area and the length of the spawning season. Even around islands, where the currents are modified to form wakes and eddies (Barkley 1972) in which zooplankton and fish larvae can be entrapped, skipjack tuna larvae were found to be randomly distributed (Nakamura and Matsumoto 1967; Powles 1977).

Skipjack tuna, as well as other tunas, require warm water for spawning and larval survival; consequently, the limits of larval distribution are governed largely by water temperature. The range of distribution can be described roughly by the location of the mean 25°C surface isotherm (Fig. 11). Others (Ueyanagi 1969; Mori 1972) have used the 24°C isotherm to describe the distributional range. This does not imply that

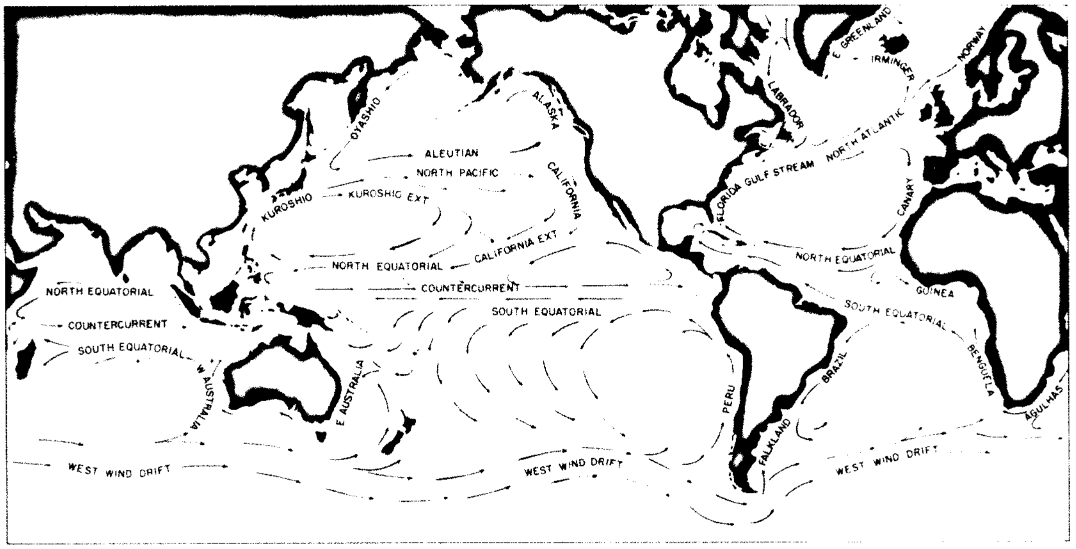


Figure 15.—Ocean current systems (from Brock 1959).

skipjack tuna larvae are not found in water temperatures below 25° or 24°C, for they have been take at surface temperatures as low as 22.1°C (Matsumoto 1974).

Both the optimum and minimum temperatures for skipjack tuna larvae differ by areas (Table 4). In the western Pacific Ocean between lat. 30°N and the Equator, all larvae taken in surface night tows from 10 cruises of the RV *Shoyo Maru* (data from Ueyanagi 1969) were from waters 25° to 29°C. The most productive tows, in occurrence and number of larvae, were made in 28°C water. The lowest and highest temperatures in which skipjack tuna larvae were caught were 23.5° and 30°C, respectively. These larvae were taken in subsurface tows at 20-30 m (not included in table). In the vicinity of the Hawaiian Islands between lat. 10° and 26°N (Table 3), nearly all larvae caught in surface night tows from nine cruises of the RV *Townsend Cromwell* in 1964 and 1965 (unpubl. data, Honolulu Laboratory), were from waters 23°-26°C, and the most productive tows, in occurrence and number of larvae, were in 25° and 24°C water, respectively. The coldest water in which skipjack tuna larvae were caught was 22.1°C. Strasburg (1960), using opening and closing plankton nets towed obliquely at 0-60, 70-130, and 140-200 m in the equatorial central Pacific, reported the capture of a skipjack tuna larva (Fig. 16) in water well below 65°F (18.5°C) and felt that 60°F (15.6°C) was the minimum temperature in which tuna larvae could occur.

Studies of tuna larvae taken in plankton nets by others (Matsumoto 1958; Strasburg 1960; Klawe 1963; Ueyanagi 1969; Richards and Simmons 1971) have shown that skipjack tuna larvae generally are limited to the upper 50 m of water, that they undergo vertical diel migration, and that the vertical migration is most pronounced in the upper 30 m. All of these studies show that surface tows at night caught considerably more larvae than day tows. Although Strasburg's results (Fig. 16) suggest that larvae may be present below the thermocline, Klawe (1963) reported that none were taken below the mixed layer in the eastern Pacific Ocean.

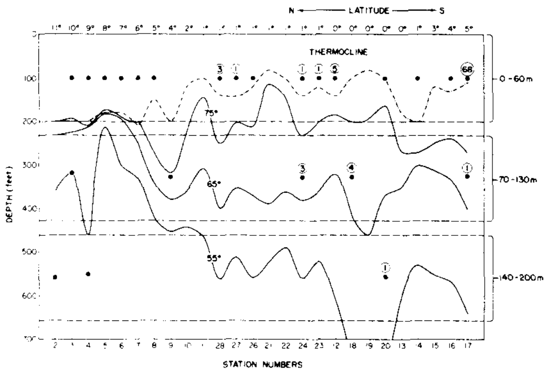


Figure 16.—Isotherm and thermocline depths at closing net plankton stations in the central equatorial Pacific Ocean (lat. 11°N-5°S; long. 140°W), *Hugh M. Smith* cruise 33. Circled numbers denote skipjack tuna larvae, dots represent closing net tows yielding other tuna larvae (modified from Strasburg 1960).

Juvenile skipjack tuna (up to about 47 mm) also are found near the surface. Sampling for juvenile tunas with a small mesh midwater trawl, Higgins (1970) found that shallow tows (maximum depth of 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.

Higgins (1970) found also that juvenile skipjack tuna were significantly larger in deep tows than in shallow tows, and night and morning tows at the deeper depth also tended to catch larger juveniles than day tows. He tentatively concluded that the smaller juveniles live primarily in the upper isothermal layer, whereas the larger juveniles tend to occur in or migrate to deeper water.

2.32 Adults

(1) Surface temperature

The temperature range within which skipjack tuna appear to be restricted has been reported on a world scale by Laevastu and Rosa (1963) as 17° to 28°C and 19° to 23°C for the major fisheries. Specific regions of the world oceans not only show some variations, but extend the range further. Uda

Table 4.—Skipjack tuna larvae taken in surface tows during 10 cruises of the *Shoyo Maru* in the western North Pacific Ocean (Ueyanagi 1969) and in 9 cruises of the *Townsend Cromwell* in the central North Pacific Ocean (unpubl. data, NMFS Honolulu Laboratory).

	Western Pacific (lat. 30°N-0°)				Central Pacific (lat. 10°-26°N)[1]			
Surface temp. (°C)	Number tows	Number larvae	Percent occurrence	Larvae per tow	Number tows	Number larvae	Percent occurrence	Larvae per tow
20	3	0	0	0	1	0	0	0
21	6	0	0	0	1	0	0	0
22	10	0	0	0	14	11	42.8	0.79
23	5	0	0	0	29	88	58.6	3.04
24	15	0	0	0	46	192	56.5	4.17
25	27	15	25.9	0.56	38	157	65.8	4.13
26	66	109	47.0	1.65	31	74	61.3	2.38
27	109	260	46.7	2.38	5	3	20.0	0.60
28	119	611	50.4	5.13	—	—	—	—
29	92	217	31.6	2.36	—	—	—	—
30	6	1	16.6	0.17	—	—	—	—

[1] Includes only tows made during the spawning season, March-September.

(1957) gave the range off Japan as 17.5° to 30°C for all occurrences; Broadhead and Barrett (1964) and Williams (1970) reported a range of 17° to 30°C in the eastern Pacific Ocean; Jones and Silas (1963) reported regular catches of skipjack tuna off southern India from 27° to 30°C water; Robins (1952) reported skipjack tuna taken in temperatures of 14.7° to 20.8°C in Tasmanian waters; and Eggleston and Paul (1978) gave a range of 16° to 22°C off New Zealand. Thus, the overall temperature range of skipjack tuna occurrence could be taken as 14.7° to 30°C. Figure 10 shows that the 15°C isotherm adequately demarks the range of skipjack tuna occurrence. (Note: The 15°C isotherms shown were for the warmest month of the year in both hemispheres and, hence, represent the maximum average poleward displacement.)

As in the distribution of the larvae, temperature plays an important role in the distribution of the adults. Its influence is usually not obvious in the tropics, where the temperature is relatively uniform throughout the year, but is most noticeable at the higher latitudes. This is readily seen in the persistence throughout the year of high catch rate cells of skipjack tuna taken on the tuna longline in the equatorial Pacific, as compared with the latitudinal shifting of such cells near the northern and southern boundaries of distribution in response to seasonal changes in temperature (Matsumoto 1975), and in the marked seasonality seen in the surface fisheries near the northern and southern limits of distribution in the northeastern and southeastern Pacific, Hawaii, northwestern Pacific, Papua New Guinea, and New Zealand (Kawasaki 1965b; Joseph and Calkins 1969; Uchida 1975; Habib 1976, 1978; Forsbergh 1980; Habib et al. 1980a, b, c; Wankowski 1980).

That skipjack tuna seek preferred temperatures is indicated by catch patterns in the various fisheries. These temperatures vary by regions: 20° to 24°C in the northwestern Pacific fishery (Uda 1957), 20° to 30°C in the eastern Pacific fishery (Williams 1970), 28° to 29°C off southern India (Jones and Silas 1963), 16° to 18°C off Tasmania (Robins 1952), and 19° to 21°C off New Zealand (Eggleston and Paul 1978). Sharp (1978) listed the optimum temperature range of commercial activities and schooling behavior of skipjack tuna for five hypothesized subpopulations in the Pacific Ocean as follows: northeastern Pacific, 20°-26°C; southeastern Pacific, 20°-28°C; New Zealand, 17°-23°C; Papua New Guinea-Solomon Islands, 28°-30°C; and northwestern Pacific, 20°-28°C. Others who have investigated the relationship of skipjack tuna and water temperature include Kuroda (1955), Kawasaki (1958, 1965a), Schaefer (1961b), Radovich (1963), Kasahara and Tanaka (1968), Uchida (1970), Seckel (1972), and Yasui and Inoue (1977).

(2) Salinity

According to Blackburn (1965), "Salinity measurements can be important in characterizing and detecting oceanic features with which tuna are associated but salinity *per se* has no known direct effect on tuna distribution." Barkley (1969), however, showed that the habitat of adult skipjack tuna in the Pacific Ocean appears to coincide geographically with areas where a shallow salinity maximum is present seasonally or throughout the year (Fig. 17), and suggested that the normal habitat of skipjack tuna is the lower salinity water which overrides the shallow salinity maximum.

Seckel (1972) observed that skipjack tuna landings in the Hawaiian skipjack tuna fishery were high in those years when initial warming of the water occurred before the end of February and the mean monthly salinity during spring was between 34.6 and 34.8‰, the latter value indicating the northern boundary of the California Current Extension water. Yasui and Inoue (1977) also noted good to excellent fishing off southern Japan in those years when the mean surface salinity was 34.81‰ and the mean surface temperature was 21.2°C. In poor years the mean salinity was 34.87‰ and the mean temperature was 19.8°C. In both instances, good fishing was related to favorable salinities, as well as favorable water temperatures.

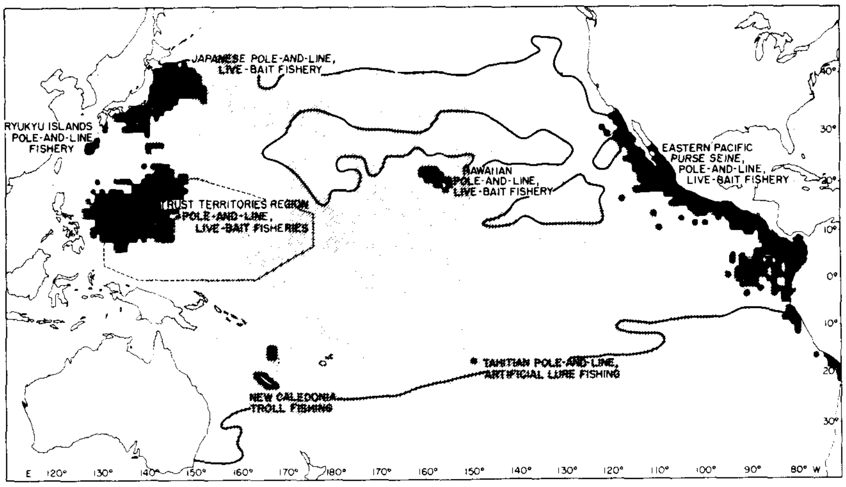


Figure 17.—Distribution of skipjack tuna in the Pacific Ocean (after Rothschild and Uchida 1968). The contours mark the boundaries of the area where a shallow subsurface salinity maximum is present either seasonally or permanently (from Barkley 1969).

Donguy et al. (1978), in comparing charts of skipjack tuna catches by the Japanese in the western Pacific for the period 1974-76 and surface salinity charts for 1957-75, noted that the catches of skipjack tuna were greater in waters with salinities of 35‰ or less in the area east of Papua New Guinea. In this instance the 35‰ isohaline in the region was found to be associated with the presence of a convergence.

(3) Surface currents

The circulation features of the major currents in both the Pacific and Atlantic Oceans, described previously in connection with distribution of larvae, also affect the distribution of adults. The flow toward the Equator of cool water on the eastern side of the oceans tends to restrict the distribution of fish in that region, and the poleward flow at the western side of the oceans permits a broader distribution there.

Surface currents affect the distribution of skipjack tuna in other ways. In currents flowing meridionally, tuna are considered to be distributed along the axis of the current and in greater abundance than in adjacent waters (Blackburn 1965). Such a relation was noted by Kawasaki (1958) and Uda (1962a) in the Kuroshio (warm current from the south) off Japan. Uda observed that more skipjack tuna became available to the fishery when the warm Kuroshio water extended over a broad area; and conversely, that a strong Oyashio (cold current from the north) hindered the movement of fish and catches were low.

Other effects of currents on the movement of fish have been indicated in the models of migration of skipjack tuna proposed by Seckel (1972), Williams (1972), Matsumoto (1975), and others. These migration models are described in Section 3.51.

(4) Hydrographic features

Fish tend to aggregate in areas where warm and cold water intrusions are well developed, in eddies, in areas of turbulent mixing, in oceanic fronts, convergences, upwelling, and other hydrographic features (Uda 1961, 1962b). Kawasaki (1958) noted that skipjack tuna fishing grounds developed off Japan when the warm Kuroshio water spread thinly over colder water and when the Kuroshio meandered in a complicated pattern. Uda (1962a) reported that good catches were also made when both the Kuroshio and the cold Oyashio currents were strong, under which conditions the skipjack tuna were concentrated along the boundary between the warm and cold water (polar front). Uda (1962b) further reported that in the eddies associated with the polar front, skipjack tuna were found in the warmer anticyclonic eddies along the front. Donguy et al. (1978) showed that skipjack tuna catches by the Japanese in the western Pacific, east of Papua New Guinea, were concentrated along and on the low salinity side of convergences (Fig. 18). Forsbergh (1969) reported that a marked salinity front was found at all seasons in the Panama Bight and that the abundance of skipjack (and yellowfin) tuna in the northern part of the Bight appeared to be related to the seasonal cycle of upwelling.

(5) Vertical distribution

Based on studies of tuna longline catches, Yabe et al. (1963) indicated that tunas are distributed by depth layers with the skipjack tuna occupying the shallowest layer, followed in order by the bluefin tuna, *Thunnus thynnus*; yellowfin tuna; bigeye tuna, *T. obesus*; and the albacore, *T. alalunga*. Skipjack tuna were 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 that the skipjack tuna are taken only incidentally on the deep-fishing longline.

Results from the use of echo sounders and underwater observations from small submarines 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 tuna when the schools subsequently rose to the surface. Strasburg et al. (1968) encountered skipjack tuna schools at depths of 98 to 152 m in Hawaiian waters during their numerous dives in a submarine. Tracking skipjack tuna tagged with ultrasonic transmitters in Hawaiian waters (Dizon et al. 1978) indicated that this species spends its time between the surface and 263 m during the day, but remains near the surface (within 75 m) at night. These depths are well within the depth range in which the yellowfin tuna are usually caught by longline.

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

The skipjack tuna is normally heterosexual; however, a few instances of hermaphroditism have been recorded (Nakamura 1935; Raju 1960; Uchida 1961; Thomas and Raju 1964). In the two specimens described by Uchida from Hawaiian waters, the left and right gonads of one fish (Fig. 19) and the left gonad of the second fish were divided into three segments: an anterior ovarian section, a middle testicular section, and a posterior ovarian section; whereas the right gonad of the second fish was divided into two segments: an anterior two-thirds testicular section and a posterior one-third ovarian section. In both fish the anterior ovarian sections contained ripe resorbing ova but not in the posterior ovarian sections, a condition that could result from extrusion of ova from the latter during spawning but not from the former, due to the lack of an adequate oviduct. The testicular portions contained no running milt, but were described as well developed. Based on the developmental stages of the ovarian and testicular sections, Uchida believed that both fish were functional males and females.

3.12 Maturity

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.

In the Pacific Ocean, Marr (1948) recorded skipjack tuna as small as 40 cm fork length (FL) with spent ovaries from

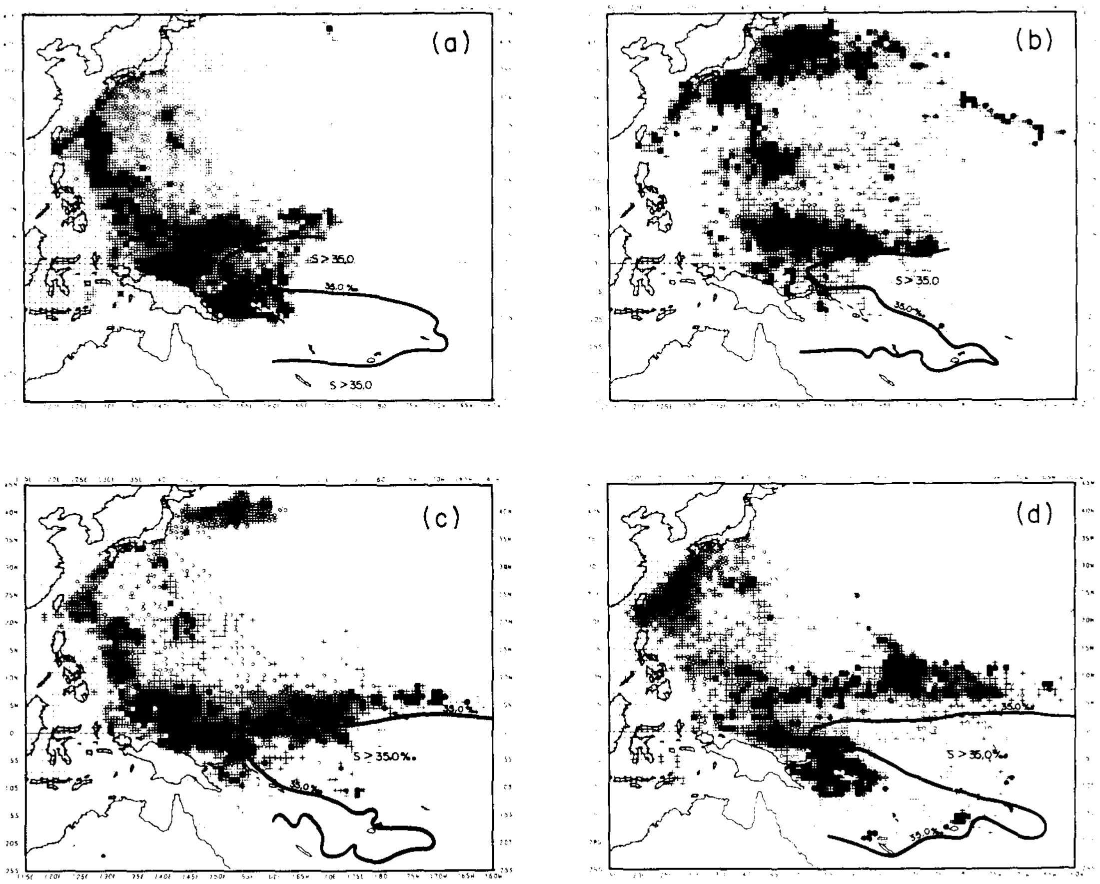


Figure 18.—Distribution of skipjack tuna catches and surface salinity in the western Pacific: a) January-March 1974, b) July-September 1974, c) October-December 1974, and d) January-March 1975. No catch denoted by 0, catches by +, and dark squares represent >700 t (from Donguy et al. 1978).

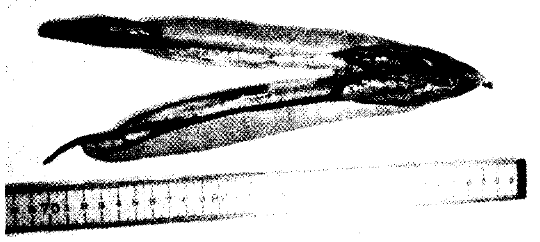


Figure 19.—Ovotestes of a hermaphroditic skipjack tuna (from Uchida 1961).

the Marshall Islands; Wade (1950) recorded fish in the 40.0 to 40.9 cm size class with ripe and spent ovaries from Philippine waters, and reported the capture of a female in the 34.0 to 34.9 cm size class having ripe ovaries; and Brock (1954) noted that the smallest fish that possessed maturing ova during the spawning season in Hawaiian waters were around 40 to 45 cm. Raju (1964c) estimated the size of sexual maturity of skipjack tuna in the Indian Ocean around Minicoy Island as about 40 to 45 cm. He derived his estimate from his observations that 1) the smallest skipjack tuna that possessed ovaries with maturing ova during the spawning season was around 40 to 45 cm and 2) remnants of mature ova were present in fish above 40 cm but none in fish below this size. Stequert (1976) reported first spawning of skipjack tuna at 41 to 43 cm off the northwest coast of Madagascar. Simmons (1969) reported minimum size of females at maturity in the Atlantic Ocean as 41 cm, as determined from fish with spawned or spent ovaries.

From the above, it appears that the minimum size of female skipjack tuna at maturity is 40 cm and that initial spawning can occur in fish between 40 and 45 cm or larger. The unusually small female (34.0-34.9 cm size class) with ripe ovaries reported by Wade (1950) could be a rarity or a case of erroneous staging of the gonads (see Section 3.15 for discussion of maturity stages of gonads).

3.13 and 3.14 Mating and fertilization

Iversen et al. (1970) observed what they believed to be courtship of skipjack tuna from an underwater sled towed from the RV *Charles H. Gilbert.* While observing a pair of skipjack tuna approximately 50 cm long, swimming close together back and forth in front of the sled, they noticed that the fish's 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 two fish swimming in tandem, one ahead of the other. The latter fish, situated slightly below the lead fish, would approach 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 trailing fish would display dark vertical bars on its side, similar to that displayed during feeding. A second pair of skipjack tuna swimming in tandem were observed from the deck of the vessel. On two occasions the lead fish was seen to wobble from side to side and the trailing 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 (see Section 3.41 on feeding behavior).

Observations of similar behavior, believed to be mating or courting acts, have been observed by longtime skipjack tuna fishermen (e.g., R. M. Oka[6]) in the Hawaiian Islands. Schools of fish displaying such behavior were reported to be reddish- or purplish-hued and as being disinterested in feeding. The senior author has observed similar schools on several occasions and when the visibility, sea, and light conditions were right, whitish trails of spawn could be seen at the point of contact when two fish came together. The contacts seemed to occur randomly throughout the rapidly moving schools.

These observations suggest that mating is most likely promiscuous, and other observations such as the collection of eggs in various stages of embryonic development in plankton nets suggest that fertilization occurs externally.

3.15 Gonads

In the early years, sexual maturity of the skipjack tuna was determined by the general appearance of the gonad (Matsui 1942; Marr 1948; Yao 1955; Williams 1964). The characters most used were size of gonad and degree of softness or turgidity. Others (Buñag 1956; Raju 1964c; Kawasaki 1965a) felt that these general characters alone were inadequate even for gross classification. Some improvements were made by including the description of ova in the various stages of development (Buñag 1956; Schaefer and Orange 1956; Raju 1964c; Yoshida 1966; Simmons 1969; Batts 1972c), but the classification still remained subjective and was prone to variations caused by the observer's interpretation of the various stages.

Buñag (1956) and Raju (1964c) classified sexual maturity on the basis of ovum diameter measurements. Yoshida (1966) and Batts (1972c) provided ovum diameter measurements along with descriptions of ova, ovaries, or both. Yet the classification by these authors differed noticeably, since a standard scale defining the various stages of development had not been established for tunas. Buñag (1956) attempted to classify the stages according to the International Maturity Scale,[7] but no one else has followed his example. A summary of the maturity stages of female skipjack tuna based on ova diameter and descriptions of ova and ovaries from the preceding studies is presented in Table 5.

To avoid measuring ova, some authors have used gonad indices (G.I.) to determine maturity (Yabe 1954; Schaefer and Orange 1965; Orange 1961; Raju 1964c; Yoshida 1966; Batts 1972c). Schaefer and Orange (1956) obtained a linear relationship between ovum diameter and G.I. (Fig. 20) of fish taken in the eastern tropical Pacific. They thus concluded that maturity of female skipjack tuna could be determined on the basis of G.I. values. Their data, however, consisted mainly of G.I. below 50 from samples that included only few fish larger than 60 cm. Raju (1964c) also obtained similar results (Fig. 21) from fish taken off Minicoy Island in the Indian Ocean; however, his sample included larger fish and the largest G.I. was about 66.

Yoshida (1966), whose study was based on fish from the Marquesas and Tuamotu Islands in the central Pacific, reported G.I. values ranging from 20 to over 90 for ovaries in the developing stage (ovum diameters 0.5 to 0.6 mm) and from 30 to nearly 100 for ovaries in the advanced stage (ovum diameters 0.6 to 0.7 mm). He noted that there was a large overlap in the G.I. values between these two stages and that the linear relationship reported by Schaefer and Orange

Table 5.—Summary of maturity stages of female skipjack tuna.

Stage	Designation	Largest ova diameter (mm)	Description of ova	Description of ovary
I	Immature	0.15	Ova transparent; with nucleus	Slender, elongate; sex determinable
II	Early maturing	0.35	Ova opaque; yolk forming	Enlarged; ova not visible
III	Late maturing	0.60	Ova opaque; yolk granular	Enlarged, turgid; ova visible
IV	Mature	0.85	Ova transparent; with oil cluster or oil droplet	Enlarged, begin losing turgidity; ova visible, easily dislodged
V	Ripe	1.00	Ova with yellow oil droplet	Greatly enlarged, not turgid; ova easily dislodged, some free in lumen; extruded by pressure
VI	Spent	0.55	Ova remnants 1.0 mm	Flaccid, with remnants of ripe ova

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[6] R.M. Oka, formerly commercial skipjack tuna pole-and-line fisherman and leading fisherman on the RV *Charles H. Gilbert*, pers. commun. June 1969.

[7] Maturity scale adopted by the International Council for the Exploration of the Sea, as cited by Clark (1934).

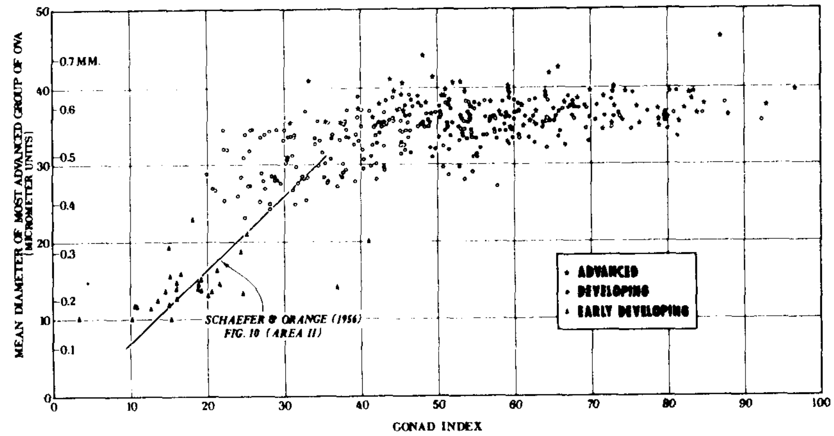

Figure 20.—Relationship between gonad index (ovary weight relative to fish length[3]) and mean diameter of most advanced group of ova of skipjack tuna from the Marquesas and Tuamotu Islands (from Yoshida 1966).

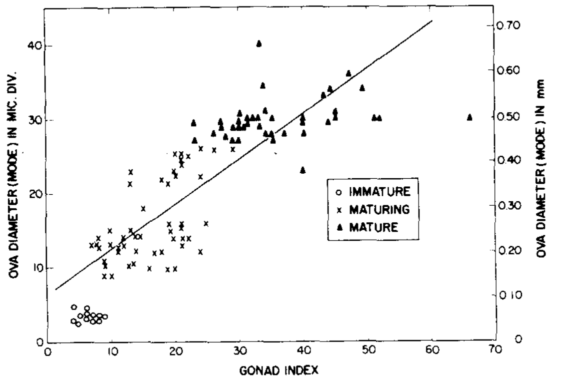

Figure 21.—Relationship between gonad index (ovary weight relative to fish length[3]) and modal length of largest group of ova of skipjack tuna from Minicoy (from Raju 1964c).

(1956) was not applicable to G.I. values above 36 (Fig. 20). We should also add that the linear relationship shown by Raju (1964c) in Figure 21 does not seem valid either. Because of the wide range of G.I. values for ovaries in the same developmental stage, the gonad index does not seem to be a sound measure of maturity for skipjack tuna.

3.16 Spawning

(1) Fecundity

Relatively little has been published concerning the fecundity of skipjack tuna. The fecundity range has been reported as 100,000 to 2 million ova for fish 43.0 to 87.0 cm long from the Pacific Ocean, 87,600 to 1,977,000 ova for fish 41.3 to 70.3 cm long from the Indian Ocean, and 141,000 to 1,331,000 ova for fish 46.5 to 80.9 cm long from the Atlantic Ocean (Table 6). Plots of number of ova in the most advanced mode against fish size by Joseph (1963), Raju (1964a), Sim-

Table 6.—Observed fecundity estimates for skipjack tuna.

Source of data	Locality	Number of fish	Fish length (range) (mm)	Estimated ova (range)
Pacific Ocean				
Yabe (1954)	Ryukyu Islands	5	468-610	113,364-859,897
Rothschild (1963)	Hawaiian Islands	3	440-870	280,000-1,900,000
Joseph (1963)	Eastern Pacific	42	614-715	210,000-1,490,000
Yoshida (1966)	Marquesas Islands	4	430-750	100,000-2,000,000
Indian Ocean				
Raju (1964a)	Minicoy Island	63	418-703	151,900-1,977,900
Stequert (1976)	Madagascar	64	441-565	87,600-824,000
Atlantic Ocean				
Simmons (1969)	Caribbean Sea	13	465-809	262,000-1,331,000
Batts (1972c)	North Carolina, U.S.A.	31	498-704	141,000-1,200,000

mons (1969), and Batts (1972c) show considerable variation among fish of the same size. All four authors fitted regression lines to the relationship between fecundity and length (Table 7; Fig. 22), but due either to inadequate sample size or to samples of limited size ranges, the regression lines varied noticeably. Raju (1964a) fitted regression lines also to the relationship between fecundity and the square of the fish length, and both he and Simmons (1969) fitted regression lines to the relationship between fecundity and the cube of the length. The latter regressions had the higher coefficients of correlation, although all four regressions were statistically significant ($P = 0.01$). Joseph (1963) and Raju (1964a) fitted regression lines to the relationship between fecundity and fish weight also. Both reported smaller standard error of estimates than those obtained from any of the fecundity-length relationships, whereas the latter obtained a coefficient of correlation only slightly higher than that of the fecundity-length cubed relationship. The closeness of the coefficients of correlation is understandable, since weight is nearly proportional to the cube of the length for skipjack tuna. Consequently, either the length cubed or weight may be used to describe the relationship between fecundity and fish size.

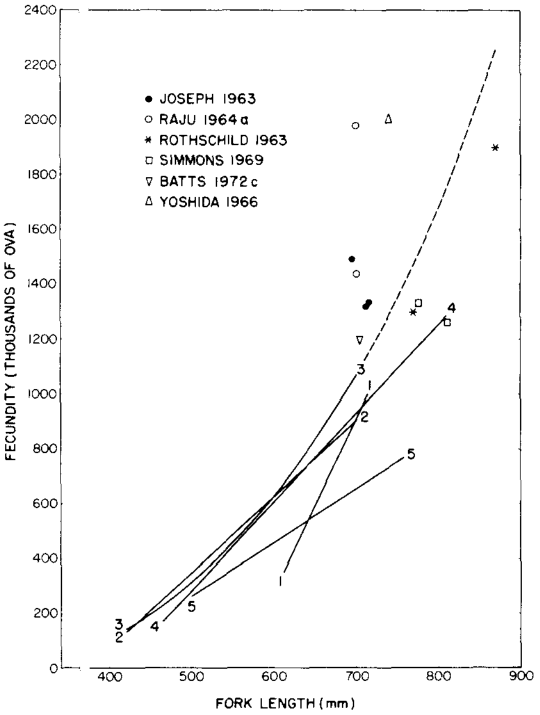

Figure 22.—Regressions of fecundity on length and observed fecundity estimates of skipjack tuna above 690 mm. 1) Joseph (1963); 2) Raju (1964a); 3) fecundity-length^3, Raju (1964a); 4) Simmons (1969); and 5) Batts (1972c).

Using Raju's (1964a) fecundity-length cubed relationship, the calculated fecundity estimate of skipjack tuna at minimum spawning size (40.0 cm) is 110,000 ova. That Raju's fecundity-length cubed relationship holds reasonably well for fish larger than about 69.0 mm is noted in Figure 22, which shows the extension of the curve and also the observed fecundity of fish above this size by various authors.

In spite of the acceptable fecundity-length cubed relationship noted above, it would be most difficult to estimate the total annual egg production of the skipjack tuna because of 1) the extremely large variation in number of ova among fish of the same size, 2) the uncertainty in the number of times a fish spawns during the year (Section 3.16), 3) the possibility of reduced fecundity at successive spawnings in the same year (Joseph 1963), and 4) incomplete knowledge concerning the size composition and total abundance of the spawning stocks.

(2) Frequency

The possibility of skipjack tuna spawning more than once during a season has been discussed by several authors. Brock (1954) was of the opinion that the multimodal distribution of ovum diameters during the spawning season and its absence at other times indicated that individual skipjack tuna taken in Hawaiian waters spawn several times. As supporting evidence, he cited the absence of an overall trend in ovum diameters during the spawning season (Fig. 23) and the absence of spawned-out fish until after the end of the spawning season. Buñag (1956) determined multiple spawning by following the movement of ovum diameter modes through the various stages of development as indicated by ovum diameter frequency plots (Fig. 24). Raju (1964c) determined multiple spawning from the Indian Ocean by satisfying the four lines of evidence used by Clark (1934): 1) The presence of multiple modes in diameter frequency polygons, 2) obtaining a high correlation in the progression of successive modes, 3) the

Table 7.—Comparison of fecundity-length and fecundity-weight relationships of skipjack tuna from various sources.

Source	Relationship	*a* (thousands)	*b*	Standard error of estimate (thousands)		*P*
Joseph (1963)	[1]$Y = a + bL$ (1)	−3,503	6.326	276	—	—
	$Y = a + bW$	−608.807	88.613	273	—	—
Raju (1964a)	[1]$Y = a + bL$ (2)	−1,004.94	2.713	28.6	0.645	≤0.01
	$Y = a + bL^2$	−292.26	0.00254	27.4	0.668	≤0.01
	[1]$Y = a + bL^3$ (3)	−109.0	0.00000342	24.7	0.741	≤0.01
	$Y = a + bW$	−67.69	67.01	22.5	0.789	≤0.01
Simmons (1969)	[1]$Y = a + bL$ (4)	−1,333.541	3.238	—	0.873	≤0.01
	$Y = a + bL^3$	—	—	—	0.886	≤0.01
Batts (1972c)	[1]$Y = a + bL$ (5)	−632.085	1.854	—	—	—

[1] Number in parentheses refers to regression line in Figure 22.

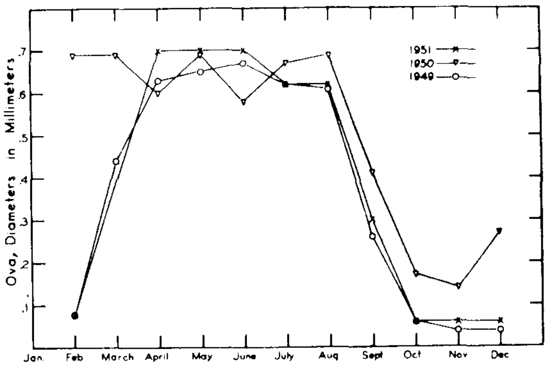

Figure 23.—Average modal diameter of the largest group of ova in skipjack tuna ovary samples collected from1949 to 1951 in Hawaiian waters (from Brock 1954).

presence of ova remnants in maturing ovaries, and 4) 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 skipjack tuna spawns more than once during a season. How many times it spawns is not yet known, but utilizing the reports by Brock (1954) and Buñag (1956), the number of spawnings can be estimated, at least for fish in Hawaiian waters.

From Brock's 1949 and 1951 data in Figure 23, we note that in Hawaiian waters, fish with immature ova (ova diameter 0.1 mm) occurred in February, and in 2 mo the ova developed into the mature stage (ova diameter 0.7 mm). If development continues at this same pace, the ova should be in the ripe stage (Yabe 1954; Yoshida 1966; Batts 1972c) with diameters from 0.8 to 1.2 mm in late April or early May. This is supported by the first captures of larval skipjack tuna in Hawaiian waters in late April and early May (Seckel 1972). Buñag (1956), as well as others, had 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. 24), i.e., ova in the most advanced group are not much larger than about 0.58 mm (18 micrometer units). Ova of this size would require about 6-7 wk to reach the ripe stage (based on Brock's data), exclusive of a probable resting period after the initial spawning. Hence, the earliest that a skipjack tuna could 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 species to spawn a third time in the area. This does not mean that a third or even a fourth spawning could not occur. In fish with ovaries developing more than two groups of ova, migration to warmer waters in the fall and winter could allow it to spawn a third or even a fourth time during a year.

Another bit of information may be gleaned from Figure 23. 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 3.5 mo.

(3) Spawning in captivity

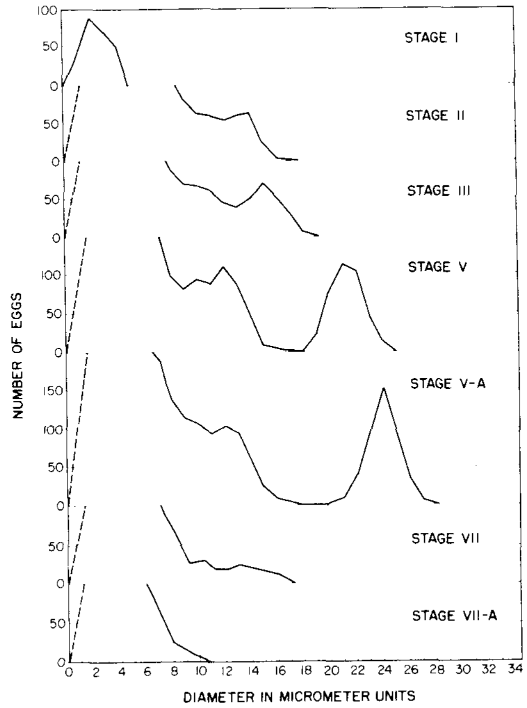

Figure 24.—Ova diameter frequency polygons of skipjack tuna with the stages of ova development (from Buñag 1956). [Each micrometer unit equals 0.0325 mm.]

Current interest in mariculture has resulted in many attempts to rear tunas in captivity. Collection of ripe ova from females at sea has only resulted in sporadic success, probably due to the paucity of running ripe females in the commercial catches and because attempts to hold adults as brood stock has proven inefficient and costly.

In June and July of 1980, female skipjack tuna (1.4-2.2 kg) confined at the Kewalo Research Facility of the U.S. National Marine Fisheries Service in Honolulu ovulated ripe ova within 8 h after capture (Kaya et al. 1982). The rapid development of the ova, followed by ovulation and spawning, apparently was induced by stresses experienced by the fish during capture and confinement. The ripe ova measured approximately 1.0 mm as compared with unovulated ova, 0.59-0.74 mm, obtained from fish taken from the same school and iced immediately upon capture. Artificial fertilization of the ripe ova resulted in successful embryonic developement and subsequent hatching of the larvae. Males brought live to the holding tanks did not respond in the same manner. Their testes were identical to those of fish iced immediately upon capture. Although all testes were mature, they failed to yield milt on moderate stripping pressure. Small amounts of thick milt obtained from excised testes, however, were successfully used in fertilizing the ripe ova stripped from captive females.

The rapid maturation and ovulation processes brought on by capture and confinement stresses are currently being exploited to routinely produce larval skipjack tunas for developmental and growth studies at the Kewalo Research Facility.

(4) Areas and seasons

Gonadal studies in the Pacific, Atlantic, and Indian Oceans indicate that skipjack tuna spawn throughout the year in tropical waters near the Equator and from spring to early fall in subtropical waters, with the spawning period becoming shorter as distance from the Equator increases. Because sampling for gonads requires the capture of adults, these studies have generally been restricted to specific areas where fishing has been done on a commerical basis or in areas subjected to heavy experimental fishing. Such areas include waters south of Japan, Philippines, Marshall Islands, Hawaiian Islands, New Caledonia, Marquesas-Tuamoto Archipelago, and off Central America in the Pacific Ocean (Kishinouye 1923; Marr 1948; Wade 1950; Brock 1954; Yabe 1954; Yao 1955; Schaefer and Orange 1956; Orange 1961; Yoshida 1966; Legand 1971; Naganuma 1979); waters off Ghana, Ivory Coast, Sierra Leone, Cape Verde Islands, Lesser Antilles, Cuba, and North Carolina in the Atlantic Ocean (Rivero and Fernandez 1954; Frade and Postel 1955; Gorbunova and Salabarría 1967; Simmons 1969; Zhudova 1969; Batts 1972c); and waters around Madagascar, Minicoy Island, and throughout the tropical zone in the Indian Ocean (Raju 1964c; Marcille and Suzuki 1974; Stequert 1976).

Larval captures, also indicative of spawning activity, have occurred not only in the areas mentioned above and in similar months, but also in intervening waters, e.g., Pacific Ocean—Matsumoto (1958), Strasburg (1960), Klawe (1963), Nakamura and Matsumoto (1967), Ueyanagi (1969, 1970); Atlantic Ocean—Richards (1969), Richards and Simmons (1971), Ueyanagi (1971); Indian Ocean—Jones (1959), Gorbunova (1963, 1965a), Jones and Kumaran (1963), Ueyanagi (1969).

3.17 Spawn

Ripe ovarian eggs are spherical, smooth, transparent, and usually contain a single yellow oil droplet (Brock 1954; Yabe 1954; Yoshida 1966). Eggs are 0.80 to 1.17 mm in diameter, with mean diameters ranging from 0.96 to 1.135 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 fully ripe and capable of being fertilized has been shown by Ueyanagi et al. (1973, 1974) and Kaya et al. (1982).

Eggs of other species of scombrids that have been fertilized artificially (frigate tuna, *Auxis thazard*; bullet tuna, *A. rochei*; and yellowfin tuna) and reared through the hatching stage are comparable in size and appearance with those of skipjack tuna (Harada et al. 1971; Harada, Murata, and Furutani 1973; Harada, Murata, and Miyashita 1973; Ueyanagi et al. 1973). Consequently, tuna eggs collected at sea in plankton nets are extremely difficult to identify to species.

The spawned eggs of tunas are buoyant in nature (Kikawa 1953; Harada et al. 1971; Harada, Murata, and Furutani 1973; Harada, Murata, and Miyashita 1973). During experiments in rearing artificially fertilized yellowfin tuna eggs, Kikawa (1953) observed that most of the eggs which were 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 buoyant eggs contained developing embryos.

3.2 Preadult phase

3.21 Embryonic phase

Development of the skipjack tuna embryo has been studied in detail by Ueyanagi et al. (1973, 1974) from artifically fertilized eggs. They noted that embryonic development proceeded rapidly after fertilization (Fig. 25) and the larvae hatched in about 1 d. The incubational period noted by the former authors was 26 to 31 h in 23° to 25°C water, 21 to 32 h in 24.2° to 27°C water, and 21 to 22 h in 26° to 29°C water; whereas, the latter reported 22 to 27 h in 27°C water. Hence, there is some indication that incubational period is related inversely to water temperature.

3.22 Larval phase

Total length (TL) is used in discussing tuna larvae. It represents the distance from the snout to the end of the longest caudal ray before the caudal fin has forked. On larger larvae total length equals fork length.

The newly hatched larva (Fig. 25) is about 2.6 mm TL (Ueyanagi et al. 1974), comparable with the size estimated by Matsumoto (1958). According to Ueyanagi et al., the larvae absorbed their yolk sac within 2 d after hatching, but due to unsuccessful initial feeding, they died within 5 d.

The development of the larvae is shown in Figures 25 and 26. 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 convergence of these melanophores at the caudal peduncle leads to the eventual formation of a single, distinct black spot (Fig. 26a-d), one of the principal identifying characters of the skipjack tuna larva. 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 which is bent slightly downward in relation to the body axis, the appearance of 2 or 3 melanophores over the forebrain area when the larvae are about 7 mm long (the number of melanophores increases 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 in larvae about 7 mm long (the number of spines increases to about 13 in larvae 11 mm TL). Pigmentation on the first dorsal fin is limited to scattered melanophores near the outer edge of the fin (Fig. 26d). 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 long. At this stage the young are considered as juveniles.

The juvenile stage is characterized by a more fusiform body and by a general increase in pigmentation over all parts of the body. Juveniles up to 47 mm (Fig. 27d) are easily identified by the concave outline of the first dorsal fin and its characteristic pigmentation, the moderately long snout, and

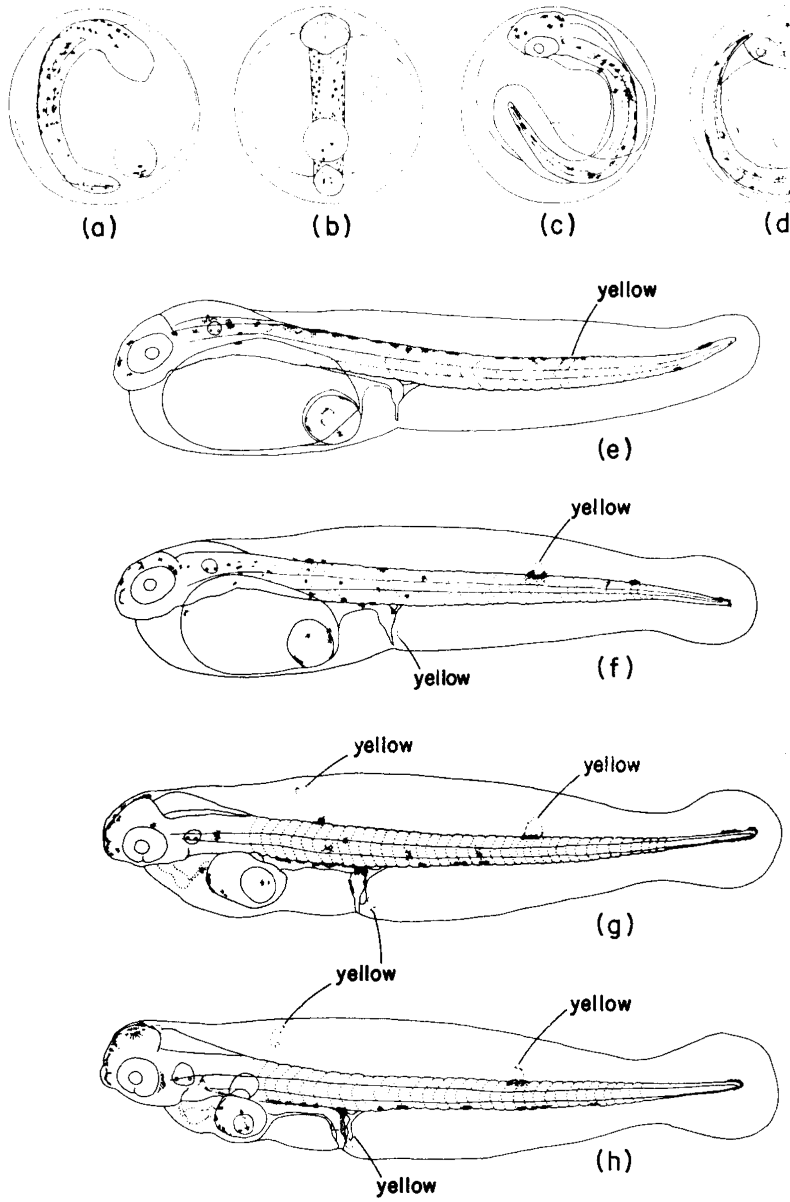

Figure 25.—Development of eggs and prelarval stage of skipjack tuna. a) 12 h after fertilization, 1.01 mm in diameter; b) 15 h, 1.00 mm; c) 22 h, 0.97 mm; d) 23 h, 0.99 mm; e) just after hatching, TL 2.65 mm; f) 4 h, after hatching, TL 2.96 mm; g) 10 h, TL 3.30 mm; h) 19 h, TL 3.36 mm; i) 33 h, TL 3.57 mm; j) 43 h, TL 3.70 mm; k) 84 h, TL 3.55 mm (from Ueyanagi et al. 1974).

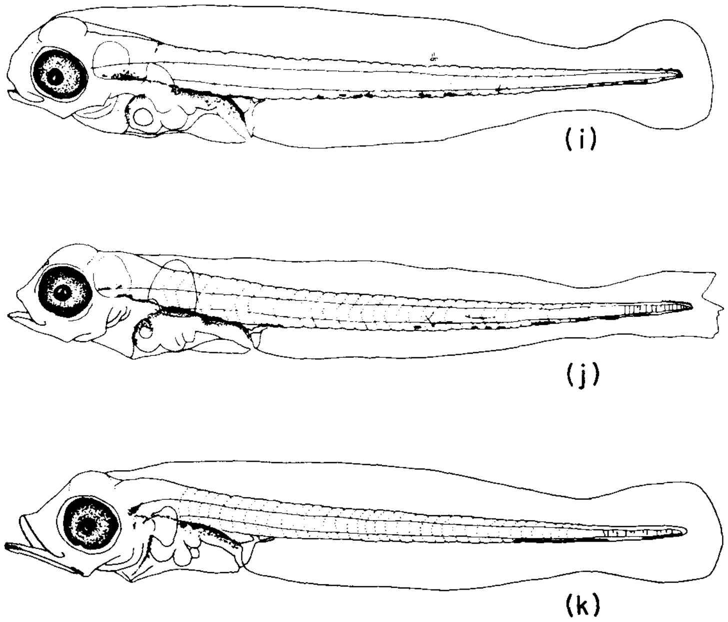

Figure 25.—*Continued.*

the number of vertebrae (20 precaudal and 21 caudal). The first dorsal fin has scattered melanophores on the first three or four 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 fins 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 tuna do not develop dark vertical bands over the dorsal half of the body.

According to Godsil and Byers (1944) and Godsil (1954), adult skipjack tuna lack a swim bladder. Richards and Dove (1971), however, reported that all tuna larvae, including larvae of the skipjack tuna, develop swim bladders and gas glands at the smallest sizes studied (2.6 mm standard length), but that the swim bladder degenerates in skipjack tuna before the fish reaches a size of 20 mm. According to these authors, degeneration of the swim bladder begins when the larvae reach a size of 9.0 mm and the swim bladder is nearly absent in specimens 24.0 mm long. Only the gas gland remains in juveniles above this size.

3.23 Adolescent phase

Juveniles below the size of first spawning (ca. 40 cm) have not been described and there is no information in the literature describing the initial appearance of the longitudinal black stripes along the sides of the body below the lateral line.

3.3 Adult phase

3.31 Maximum size and longevity

It is common practice to fit a von Bertalanffy or negative exponential curve to a set of size data and report the estimate of L_∞ thus obtained as the maximum size of a fish. It should be remembered that L_∞ is a parameter mathematically characterizing the asymptotic phenomenon we call maximum size of a fish. Our estimate of it is a statistic whose accuracy is dependent upon the representativeness of the sample used in the calculation, and whose variance is, among other things, dependent upon the sample size. Thus if we need an estimate of maximum size for other model building, e.g., estimating sustainable yield, then a statistic is what is needed. If we want to describe the maximum size of a fish, then it may suffice to report the largest fish recorded to date. In the following paragraphs we will follow the latter procedure, while later in Section 3.43, we will present estimates of L_∞.

Miyake (1968) listed a skipjack tuna in the 106.5 to 108.4 cm size class taken on tuna longline. Although he made no reference to this fish, it could well be the largest skipjack tuna ever recorded. A fish of this size class, using the length-weight relation developed for fish in the central North Pacific (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 computed from data on modal progression and otolith readings (Table 8), such a fish would have a minimum age of 8-12 yr.

3.32 Hardiness

As already discussed under Section 2.32, skipjack tuna can withstand a wide range of temperatures. At sea they have been found in water with temperatures as high as 30 °C and as low as 14.7 °C, which approaches the lower lethal ambient temperature of 13 °C, as proposed by Stevens and Fry (1971). However in the short term and locally, skipjack tuna inhabit epipelagic waters characterized by narrow variations in oceanographic features. (Additional discussion in Section 3.6.)

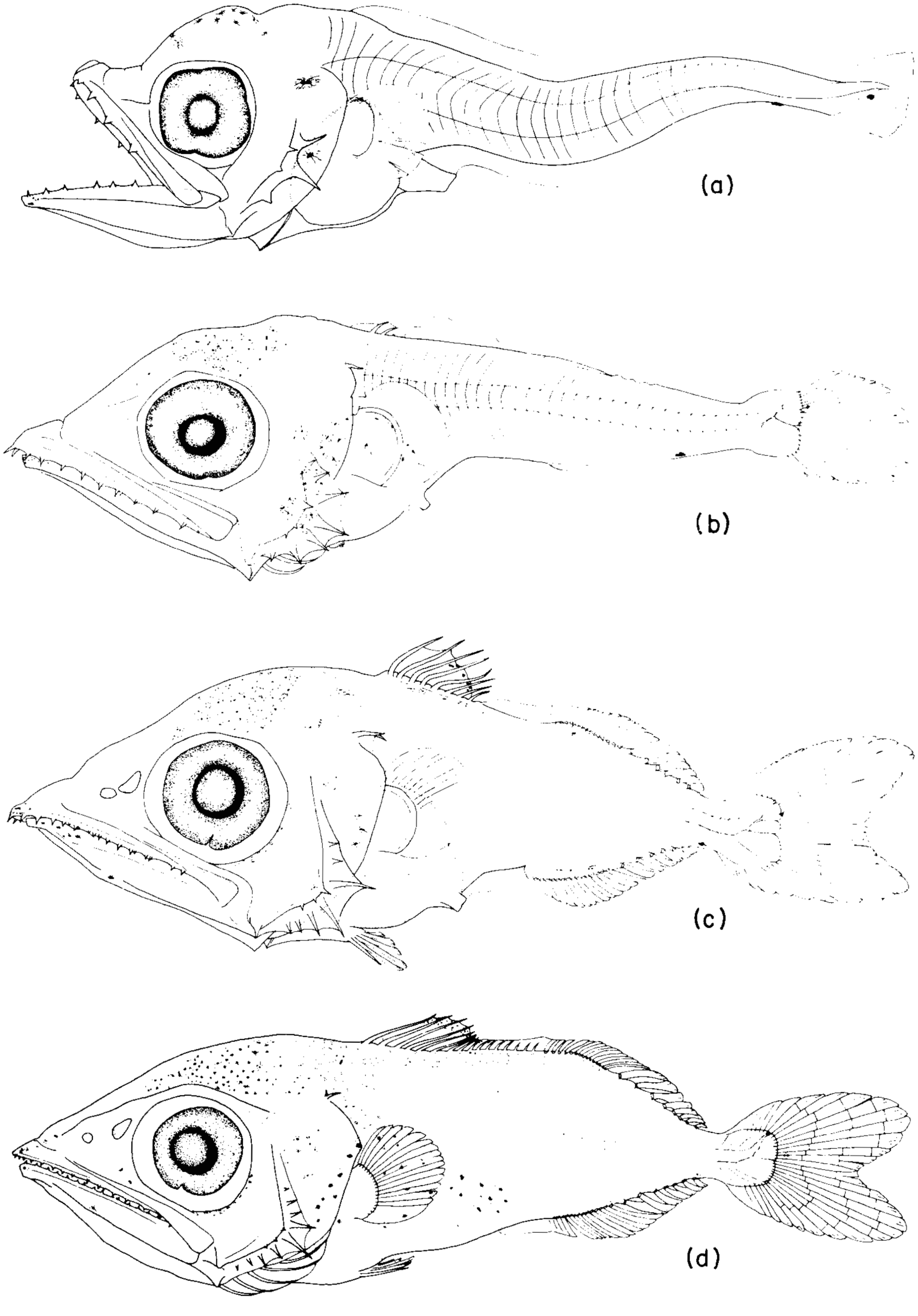

Figure 26.—Skipjack tuna larvae. a) 3.7 mm TL; b) 6.7 mm TL; c) 8.75 mm TL; d) 10.9 mm TL (from Matsumoto 1958).

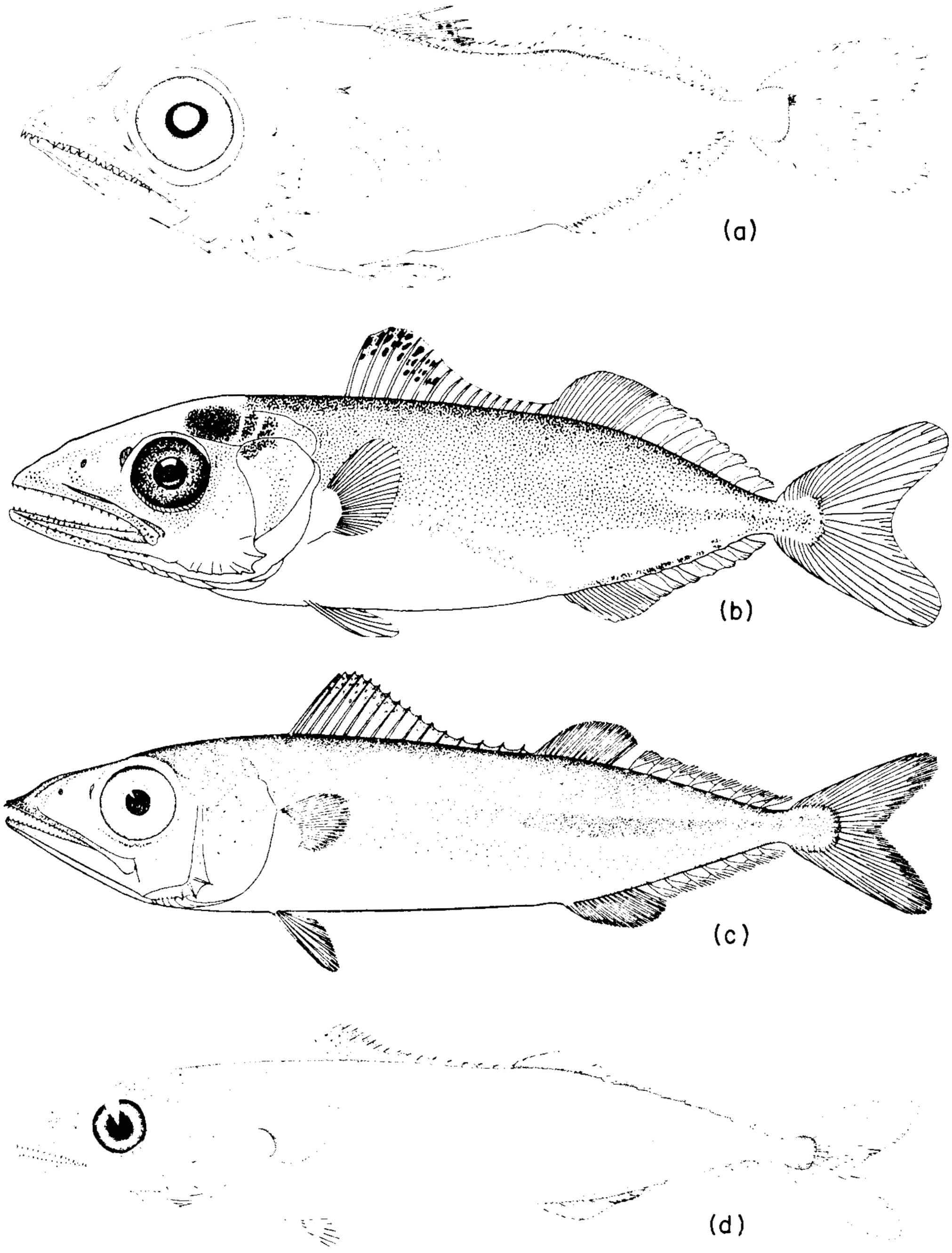

Figure 27.—Juvenile skipjack tuna. a) 14.5 mm TL; b) 21.0 mm TL; c) 27.0 mm TL; d) 47.0 mm TL (from Schaefer and Marr 1948; Wade 1950; Matsumoto 1958, 1961).

Table 8.—Size (fork length in centimeters) at age and growth parameters of skipjack tuna from the Pacific, Indian, and Atlantic Oceans.

Source	Area	Age in years								Growth parameters			Method
		0	1	2	3	4	5	6	7	t_0	K	L_∞(cm)	
Pacific Ocean													
Aikawa (1937)	East of Japan	<26	26	34	43	54	—	—	—	—	—	—	Vertebrae
Aikawa and Kato (1938)	Palau	<27	27	37	46	55	64	72	80	—	—	—	Vertebrae
Chi and Yang (1973)	Taiwan	<27	27	47	62	73	81	—	—	−0.016	0.302	103.6	Vertebrae
Yokota et al. (1961)	South of Japan-Sulu Sea	—	37	52	64	73	85	—	—	—	—	140.0	Modal analysis
Joseph and Calkins (1969)	East of Japan	0.3	25	45	62	75	—	—	—	—	0.19	141.8	Modal analysis; Kawasaki's (1963) data
Kawasaki (1965a)	South of Japan and Hawaii	—	15	45	63	73	77	—	—	—	—	—	Modal analysis
Chi and Yang (1973)	Taiwan	<36	36	60	75	—	—	—	—	−0.016	0.432	103.8	Modal analysis
Yoshida (1971)	Central Pacific	—	35	—	—	—	—	—	—	—	—	—	Modal analysis; juveniles
Uchiyama and Struhsaker (1981)	Hawaii	—	43	68	79	83	—	—	—	—	0.92	85.5	Modal analysis; Brock's (1954) data
Joseph and Calkins (1969)	Eastern Pacific	0.3	30	50	62	70	—	—	—	—	0.44	85.1	Modal analysis; Schaefer's (1961a) data
Joseph and Calkins (1969)	Eastern Pacific	0.3	37	60	76	87	—	—	—	—	0.41	107.5	Modal analysis
Joseph and Calkins (1969)	Hawaii	0.3	44	65	74	78	—	—	—	—	0.77	82.3	Tagging; corrected data from Rothschild (1967)
Joseph and Calkins (1969)	Hawaii	0.3	40	63	75	82	—	—	—	—	0.59	90.6	Tagging; uncorrected data from Rothschild (1967)
Skillman[1]	Hawaii	—	43	61	74	83	—	—	—	—	0.39	101.1	Tagging; males only
Skillman[1]	Hawaii	—	43	61	73	80	—	—	—	—	0.47	92.4	Tagging; males and females
Joseph and Calkins (1969)	Eastern Pacific	0.3	31	51	64	72	—	—	—	—	0.431	88.1	Tagging; averaged data
Joseph and Calkins (1969)	Eastern Pacific	0.3	41	59	67	70	—	—	—	—	0.829	72.9	Tagging; non-averaged data
Uchiyama and Struhsaker (1981)	Hawaii	—	44	68	83	91	—	—	—	−0.02	0.55	102.0	Otolith
Indian Ocean													
Shabotiniets (1968)	Indian Ocean	—	—	—	40-45	40-60	—	—	—	—	—	—	First dorsal spine
Atlantic Ocean													
Batts (1972a)	Western North Atlantic	—	41	49	57	64	—	—	—	−4.329	0.195	79.6	First dorsal spine

[1] See text footnote 10.

Under abnormal conditions, such as when fish are caught and handled for experimental purposes, skipjack tuna are not quite as hardy as other tunas and not nearly as hardy as some other marine or freshwater species commonly used in laboratory experiments. Skipjack tuna can be used as an experimental animal but laboratory procedures must be designed with care. Mark-recapture experiments have been conducted successfully, but the animals must be handled quickly and with care.

3.33 Competitors

Fish that have been observed or taken with feeding aggregations of skipjack tuna (Gudger 1941; Waldron 1963) have been considered as competitors of skipjack tuna. These fish include yellowfin tuna; albacore; kawakawa, *Euthynnus affinis*; frigate tuna; dolphin, *Coryphaena hippurus*; rainbow runner, *Elagatis bipinnulata*; and whale shark, *Rhineodon typus*.

In addition, seabirds may be considered as competitors, for both they and skipjack tuna feed on the same aggregations of forage fishes at the sea surface.

3.34 Predators

Predators of either juvenile or adult skipjack tuna are listed in Table 9.

3.35 Parasites, diseases, injuries, and abnormalities

Parasites found in skipjack tuna have been listed by Waldron (1963), Silas (1967), and Silas and Ummerkutty (1967). The list by Waldron includes 26 trematodes, 4 cestodes, 2 nematodes, 1 or more acanthocephalids, and 10 copepods; that by Silas includes 33 trematodes and 1 cestode; and that by Silas and Ummerkutty includes 10 copepods. The last two studies also provide information such as host, locality, location of infestation, and pertinent remarks on nomenclature or occurrence. Chen and Yang (1973) listed one species each of trematode, cestode, and nematode, and two species of acanthocephalids in skipjack tuna from waters off Taiwan. We have not seen the report by Love and Moser (1977), however, Forsbergh (1980) stated that these authors listed 36 species of trematodes, 1 specie of cestode, 12 species of copepods, and 6 species of nematodes and acanthocephalids. Cressy and Cressy (1980) presented a comprehensive account of copepods parasitic on tunas and tunalike fishes on a worldwide basis. Because of the unreliability of most past literature, they attempted to clarify the taxonomic status of both parasites and hosts. They resolved problems of synonymy of several species of copepods and listed five species parasitic on skipjack tuna which they had collected during the course of their study.

The list of parasites (Table 10) was compiled from the papers examined above.

Table 9.—Predators of either juvenile or adult skipjack tuna.

Predator	Source
Skipjack tuna	Kishinouye (1926); Marr (1948); Eckles (1949); Hotta (1953); Hotta and Ogawa (1955); E. Nakamura (1965); Matsumoto (1961); Waldron and King (1963); Dragovich (1971)
Yellowfin tuna	Kishinouye (1923); Shimada (1951); Reintjes and King (1953); Suda (1953); King and Ikehara (1956); Koga (1958); Matsumoto (1961); Alverson (1963); Mori (1972)
Albacore	Koga (1958); Mori (1972)
Bigeye tuna	Suda (1953); Koga (1958); Mori (1972)
Black marlin, *Makaira indica*	Shimada (1951); Suda (1953); Royce (1957); Yoshida (1971); Mori (1972)
Blue marlin, *Makaira nigricans*	Suda (1953); Royce (1957); Koga (1958); Yoshida (1971); Mori (1972)
White marlin, *Tetrapturus albidus*	Mori (1972)
Striped marlin, *Tetrapturus audax*	Shimada (1951); Royce (1957); Yoshida (1971); Mori (1972)
Longbill spearfish, *Tetrapturus pfluegeri*	Mori (1972)
Shortbill spearfish, *Tetrapturus angustirostris*	Yoshida (1971); Mori (1972)
Sailfish, *Istiophorus platypterus*	Shimada (1951); Yoshida (1971); Mori (1972)
Swordfish, *Xiphias gladius*	Yoshida (1971); Mori (1972)
Chinese mackerel, *Scomberomorus sinensis*	Imamura (1949)
Wahoo, *Acanthocybium solandri*	Iversen and Yoshida (1957)
Escolares, Gempylidae	E. Nakamura (1965)
Thresher shark, *Alopias* sp.	Strasburg (1958)
Requiem shark, *Carcharhinus albimarginatus*	Fourmanoir (1960)
Seabirds	Simmons (1969); Potthoff and Richards (1970)

Fourmanoir, P. 1960. Rapport sur *Katsuwonus pelamis* dans l'ouest de l'océan Indien. CCTA CSA (Commission for Technical Cooperation in Africa Scientific Council for Africa). Colloque sur les Thonidés, Dakar, 12-17 décembre 1960. Tunny (60)9, 9 p.

Table 10.—Parasites of skipjack tuna.

Parasites	Source	Parasites	Source
Trematodes		*Koellikeria orientalis* (Yamaguti)	
Monogenetic		*Koellikeria reniformis* Ishii	
Capsala interrupta (Monticelli)	Silas (1967)	*Lobatozoum multisacculatum* Ishii	
Capsala katsuwoni (Ishii)		*Neodiplotrema pelamydes* (Yamaguti)	
Capsala laevis (Verrill)		*Syncoelium katuwo* Yamaguti	
Capsala lintoni (Price)		Cestodes	
Capsala nozawae (Goto)		*Tentacularia coryphaenae* (Bosc)	Waldron (1963)
Hexostoma grossum (Goto)		*Callotetrarhynchus speciosus* (Linton)	
Pricea minimae Chauhan		*Pelichnibothrium* [larva]	
Pseudaxine katsuwoni Ishii		*Rhyncobothrium*	
Pseudaxine vagans Ishii		*Tentacularia bicolor* (Bartels)	Silas (1967)
Digenetic		Nematodes	
Atalostrophium (*Atalospargarum*) sp. Ishii	Silas (1967)	*Anisakis* sp. [larva]	Waldron (1963)
		Philometroides sp.	
Atalostrophion sardae MacCallum		Acanthocephalids	
Didymocylindrus filiformis Ishii		*Nipporhynchus ornatus* (Van Cleave)	
Didymocystis abdominalis Yamaguti		*Nipporhynchus trachuri* (Harada)	Chen and Yang (1973)
Didymocystis bilobata Ishii		Copepods	
Didymocystis dissimilis Yamaguti		?*Anuretes branchialis* Rangneker	Silas and Ummerkutty (1967)
Didymocystis ovata Ishii		*Caligus bonito* Wilson	
Didymocystis simplex Ishii		*Caligus mutabilis* Wilson	
Didymocystis soleiformis Ishii		*Caligus pelamydis* Kroyer	
Didymocystis submentalis Yamaguti		*Caligus quadratus* Shiino	
Didymocystis wedli Ariola		*Caligus coryphaenae* Steenstrup and Lütken	Cressey and Cressey (1980)
Didymoproblema fusiformes Ishii		*Caligus productus* Dana	
Didymozoon filicolle Ishii		*Caligus asymmetricus* Kabata	
Didymozoon longicolle Ishii		*Pseudocycnus appendiculatus* Heller	
Didymozoon minor Yamaguti	Silas (1967)	*Unicolex reductis*, new species	
Dinurus euthynni Yamaguti		*Lepeophtheirus dissimulatis* Wilson	Silas and Ummerkutty (1967)
Hirudinella marina (Garsin)		*Lepeophtheirus salmonis* Kroyer	Waldron (1963)
Koellikeria globosa Ishii		*Homoiotes bermudensis* Heegaard	

3.4 Nutrition and growth

3.41 Feeding

(1) Time

Feeding by skipjack tuna follows a more or less regular pattern. From studies of stomach contents, Yuen (1959), Waldron and King (1963), E. Nakamura (1965), and Dragovich (1971) determined that feeding peaks in the early morning from about 0800 to 1200, drops to a low between 1300 and 1600, and peaks again in the late afternoon, roughly from about 1600 to sunset (Fig. 28). E. Nakamura (1965) associated this feeding pattern with the availability of food. He stated, "Zooplankters move downward during the early daylight hours, presumably to reach a preferred level of illumi-

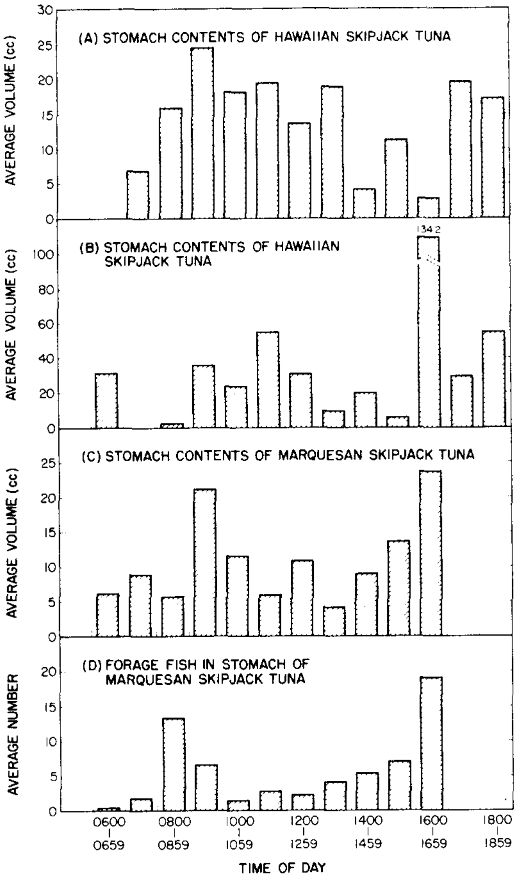

Figure 28.—Diurnal variation in volumes of stomach contents of Hawaiian skipjack tuna (panels A and B) and diurnal variation in volumes (panel C) and number of forage fish (panel d) in stomachs of Marquesan skipjack tuna (data from Waldron and King 1963 (A); Yuen 1959 (B); and E. Nakamura 1965 (C and D)).

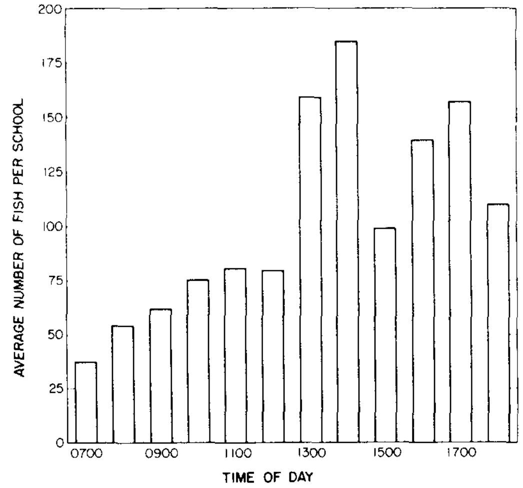

Figure 29.—Skipjack tuna catches by time of day for several Hawaiian bait boats during the 1956 and 1957 fishing seasons (data from Yuen 1959).

nation. 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 zooplanters and forage fish begin their upward movement. Skipjack begin feeding heavily in the late afternoon hours before dark as food becomes more available." He suggested also that the diurnal variation in the volumes of stomach contents may also reflect the effects of satiation. 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 always be the case is suggested in the hourly catches of skipjack tuna in the Hawaiian fishery (Fig. 29). 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, E. Nakamura's observation on the association of feeding with the availablility of food is preferable to the latter hypothesis based on volume of stomach content.

Some seasonal variations in feeding are indicated in studies of stomach content volumes but for the most part, the variations reflect the seasonal changes in abundance of forage organisms. Waldron and King (1963) observed a noticeable decrease in the average volumes of food in stomachs collected in Hawaiian waters during midsummer as compared with stomachs collected in late spring and early fall. The trend of the average volume followed closely that of the forage fish component. E. 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 the Laccadive Islands, Raju (1964b) found that the total average forage volume showed a peak in early spring and a lesser peak in the fall. The trend closely followed that of crustaceans, which dominated the food category in the areas sampled.

(2) Food selectivity

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 1964b; E. Nakamura 1965) agree that the average volume of food in skipjack tuna stomachs increases with size of fish. Differences in the 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 and small fishes. Yuen (1959) observed that the percent either by volume or occurrence of fish in stomachs of skipjack tuna collected near Hawaii increased with an increase in size, whereas the percent of molluscs and crustaceans decreased. Similar observations were noted generally for skipjack tuna in the Marquesas Islands (E. Nakamura 1965), eastern Pacific Ocean (Alverson 1963), central Indian Ocean (Raju 1964b), and western Atlantic Ocean, off North Carolina, U.S.A. (Batts 1972b).

Magnuson and Heitz (1971), in their study of the gill raker apparatus among scombrids and dolphins (Coryphaenidae), found that gill raker gap differed markedly among species and lengths of fish. A 50 cm skipjack tuna, a 30 cm yellowfin tuna, and a 10 cm striped bonito, *Sarda orientalis*, all had an estimated gill raker gap of 1 mm; and conversely, the gaps of a 50 cm fish of each species were estimated to be ca. 1.0, 1.7, and 4.5 mm, respectively (Fig. 30). Comparing mean gill raker gap with the stomach contents of fishes based on the literature, they showed that the percent volumes of crustaceans were inversely related to mean gill raker gaps and concluded that gill raker gap was related functionally with the quantity of smaller organisms in the stomachs. The presence of euphausids in stomachs of skipjack tuna and their absence in yellowfin tuna were cited as evidence for selection of organisms as determined by the magnitude of the gill raker gaps.

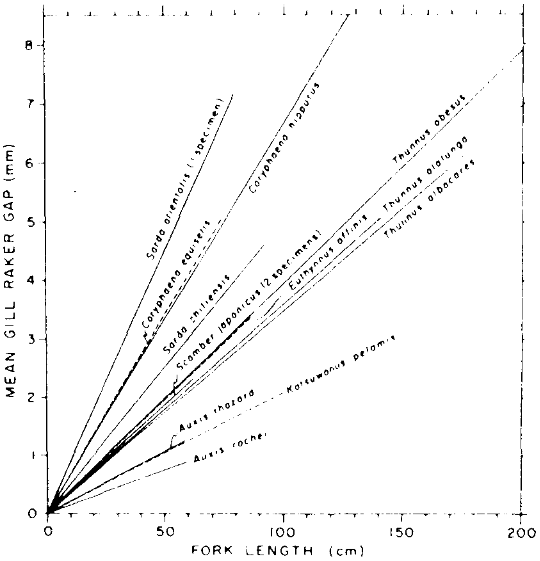

Figure 30.—Comparison of the mean gill raker gap and fork length relationship for various scombrid and coryphaenid fishes. Lengths are approximate ranges known for each species (from Magnuson and Heitz 1971).

(3) Distance from land

In examining feeding with respect to distance from land, arbitrarily zoned at 16, 40, 80, 161, and 322 km (10, 25, 50, 100, 200, and over 200 mi), Waldron and King (1963) found the average volume of stomach contents increased with distance from shore up to 50 mi and varied irregularly at greater distances. The trend was due largely to variation in the volume of fishes, which were the dominant food element. Among the families of fish consumed, Scombridae, Mullidae, and Carangidae were important within 16 km; Scombridae was dominant between 40 and 80 km, followed by Carangidae, Gempylidae, and Holocentridae; and Scombridae, Gempylidae, and Exocoetidae were important in offshore areas between 161 and 322 km. E. Nakamura (1965) found no relationship between stomach content volumes and distance from land of skipjack tuna taken around the Marquesas Islands. He noted, however, that food items categorized as reef-originating forms decreased significantly from inshore to offshore along four 362 km (225 mi) survey tracks. The percentages of reef-originating forms in the inner, middle, and outer 121 km (57 mi) sectors were 61.5, 39.9, and 8.8, respectively.

(4) Feeding behavior

Only a few studies have been made of the feeding behavior of skipjack tuna both in the wild and in captivity, but these have provided a wealth of information. Nakamura (1962), from his study of skipjack tuna in captivity, found that 1) when fed hourly until satiated, skipjack tuna exhibited an initial high feeding followed by feeding of small amounts throughout the day; 2) skipjack tuna had difficulty in seizing the food at night; 3) new fish introduced into tanks learned to feed faster when experienced fish were already in the tanks; 4) food particles were always taken at the surface or mid-depth, never off the bottom, and swimming was often accelerated prior to taking the food; 5) they rejected whole shrimp or squid after ingesting a few pieces, but when the rejected pieces were cut up into smaller pieces, the food was again accepted; and 6) captive skipjack tuna were never seen to prey upon small fish which were present in the pool.

Magnuson (1969) studied other aspects of feeding behavior of skipjack tuna in captivity. In one experiment, skipjack tuna were fed at intervals of 15 min throughout the day. A period of intense feeding occurred between 0630 and 0830 (Fig. 31). During this period the fish 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 the whole 2-h 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, and the stomachs were completely empty by dawn. In another experiment, skipjack tuna that had been deprived of food for 24 h were fed at a uniform rate for 45 min from 0900 to 0945. The stomach contents approached a maximum after about 30 min (Fig. 32-I). The proportion of food particles attacked decreased as the stomachs filled (Fig. 32-II), but very little change was noted until the contents exceeded 50% of the stomach's capacity. Then the likelihood that a skipjack tuna 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 (Fig. 32-III).

Passage of food through the alimentary canal was estimated from 54 fish, 39 to 50 cm FL, that had been denied food during the previous 24 h. These fish were fed as many thawed smelt as they would eat and their stomachs and intestines were examined at intervals over a 24-h period. The skipjack tuna ate the equivalent of about 8.6% of their body

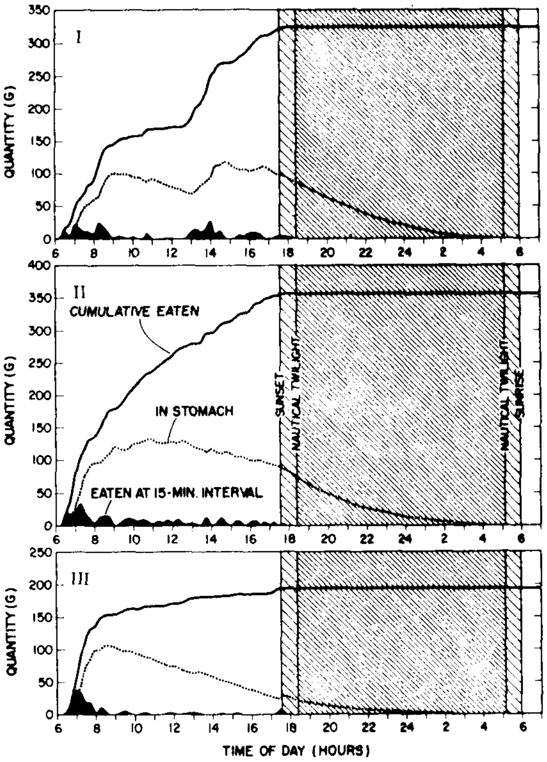

Figure 31.—Diel changes in the feeding of skipjack tuna in captivity. I. Quantity of food eaten. II. Cumulative weight of food eaten. III. Estimated weight of material in the stomach prior to each meal. Food was offered at 15-min intervals from 0600 to 1845 (from Magnuson 1969).

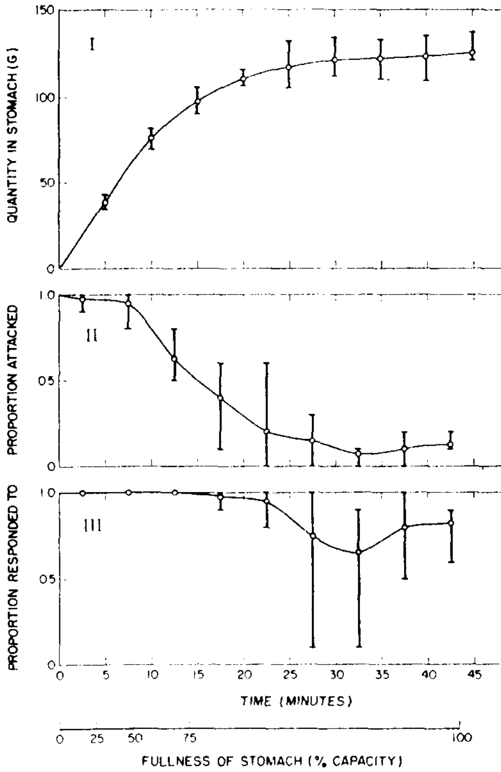

Figure 32.—Changes in feeding behavior as skipjack tuna eats a meal. I. Estimated weight of material in stomach. II. Proportion of food particles attacked. III. Proportion of particles eliciting a response. Means and ranges shown in each plot. Proportion of stomach filled, shown along the time axis, was estimated from panel I (from Magnuson 1969).

weight; about 10% of the initial quantity eaten had passed from the stomach each hour during the first 8 h; and the stomachs were essentially empty within 12 h after a meal. Magnuson (1969) noted also that the contents of the intestine increased rapidly during the first 3 h after the meal and the intestine was essentially empty about 14 h after the meal. Most waste material was evacuated from the intestine while the intestine was being filled from the emptying stomach. Defecation soon after eating was not surprising because of the short intestine in skipjack tuna.

Another aspect of feeding behavior is the appearance of banded color patterns on the skipjack tuna. Strasburg and Marr (1961) reported the appearance of such coloration on 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 is likely under various conditions and is produced presumably by the contraction of melanophores. The vertical bars were noticed from a ship's subsurface viewing chamber 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), kawakawa (Nakamura and Magnuson 1965), and dolphin (Strasburg and Marr 1961).

3.42 Food

Various authors have examined the food of skipjack tuna (Kishinouye 1923; Suyehiro 1938; Welsh 1949; Ronquillo 1954; Hotta and Ogawa 1955; Postel 1955; Tester and Nakamura 1957; Yuen 1959; Alverson 1963; Waldron and King 1963; Raju 1964b; Thomas 1964; E. Nakamura 1965; Sund and Richards 1967; Dragovich 1971; Batts 1972b; Roberts 1972). In addition, there are other reports with brief mention of the food of skipjack tuna. The most comprehensive studies to date are those by Hotta and Ogawa (1955), Alverson (1963), Waldron and King (1963), and E. Nakamura (1965) in the Pacific Ocean; Dragovich (1971) and Batts (1972b) in the Atlantic Ocean; and Raju (1964b) in the Indian Ocean.

The major food items fall into three groups: fishes, crustaceans, and molluscs. Although fishes comprise the most important source of food for skipjack tuna in most of the oceans, variations in the order of importance of the major groups of food organisms are found in different areas and seasons (Table 11). In the western and central Pacific and western Atlantic Oceans, fishes (49-95% of total volume) comprised the most important group, followed by molluscs (4-50%), and crustaceans (1-23%) (Welsh 1949; Ronquillo 1954; Waldron and King 1963; Dragovich 1971; Batts 1972b). Waldron and King (1963) reported differences in the food composition of skipjack tuna by island areas in the central Pacific: "(1) Skipjack from the Hawaiian area depended on fishes to a greater extent than those from the Phoenix or Line Islands; (2) skipjack from the Phoenix Island area utilized molluscs, crustaceans, and fishes equally as sources of food; and (3) skipjack from the Line Islands area depended on fishes to a lesser degree than those from the other two areas and to a greater extent on squids and crustaceans." In the eastern sides of the Pacific and Atlantic Oceans, crustaceans were the main source of food. They comprised 50-62% of the food, fish comprised 33-37%, and molluscs, 4-13% (Schaefer 1960; Alverson 1963; Dragovich 1971). In the Indian Ocean around the Laccadive Islands, crustaceans were the most important food group. They made up 59% of the total volume, molluscs were 22%, and fish were 10% (Raju 1964b). At nearby Minicoy Island fishes formed 48% of the food, crustaceans 47%, and miscellaneous items, mostly molluscs, 5% (Thomas 1964).

The food of skipjack tuna in all the major oceans includes a wide variety of organisms, representing 11 invertebrate orders and 80 or more fish families (Table 12). Past studies show that of the invertebrates, two groups of arthropods (decapods and stomatopods) and two groups of cephalopods (octopods and squids) were found in stomachs from nearly all localities. The fish families represented in stomach contents vary considerably, with samples taken in the Pacific Ocean having the greatest number by far. Hotta and Ogawa (1955) listed 48 families, Waldron and King (1963) listed 42, and both Ronquillo (1954) and E. Nakamura (1965) listed 33. In the Atlantic Ocean, Dragovich (1970) listed 28 fish families in the western and 21 in the eastern sectors. Raju (1964b) listed only 10 fish families in the stomachs of skipjack tuna collected from inshore waters (about 8 km) around Laccadive Islands and Thomas (1964) listed 11 fish families from Minicoy Island in the Indian Ocean. 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 the tunas), Ostraciidae, and Tetraodontidae.

The presence of scombrids in the stomachs of skipjack tuna deserves special consideration, since this group of fish occasionally constitute a major portion of the skipjack tuna diet. Data from Waldron and King (1963) indicate that scombrids occurred in 10.6% of 707 skipjack tuna stomachs examined and that this group comprised 25.0% of the total volume, the highest of all fish families and larger than the entire mollusc group. E. Nakamura (1965) reported the occurrence of juvenile tuna in 24.8 to 44.2% of 603 stomachs examined from five cruises around the Marquesas and Tuamotu Islands. This group ranked the highest among all fish families on four cruises and fifth on one cruise. Dragovich (1971) also indicated high (25.0%) occurrence of scombrids in 369 skipjack tuna stomachs from the Caribbean Sea and adjacent waters. This group ranked second only to the large unidentified fish group.

The wide variety of food organisms in the stomach contents and the variations in the importance of the major food groups have led to the conclusion that skipjack tuna are opportunistic feeders and will prey upon any forage organisms that are available to them. Cannibalism among the skipjack tuna lends additional support to this conclusion. In the central Pacific Ocean, E. Nakamura (1965) reported juvenile skipjack tuna in 12.4% of the skipjack tuna stomachs containing food. He also indicated that 7.8% of 707 stomachs collected by Waldron and King (1963) contained juvenile skipjack tuna. Conand and Argue (1980) reported that 3.3% of 5,956 stomachs of skipjack tuna from the western Pacific Ocean (lat. 25°N-42°S, long. 134°E-140°W) contained juvenile skipjack tuna. In the Atlantic Ocean, Suarez Caabro and Duarte-Bello (1961) and Dragovich (1971) also reported the occurrence of juvenile skipjack in stomachs of skipjack tuna.

3.43 Growth rate

Various methods have been used to determine the growth of skipjack tuna and other tunas, including analyses of growth

Table 11.—Percent composition of the three major food groups of skipjack tuna in various localities.

Author	Locality	Percent of total volume		
		Fishes	Crustaceans	Mollusks
Ronquillo (1954)	Western Pacific-Sulu, Celebes Sea	66	23	11
Waldron and King (1963)	Central Pacific-Hawaii, Line, Phoenix Is.	75	4	20
Welsh (1949)	Central Pacific-Hawaii (live-bait fishery)	63	9	28
Welsh (1949)	Central Pacific-Hawaii (trolling)	51	27	22
Schaefer (1960)	Eastern Pacific	33	62	4
Alverson (1963)	Eastern Pacific	37	59	3
Batts (1972b)	Western Atlantic-Cape Hatteras	90	3	7
Batts (1972b)	Oregon Inlet, western Atlantic-North Carolina, U.S.A.	49	1	50
Dragovich (1971)	Western Atlantic, Equatorial	95	1	4
Dragovich (1971)	Eastern Atlantic, Equatorial	37	50	13
Raju (1964a)	Central Indian-Laccadive Islands	19	59	22
Thomas (1964)	Central Indian-Minicoy Islands	48	47	5

[1] The percentages are of number of organisms. Conversion to percentages of volume would rank the mollusks second and the crustaceans third.

Table 12.—Organisms found in skipjack tuna stomachs by various authors.

	Pacific Ocean							Atlantic Ocean			Indian Ocean
	Hotta and Ōgawa (1955) Japanese waters	Ronquillo (1954) Philippine waters	Welsh (1949) Hawaiian waters	Yuen (1959) Hawaiian waters	*Waldron and King* (1963) Hawaii, Line, and Phoenix	Nakamura, E. (1965) Marquesas and Society Is.	Alverson (1963) Eastern Pacific	Dragovich (1971) Western Atlantic	Batts (1972b) Western Atlantic	Dragovich (1971) Eastern Atlantic	Raju (1964b) Central Indian
	Number of samples										
Taxonomic group	2,900	115	224	573	707	603	2,317	1,060	705	1,060	2,609
Arthropoda	x	x	x	x	x	x	x	x	x	x	x
Crustacea	x	x	x	x	x	x	x	x	x	x	x
Copepoda					x						
Mysidacea					x		x			x	x
Isopoda				x	x		x	x	x		
Amphipoda		x		x	x	x	x	x	x	x	
Euphausiacea	x			x	x	x	x			x	x
Decapoda	x	x	x	x	x	x	x	x	x	x	
Stomatopoda		x	x	x	x	x	x	x	x	x	x
Mollusca	x	x	x	x	x	x	x	x	x	x	x
Gastropoda					x	x	x	x	x	x	
Heteropoda					x	x		x	x	x	
Pteropoda					x	x	x	x	x	x	
Cephalopoda	x	x	x	x	x	x	x	x	x	x	x
Octopoda	x	x	x	x	x	x	x	x	x	x	x
Decapoda	x	x	x	x	x	x	x	x	x	x	x
Chordata	x	x	x	x	x	x	x	x	x	x	x
Tunicata					x	x	x			x	x
Pisces	x	x	x	x	x	x	x	x	x	x	x
Albulidae					x						
Clupeidae	x	x			x				x		
Dussumieriidae (= Clupeidae)	x		x								
Engraulidae							x				
Gonostomatidae	x						x				
Sternoptychidae	x	x			x		x				
Stomiatidae		x			x						
Idiacanthidae						x					
Synodontidae		x	x	x	x	x				x	
Paralepidae (= Sudidae)	x	x		x	x		x	x		x	
Alepisauridae	x	x			x						
Myctophidae (= Scopelidae)	x	x			x	x	x			x	
Congridae									x	x	
Belonidae					x	x					
Scomberesocidae	x				x		x				
Hemiramphidae		x			x		x				
Exocoetidae	x	x				x	x	x	x		
Oxyporhamphidae (= Hemiramphidae)	x	x				x	x	x	x		
Gadidae							x		x		
Aulostomidae			x								
Fistulariidae		x		x	x	x	x				
Macrorhamphosidae	x										
Syngnathidae		x	x	x	x			x	x	x	
Holocentridae	x	x	x	x	x	x		x	x		
Grammicolepidae	x										
Antigoniidae (= Caproidae)		x		x				x			
Sphyraenidae	x			x	x	x					
Atherinidae					x						
Polynemidae	x						x	x			
Serranidae	x			x		x	x	x		x	
Epinephelidae (= Serranidae)	x										
Kuhlidae					x						
Priacanthidae	x	x	x	x	x	x		x		x	
Malacanthidae								x			
Scombropidae					x						
Labracoglossidae	x										
Carangidae	x	x	x	x	x	x	x	x	x	x	x
Menidae	x										

Table 12.—*Continued.*

	Pacific Ocean							Atlantic Ocean			Indian Ocean
	Hotta and Ogawa (1955) Japanese waters	Ronquillo (1954) Philippine waters	Welsh (1949) Hawaiian waters	Yuen (1959) Hawaiian waters	Waldron and King (1963) Hawaii, Line, and Phoenix	Nakamura, E. (1965) Marquesas and Society Is.	Alverson (1963) Eastern Pacific	Dragovich (1971) Western Atlantic	Batts (1972b) Western Atlantic	Dragovich (1971) Eastern Atlantic	Raju (1964b) Central Indian
	Number of samples										
Taxonomic group	2,900	115	224	573	707	603	2,317	1,060	705	1,060	2,609
Bramidae		x	x	x	x	x		x	x	x	
Coryphaenidae	x	x			x	x		x	x		
Emmelichthyidae	x					x					
Lutianidae	x					x					
Caesionidae (= Lutianidae)	x	x									
Sciaenidae							x				
Denticidae (= Lethrinidae)	x										
Mullidae	x	x	x	x	x	x		x			
Pampheridae	x										
Kyphosidae						x					
Ephippidae									x		
Chaetodontidae	x	x	x	x	x	x	x	x		x	
Pomacanthidae (= Chaetodontidae)					x						
Pomacentridae		x		x		x					
Cirrhitidae				x							
Chiasmodontidae		x						x		x	
Blenniidae				x	x	x					
Brotulidae					x						
Ophidiidae									x		
Ammodytidae	x			x	x	x					
Callionymidae							x				
Siganidae	x	x									
Zanclidae	x										
Acanthuridae	x		x	x	x	x		x	x		
Teuthidae (= Acanthuridae)		x								x	
Gempylidae	x	x	x	x	x	x		x	x	x	
Trichiuridae	x	x					x			x	
Scombridae (+ Thunnidae)	x	x	x	x	x	x	x	x	x	x	
Scomberomoridae (= Cybiidae)	x				x						
Istiophoridae	x								x		
Tetragonuridae					x						
Stromateidae								x	x		
Nomeidae	x			x	x	x					
Centrolophidae (= Nomeidae)			x								
Scorpaenidae				x	x	x		x		x	
Triglidae			x								
Peristediidae (= Triglidae)	x										
Platycephalidae						x					
Dactylopteridae		x		x		x		x	x	x	x
Bothidae										x	
Echeneidae	x										
Triacanthidae		x									x
Balistidae	x	x	x	x	x	x	x	x		x	x
Monacanthidae (= Balistidae)	x		x		x	x		x	x	x	x
Ostraciidae	x	x	x	x	x	x	x	x			x
Tetraodontidae	x	x		x	x			x	x	x	x
Canthigasteridae (= Tetraodontidae)	x				x						
Diodontidae	x	x		x	x	x		x			
Molidae	x			x	x			x			
Lophiidae							x				
Antennariidae											x
Pegasidae				x		x					

marks on hard parts such as vertebrae (Aikawa 1937; Aikawa and Kato 1938; Yokota et al. 1961; Chi and Yang 1973), first dorsal spine (Shabotiniets 1968; Batts 1972a), and otoliths (Wild and Foreman 1980; Uchiyama and Struhsaker 1981); temporal progression of length-frequency modes (Brock 1954; Kawasaki 1955a, b, 1963, 1965a; Schaefer 1961a; 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; Josse et al. 1979). Reviews of some of these studies were given by Shomura (1966a), Rothschild (1967), Joseph and Calkins (1969), Chi and Yang (1973), and Josse et al. (1979). A summary of the results of these studies is presented in Table 8 and representative growth curves are shown in Figures 33-35.

Josse et al. (1979) reviewed the methods and results of most of the studies made to date and have concluded that counting seasonal growth marks on vertebrae, scales, and dorsal spines and following modal progressions of length frequencies were least reliable, that counting daily increments on otoliths was more reliable, and that measuring growth between tagging and recapture was the most reliable. Their low regard for counting growth marks and for following modal progressions stemmed from the failure of investigators to show irrefutably the periodicities in the appearance of growth rings and from the results of their own analysis of length-frequency data. They found that clear progressions of modes for more than a few months, other than in exceptional instances, were difficult to demonstrate and that the apparent modal progression could give in a single region, in different years, growths which were rapid, slow, nil, and even negative. They pointed out, first, the inadequacy of determining growth from otolith increments to resolve the problem of age, should the skipjack tuna pass through phases of no growth during the breeding period, and second, the uncertainty in reading daily marks close to the nucleus (Lewis[8]).

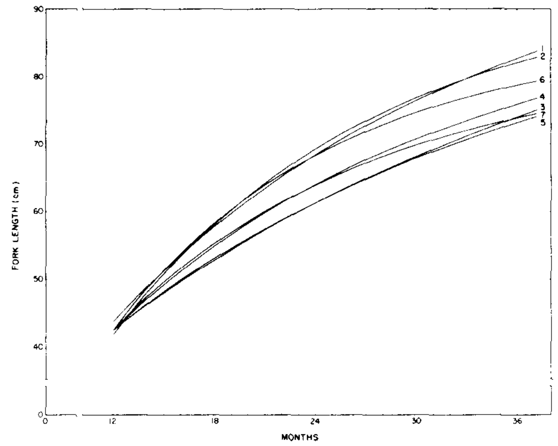

Figure 34.—Growth estimates of central Pacific skipjack tuna. 1) Uchiyama and Struhsaker (1981), otolith increments; 2) Skillman, tag returns, males only (see text footnote 10); 3) Rothschild (1967), tag returns, uncorrected data; 4) Skillman, tag returns, males and females (see text footnote 10); 5) Brock (1954), modal progression; and 6) Rothschild (1967), tag returns, corrected data (from Uchiyama and Struhsaker 1981).

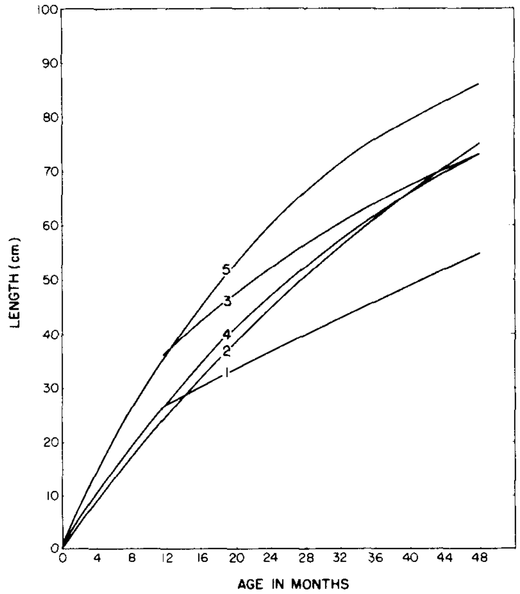

Figure 33.—Growth estimates of western Pacific skipjack tuna. 1) Aikawa and Kato (1938), vertebral rings; 2) Kawasaki (1963), modal progression (Joseph and Calkins 1969; 3) Yokota et al. (1961), modal progression; 4) Chi and Yang (1973), vertebrae; and 5) Chi and Yang (1973), modal progression.

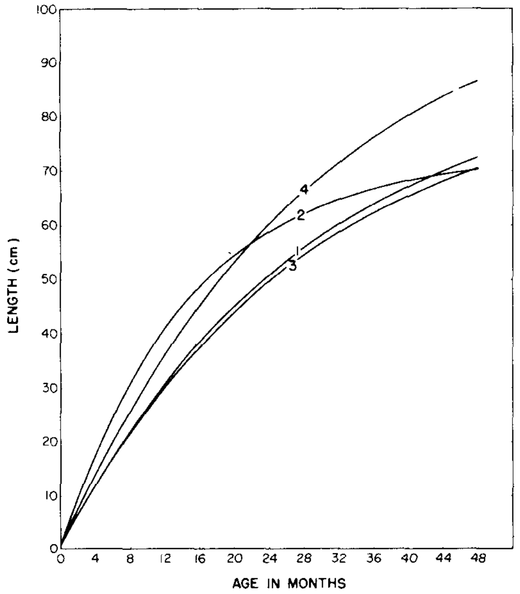

Figure 35.—Growth estimates of eastern Pacific skipjack tuna. 1) Joseph and Calkins (1969), tag returns, averaged data; 2) Joseph and Calkins (1969), tag returns, nonaveraged data; 3) Schaefer (1961a), modal progression; and 4) Joseph and Calkins (1969), modal progression (from Joseph and Calkins 1969).

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[8] Lewis, A. D. 1976. The relevance of data collected in Papua New Guinea to skipjack population studies in the western Pacific. Document 1066/76, 5 p. Department of Primary Industry, Papua New Guinea. Ministry of Agriculture, Forests, and Fisheries, Fisheries Division, Suva Fiji.

While Josse et al. (1979) considered tagging data to be the most reliable, the possibility of an interruption in growth caused by tagging itself has yet to be determined. We cite as an example the work by Wild and Foreman (1980), who investigated the relation of otolith increments and time for tagged and recaptured skipjack and yellowfin tunas marked with tetracycline. They observed that the number of increments underestimated time by approximately 24% during growth from 42 to 64 cm over a period of up to 249 d. They further reported that the growth rate of skipjack tuna, estimated from the length at recapture and linear change in otolith dimension of tagged fish injected with tetracycline was 1.15 cm/mo. The growth rate was comparable with that obtained from earlier tagging studies by Joseph and Calkins (1969) in the eastern Pacific, but much less than that estimated from the latter's results based on modal progression. The agreement of the growth rates from otolith increments after tetracycline treatment and from incremental change in size indicates that both methods are equally good at measuring growth rate of tagged fish but provide no information on the effect of tagging itself.

The matter of reliability in the length of fish at release should be considered also in tagging data. In most past studies the average length of fish from the same school was assigned to the tagged fish or tagged fish were measured to the nearest 5 cm. Only recently in Papua New Guinea (Josse et al. 1979) and in the eastern Pacific (IATTC[9]) have tagged fish been measured more closely at time of release, i.e., to the nearest centimeter. Until similar data are obtained from other areas and the adverse effects of handling fish during tagging have been clarified, the age and growth of skipjack tuna must be considered only as approximations.

Growth estimates of skipjack tuna in the western North Pacific have been determined only from analysis of vertebrae and modal progression. Aikawa (1937) and Aikawa and Kato (1938) made no serious attempt to validate growth rings as annual marks. Their lengths at age appear to be greatly underestimated. Chi and Yang (1973), using both methods, observed that two rings were formed annually on vertebrae of skipjack tuna taken from waters around Taiwan and that growth estimates from modal progression were higher than those obtained from growth marks on vertebrae (Table 8; Fig. 33). The growth of skipjack tuna, based on modal progression, was 24 cm from age 12 to 24 mo and 15 cm from age 24 to 36 mo. Growth estimates from modal analysis by Yokota et al. (1961) were lower than those obtained by Chi and Yang (1973) and comparable with the latter's estimates from vertebral analysis.

Growth estimates of skipjack tuna in the central and eastern Pacific have been obtained from modal progression, otolith increments, and tagging (Figs. 34, 35). Growth estimated from modal progresssion in both areas was comparable with that obtained by Chi and Yang (1973) in the western North Pacific and generally higher than that estimated from tagging. Growth between ages 12-24 and 24-36 mo were 25 and 11 cm, respectively, in the central Pacific (Uchiyama and Struhsaker 1981) and 23 and 16 cm, respectively, in the eastern Pacific (Joseph and Calkins 1969).

Uchiyama and Struhsaker (1981) obtained growth estimates from otolith increments of skipjack tuna in Hawaiian waters. Their estimates varied somewhat from those obtained from modal progressions in the same area and in the eastern and western Pacific (Joseph and Calkins 1969; Chi and Yang 1973). Although growth was similar for fish increasing in age from 12 to 24 mo (24 cm), it was much higher for fish increasing in age from 24 to 36 mo (25 cm).

Growth estimates derived from tagging show little or no difference for fish in the central and eastern Pacific (Table 8). Growth of fish increasing in age from 12 to 24 mo and 24 to 36 mo were 18-23 and 9-13 cm, respectively, in Hawaiian waters (Joseph and Calkins 1969, Skillman[10]) and 18-20 and 8-13 cm, respectively, in the eastern Pacific (Joseph and Calkins 1969).

Tagging studies in Papua New Guinea by Kearney (1978) have indicated that skipjack tuna in that region grew at an average annual rate of 7 cm. The estimate was derived from fish between 2 and 6 kg (ca. 38.0-64.4 cm) which were at liberty for up to 789 d. Kearney stated "The available tagging information . . . leaves little doubt that the growth rate and maximum size of skipjack in the western subpopulation are much lower than that for the more easterly subpopulations." Subsequent aging studies from otoliths (Uchiyama and Struhsaker 1981; Fig. 36) and tagging by Josse et al. (1979) and the IATTC (footnote 9) have confirmed this. Josse et al. (1979) analyzed published and unpublished tagging data from the eastern Pacific, Hawaii, and Papua New Guinea and determined that the lowest growth rates were observed in skipjack tuna from Papua New Guinea and the highest from Hawaii. The IATTC (footnote 9) compared new tagging data (fish length at release measured to nearest centimeter) from the eastern Pacific with similar data from Papua New Guinea

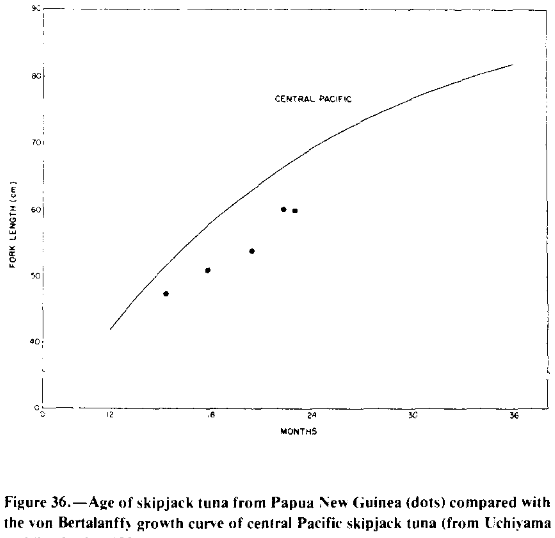

Figure 36.—Age of skipjack tuna from Papua New Guinea (dots) compared with the von Bertalanffy growth curve of central Pacific skipjack tuna (from Uchiyama and Struhsaker 1981).

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[9] Inter-American Tropical Tuna Commission. 1981. The bi-monthly report. January-February 1981. Inter-Am. Trop. Tuna Comm., 21 p. Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92037.

[10] Skillman, R. A. Estimates of von Bertalanffy growth parameters for skipjack tuna, *Katsuwonus pelamis*, from capture-recapture experiments in the Hawaiian Islands. Manuscr. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.

and found that skipjack tuna in the eastern Pacific grew at a significantly faster rate than those in the Papua New Guinea region.

Studies of skipjack tuna 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 8). Since he did not validate these marks as annuli, the size at age he obtained thus appears questionable. Batts (1972a) 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 that obtained by others using data on modal progression or tag returns (Table 8).

3.5 Behavior

See Section 3.41(4) for feeding behavior; Section 3.13 for reproductive behavior.

3.51 Migrations and local movements

Migrations of skipjack tuna have been determined for certain areas and hypothesized for others through various methods, such as following the movement through a fishery of fish groups identified by size or age, from tagging, population genetic studies, and from tuna longline catch data. The most direct evidence has been from tagging data, but there is one weakness in this method—it only gives the net movement from point of release to point of recapture and does not show the actual path taken by the fish in the interim.

In the central-eastern Pacific, Rothschild (1965), on the basis of available evidence on larval distribution, gonad indices, size distributions, tag recoveries, catch predictions, and immunogenetic studies, hypothesized that a large portion of the skipjack tuna taken in the eastern Pacific Ocean originate in the equatorial Pacific; that a large component of prerecruits (<35 cm) moves eastward and is split into a northern group that enters the Baja California fishery area and a southern group that enters the Central and South American fishery areas; and that the skipjack tuna remain in the eastern Pacific for several months before they move offshore into equatorial waters to spawn (Fig. 37).

A tagging study by Fink and Bayliff (1970) showed detailed movements of skipjack tuna in the eastern Pacific fisheries (Fig. 38). They reported that there appear to be two main

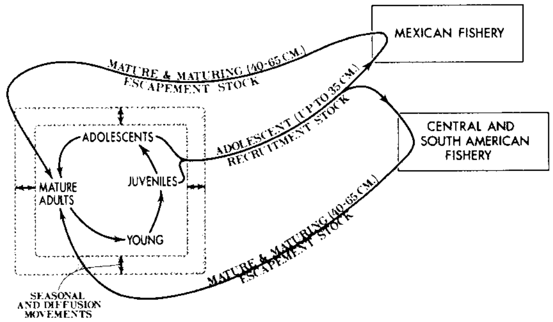

Figure 37.—Hypothesized origin and migration of skipjack tuna between the central equatorial Pacific and the northern (Mexican) and southern (Central and South America) fisheries of the eastern Pacific Ocean (from Rothschild 1965).

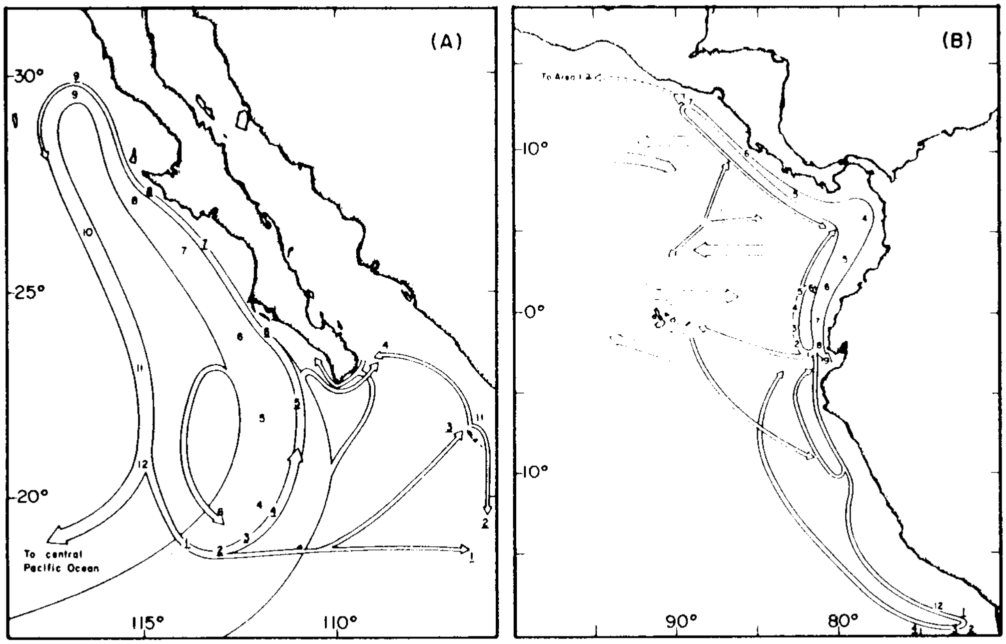

Figure 38.—Inshore migration of skipjack tuna of the A) northern fishery group and B) southern fishery group based on tagging data; numbers refer to months (from Fink and Bayliff 1970).

groups of skipjack tuna in the eastern Pacific; that recruits to the northern fishery first enter the fishery in the Revillagigedo Islands in April, migrate north along the Baja California coast during spring and summer, return south in the fall, and then migrate to the central Pacific; and that recruits to the southern fishery enter the fishing area in or near the Panama Bight and migrate both northwest to Central America and south to the Gulf of Guayaquil. Although a few fish tagged off Ecuador in the Gulf of Guayaquil were recovered off Baja California, they reported little interchange of skipjack tuna between the northern and southern fisheries.

Williams (1972) has extended Rothschild's hypotheses by proposing three migration models for the recruitment of skipjack tuna into the eastern Pacific fisheries: An active migration model (Fig. 39A), where the fish migrate eastward actively along zonal productivity bands at the northern and southern edges of the North Equatorial Countercurrent (NECC); a passive migration model (Fig. 39B), where the fish are passively carried eastward in the equatorial countercurrents; and a gyral migration model (Fig. 39C), which involves both active and passive migration. In the last model Williams proposed that the fish of the northern group move counterclockwise around a zonally narrow equatorial gyre consisting of the NECC and the North Equatorial Current, with the western limit some distance west of long. 130°W; and that fish of the southern group move eastward in the NECC and return to the central Pacific in the South Equatorial Current.

Recoveries in Hawaii of skipjack tuna tagged in the eastern Pacific showed the capability of the skipjack tuna to negotiate long migrations. Seckel (1972) developed a numerical drift simulation model based on geostrophic and wind-driven currents as a potential mode of skipjack tuna migration from the eastern Pacific northern fishery into Hawaiian waters. He 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 mo (Fig. 40). Although the time intervals are within the range of values for skipjack tuna tagged in the eastern Pacific and recaptured in Hawaii, they are, by far, longer than most (Table 13).

In the northwestern Pacific for fish caught in the Japanese coastal fisheries, Imamura (1949) noted that skipjack tuna migrated annually from the southern seas northward in the warm Kuroshio in the spring and summer and returned south as the cold Oyashio became stronger in the fall. Kawasaki (1955a, b) proposed that there are two groups of skipjack tuna in the southwestern Japanese waters which migrate north from the Ryukyu Islands to southern Japan and back,

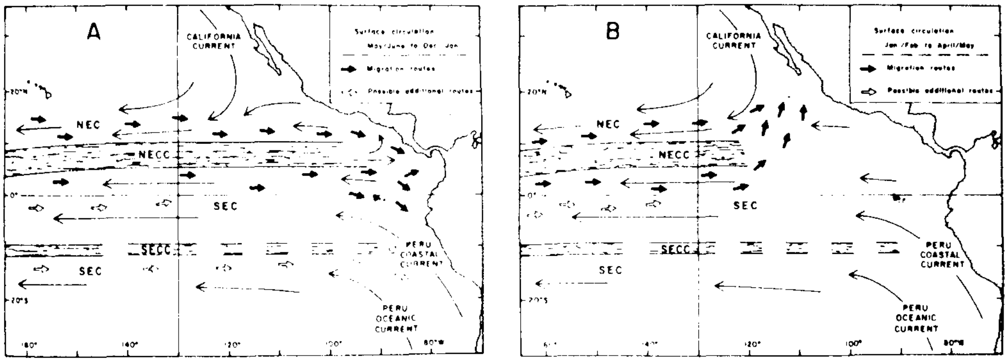

Figure 39A.—Active migration model: A) routes of young skipjack tuna into the southern fishery and B) routes of young skipjack tuna into the northern fishery. NEC = North Equatorial Current; NECC = North Equatorial Countercurrent; SEC = South Equatorial Current; SECC = South Equatorial Countercurrent. (From Williams 1972.)

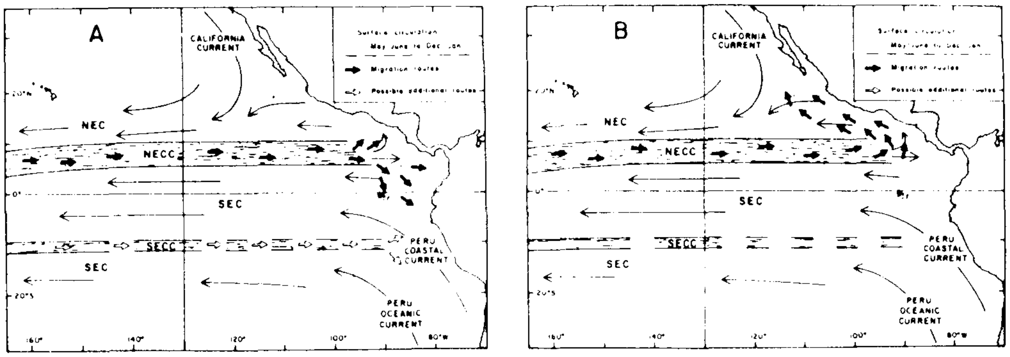

Figure 39B.—Passive migration model: A) routes of young skipjack tuna into the southern fishery and B) routes of young skipjack tuna into the northern fishery. See Figure 39A for abbreviations. (From Williams 1972.)

and two groups (coastal and offshore) in the southeastern and eastern Japanese waters which migrate north and south at different times of the year. Based on the similarity of fish sizes taken in the Japanese, Hawaiian, and eastern Pacific fisheries, he proposed (1964, 1965b) that the skipjack tuna in the northwestern Pacific is closely related to skipjack tuna taken in Hawaii and the eastern Pacific; that the major spawning area is centered along the Equator west of long. 140°W; that the larvae spawned there in summer migrate to the fisheries area by winter and are recruited into the fisheries at age 2; and that these fish migrate southward at age 3 and remain in the equatorial spawning area from ages 3.5 to 5.5.

Fujino (1972), on the basis of population genetic studies (see Section 1.33), recognized two subpopulations of skipjack

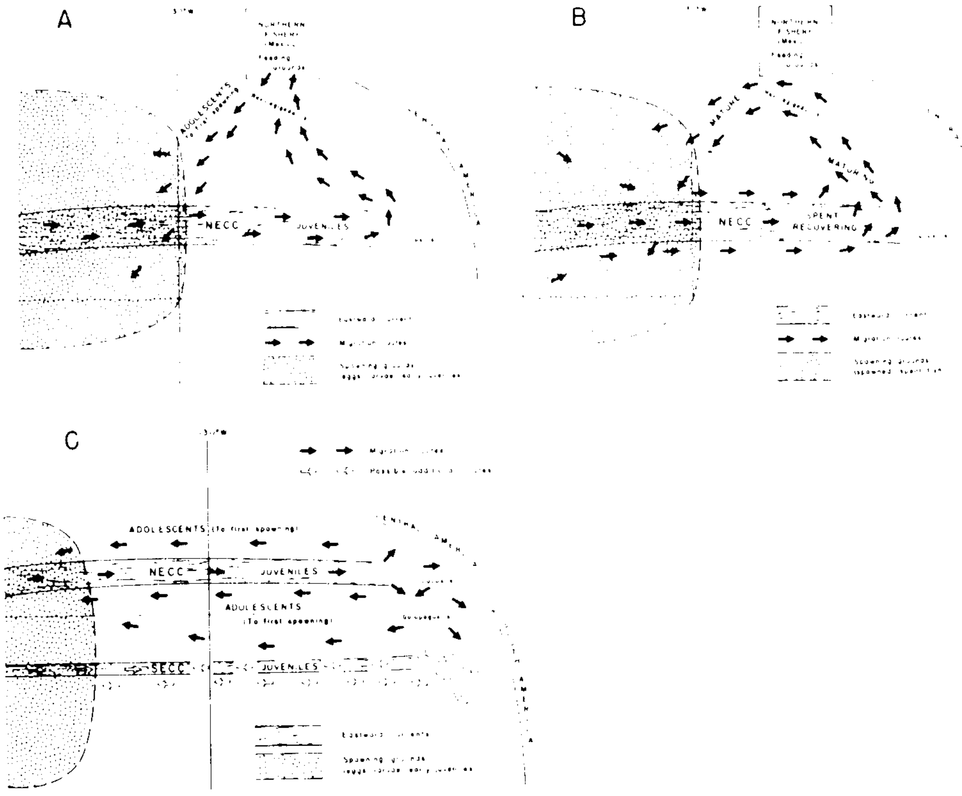

Figure 39C.—Schematic representation of gyral migration model: A) routes of young skipjack tuna into the northern fishery, B) routes of adult skipjack tuna of northern fishery, and C) routes of young skipjack tuna into the southern fishery. See Figure 39A for abbreviations. (From Williams 1972.)

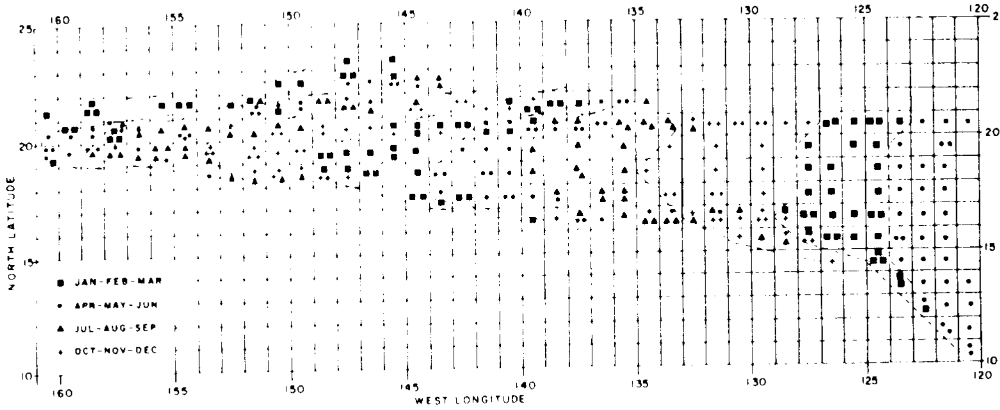

Figure 40.—Locations of drifting objects in June of the third model year that were introduced in each of the previous 30 mo at long. 120°W. Dashed lines indicate most westerly location reached by objects introduced every quarter (from Seckel 1972).

Table 13.—Recapture data for skipjack tuna tagged by IATTC from 1960 to 1976 (from Josse et al. 1979).

Date			Position		Fork length (cm)		
Recapture	Tagging/release	Days at liberty	Recapture	Tagging/release	Recapture	Tagging/release	Tag number
6/12/62	9/05/60	646	Hawaii	Baja California	77.4	—	—
8/22/62	4/17/60	848	Hawaii	Revillagigedo Island	78.0	—	—
4/05/63	9/22/61	561	Christmas Island	Baja California	70.0	—	—
6/27/67	6/05/65	753	Hawaii	Revillagigedo Island	81.4	45.0	—
7/21/70	11/06/69	258	Hawaii	Clipperton	70.3	66.0	—
8/08/70	11/06/69	276	Hawaii	Clipperton	71.5	65.0	—
9/01/76	7/06/75	422	Molokai	Baja Magdalena, Calif.	72.7	59.0	J5242
9/01/76	7/20/75	408	South of Pearl Harbor	Cabo San Lucas, Calif.	75.1	45.0	J8250
8/22/76	7/06/75	410	Lat. 21°14′N, long. 171°51′W	Lat. 24°07′N, long. 113°45′W	80.0	65.0	J5543
[1]12/09/76	5/17/76	206	Waianae, Oahu	Lat. 31°57′N, long. 159°12′E	68.0	42.0-59.0	None
6/10/77	6/17/76	357	Kahuku, Oahu	Lat. 21°16′N, long. 111°04′W	73.0-75.0	46.0	K4105
6/28/77	6/18/76	375	Kaneohe, Oahu	Lat. 21°07′N, long. 111°16′W	76.0	53.0	L0263
7/26/77	10/04/76	295	Kaneohe, Oahu	Lat. 25°45′N, long. 112°47′W	72.3	44.0	L0222
7/29/77	6/17/76	407	Kaneohe, Oahu	Lat. 21°16′N, long. 111°04′W	75.0	47.0	K7250
8/19/77	6/18/76	427	Hawaii	Lat. 21°07′N, long. 111°16′W	74.9	47.0	L0047
9/14/77	6/17/76	454	Barbers Point, Oahu	Lat. 21°16′N, long. 111°04′W	76.0	43.0	K7182
9/20/77	6/17/76	460	Waianae, Oahu	Lat. 21°16′N, long. 111°04′W	75.2	49.0	K8615

[1] Recaptured by a Japanese vessel.

[2] Tagged by Japanese fishery scientists.

tuna in the Pacific, a western and an eastern central subpopulation, and two groups of skipjack tuna within the western Pacific subpopulation, an A group, derived from spawning in the northern winter, and a B group, derived from spawning in the northern summer. The migratory paths of these groups (Fig. 5) are clearly restricted to the western Pacific west of long. 170°E and the migratory paths in Japanese coastal waters agree with the paths proposed by Kawasaki (1955a, b).

In the western equatorial Pacific intensive tagging of skipjack tuna has been carried out in recent years by the Tohoku RFRL (Japan), the Department of Agriculture, Stock and Fisheries (Papua New Guinea), and the Far Seas Fisheries Research Laboratory (Japan). Preliminary analyses of tag recoveries have revealed considerable poleward migration of skipjack tuna within the boundaries of long. 130° and 160°E with none being captured farther east than long. 173°E (Kearney 1975). For the Papua New Guinea area, Lewis (1980) reported that the essential features of migration were the interchange of skipjack tuna between the Bismarck and Solomon Seas during November-April and the northerly movement from the Bismarck Sea in the July-October period. Long-term recoveries (fish 60-390 d at large) in other southern and western Pacific areas indicate straight-line migrations in excess of 1,000 mi (South Pacific Commission 1981). Fish tagged off New South Wales, Australia, were recovered in the Solomon, Samoa, and Society Islands, Kiribati, and northern New Zealand; fish tagged off northern New Zealand were recovered in West Samoa, Loyalty, and Society Islands; fish tagged off Tuvalu were recovered in the northwestern Hawaiian Islands and near Palmyra Island; fish tagged north of New Ireland were recovered in Kiribati and the Marshall Islands; and fish tagged off Volcano Island were recovered in Kiribati (South Pacific Commission 1981, Fig. 6). While straight lines connecting tag release and recovery points do not necessarily represent the actual paths of the fish, the net movement of fish from the south equatorial Pacific to the North Pacific and vice versa is significant.

Migrations of skipjack tuna have been examined on a wider scope in the Pacific. Kasahara (1968) cited Naganuma,[11] who postulated several migratory routes of skipjack tuna (Fig. 41), based on the catch as well as monthly length fre-

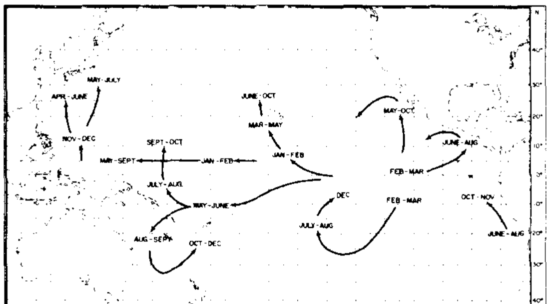

Figure 41.—Origin and migration routes of skipjack tuna as postulated from tuna longline data (from Kasahara 1968).

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[11] Naganuma, A. Unpubl. manuscr. Tohoku Regional Fisheries Research Laboratory, Shiogama City, Miyagi Prefecture, Japan.

quencies of skipjack tuna taken in the tuna longline fishery. Matsumoto (1974, 1975), on the basis of tuna longline catch data for four successive years (1964-67), proposed that there are a number of semi-independent stocks of skipjack tuna in the Pacific Ocean and that these stocks migrate in roughly circular paths (Fig. 42). The migratory paths were shown to follow a clockwise direction in the central and western North Pacific, and counterclockwise in the eastern North Pacific and in the Southern Hemisphere, corresponding with the flow of surface currents of the major water masses. By following the movement of high catch rate cells by quarters over several successive years, Matsumoto (1975, Fig. 12) has shown the probable routes by which fish can move from one area to the next and from the eastern to the western Pacific in the Northern Hemisphere and vice versa in the Southern Hemisphere within a period of 2 or more years.

Long distance migrations recorded for skipjack tuna in the Pacific Ocean are shown in Figure 43. The migrations are shown as straight-line movements between tagging and recapture sites, and do not necessarily reflect the actual paths taken by the fish in migrating from one point to another, nor the time required to negotiate the distances. Nevertheless, most of the midoceanic movements reflect the routes proposed by Matsumoto (1975).

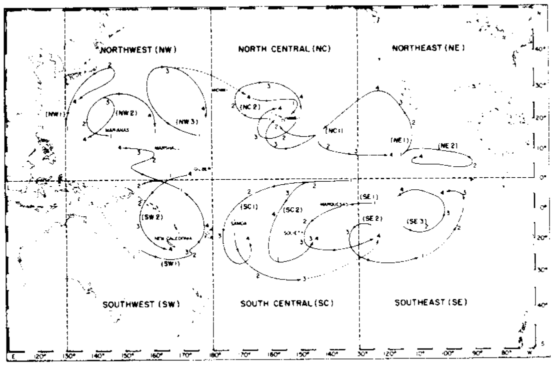

Figure 42.—Movement of the various geographic stocks of skipjack tuna in the Pacific Ocean. The numerals along the migratory routes represent quarters and locations of high catch-per-effort cells of skipjack tuna taken by the Japanese longline fishery, 1964-67. Stock designations are shown in parentheses (from Matsumoto 1974).

Local movements of skipjack tuna have been studied by tracking fish tagged with ultrasonic transmitters. A small skipjack tuna (44 cm) tracked for 8 d in Hawaiian waters by Yuen (1970), made nightly journeys of 25-106 km away from a bank and, with one exception, returned to the bank each morning (Fig. 44A, B, C). On the one exception, the fish was 9 km short of the bank; however, it remained there all day and returned to the bank on the following morning (Fig. 44D, E). The movement of the tracked fish was typical of fish which frequented the banks for feeding. Because of the repeated returns to the same spot and their consistent arrival times, Yuen suggested that skipjack tuna can navigate and that they are able to sense the passage of time.

In another study, one small (ca. 45 cm) and three large (ca. 70 cm) skipjack tuna were tagged with ultrasonic transmitters

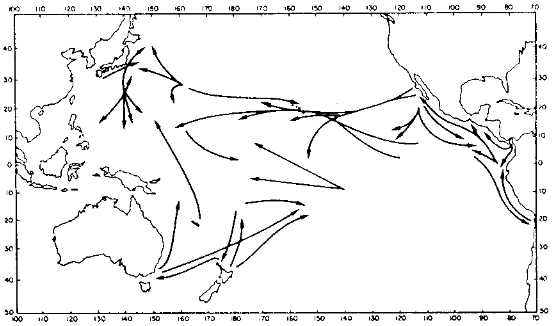

Figure 43.—Some long distance migrations of tagged skipjack tuna in the Pacific Ocean (from Forsbergh 1980).

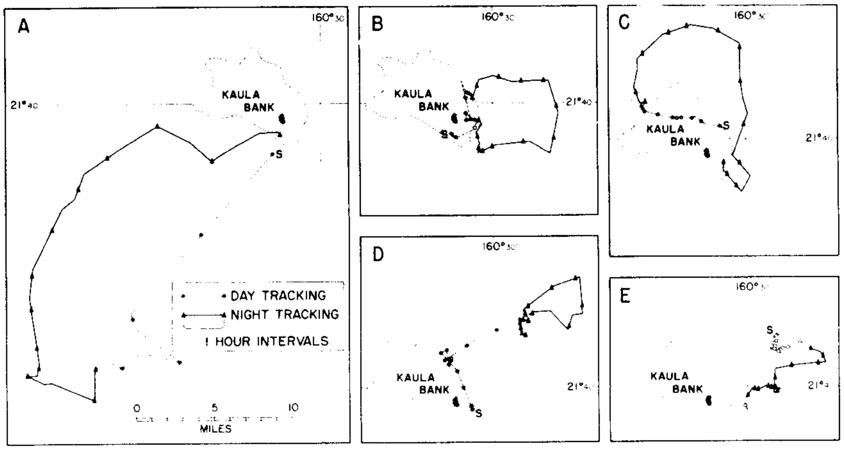

Figure 44.—Track of tagged skipjack tuna at Kaula Bank, Hawaii: (A) from 2:52 p.m., 30 August, to 6:00 a.m., 31 August; (B) from 6:00 a.m., 31 August, to 6:00 a.m., 1 September; (C) from 7:38 a.m., 3 September, to 6:00 a.m., 4 September; (D) from 6:00 a.m., 4 September, to 6:00 a.m., 5 September; (E) from 6:00 a.m., 5 September, to 7:30 a.m., 6 September (from Yuen 1970).

and tracked (Dizon et al. 1978). Behavior of the small skipjack tuna was identical to that in Yuen's (1970) study. Behavior of the larger fish, however, seemed independent of the banks. Movement during the day was characterized by many rapid vertical excursions superimposed on horizontal movement. The three fish traveled 142 km in 24 h, 50 km in 11 h, and 25 km in 10 h.

3.52 Schooling

It is well known that the skipjack tuna have a strong tendency to form schools; yet, very little is known about the mechanism involved in schooling nor the reasons which compel the species to school. Sette (1950) suggested that schooling of predators may assist in the capture of prey, whereas Breder and Halpern (1946) discussed the possibility that schooling may confer some protection from predation. Brock and Riffenburgh (1960), in treating the predator-prey relationship quantitatively, also were of the opinion that schooling of fish is a mechanism for protection against predation. The study of the courting behavior of skipjack tuna (Iversen et al. 1970) suggests yet another factor contributing to schooling. These studies, thus, point to at least three basic biological phenomena that could be responsible for causing fishes, including skipjack tuna, to school.

(1) 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: 1) By their association with birds, drifting objects, sharks, whales, or other tuna species; 2) by their behavior at the surface, such as milling, breezing, jumping, or feeding; and 3) by a combination of 1 and 2. The following list includes the various types of schools likely to be encountered in the oceans:

- Schools unassociated with birds
  - Milling or swirling in slow circular paths
  - Breezing or traveling
  - Jumping
- Schools associated with birds or bird flocks
  - Same as above
- Schools associated with drifting objects
- Schools associated with sharks
- Schools associated 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 or other fishes.

Schooling behavior is relatively easy to observe at the surface, but such is not the case of fish 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 et al. 1952) and from 25 to 200 m (Iwasaki and Suzuki 1972). Strasburg et al. (1968) reported seeing a school of approximately 250 skipjack tuna at depths over 90 m from a small submarine.

(2) 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 et al. 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, 1968a, b; Hunter and Mitchell 1967); rafts (Kojima 1960; Gooding and Magnuson 1967; Murdy 1980; Aprieto 1981; Matsumoto et al. 1981); other flotsam, such as ship's material, airplane fuel tanks, carcasses of dead whales, etc. (Inoue et al. 1963); and sharks (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 Ocean, 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 tuna and other tuna species is relatively common. In the eastern Pacific Ocean, Orange et al. (1957) and Broadhead and Orange (1960) reported that 72 and 62% of the yearly catches of skipjack tuna by purse seiners and bait boats, respectively, were made from pure schools, or conversely, 28 and 38%, respectively, from mixed schools. Kawasaki (1959, 1965a) reported that aside from mixed schools containing yellowfin tuna, fish species most frequently found with skipjack tuna are the kawakawa, frigate tuna, bluefin tuna, albacore, bigeye tuna, and dolphin. Yabe and Mori (1950) reported other fishes, including wahoo, *Acanthocybium solandri*; rainbow runner; amberjack, *Seriola intermedia*; triggerfish, *Canthidermis rotunadatus*; and jack, *Caranx equula*, are taken along with skipjack tuna associated with driftwood in waters off southern Japan. However, it is doubtful whether these fishes were truly mixed with the skipjack tuna schools per se.

Associations of fishes with floating objects have been studied by a number of workers. While protection from predators or availability of food was given as the reason for attraction by some (Hardenberg 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 tuna, 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) that 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 marlin. The latter's 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 tuna 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 may also be 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 marlin, the skipjack tuna merely comes in the vicinity of the whale. In this association, the skipjack tuna always precede the whale and may abandon the whale while the school is being fished.

Skipjack tuna are found associated also with anchored floating objects. Fishing for tunas around such objects (bamboo rafts) has been done for many years in the Philippines, where tuna were caught by hook and line (Murdy 1980). The introduction of purse seiners in the early 1960's (Aprieto 1981) and the rapid development of techniques for purse seining around the rafts have resulted in a highly successful commercial fishery for tunas (Matsumoto[12]). Recent experiments with fish aggregating devices constructed of two 55-gal steel drums and moored in depths of 400-2,200 m in waters around the Hawaiian Islands have been successful in attracting skipjack tuna and other tuna schools in sufficient quantities for commercial pole-and-line fishing (Matsumoto et al. 1981). Similar experiments are being conducted by several island states in the South Pacific and in the Indian Ocean.

(3) Distribution of types of schools

The distribution of the various types of schools differ by area and time. In the northwestern Pacific Ocean, off northeastern Japan, Uda (1933) reported that 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 cells 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 more extensive study off northeastern Japan, 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 in warmer waters slightly south of the two current boundaries, and 3) schools associated with birds were seldom seen in offshore waters (ca. 800 km). He further determined the percent occurrence of the various types of schools and plotted the average occurrence of the three most common types of schools in the area (Fig. 45). 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.

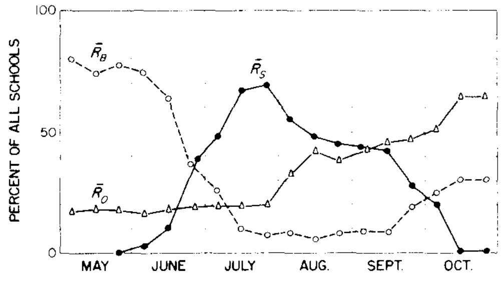

Figure 45.—Ratio of detection of schools with birds ($\bar{R}_B$), schools without birds ($\bar{R}_O$), and schools with sharks ($\bar{R}_S$) to total schools in each 10-d period (from Kimura 1954).

In more southern areas west of the Bonin Islands (lat. 19°-24°N, long. 136°-147°E), schools associated with whale sharks have been reported in October and schools associated with logs in February (Tohoku Regional Fisheries Research Laboratory undated a). Further south, in the area lat. 2°-5°N, long. 134°-150°E, schools associated with logs and bird flocks regularly occurred from December through February. Lastly, in waters south of the Equator, around Papua New Guinea and the Solomon Islands, schools were generally associated with bird flocks, with few instances of association with sharks or logs (Tohoku Regional Fisheries Research Laboratory undated b, d). Living Marine Resources (1977), however, reported that numerous logs of all sizes from twigs to entire trees were sighted and fished by three U.S. purse seiners in August-October 1976 in the area northeast of Papua New Guinea (lat. 3°N-4°S, long. 138°-154°E) in the South Equatorial Current. More specifically, T. K. Kazama[13] reported few log sightings in the area lat. 8°-3°N, long. 147°E, but that sightings increased considerably to the south (lat. 2°-4°S, long. 138°-147°E), numbering several hundred per day with the greatest single concentration of logs extending over an area approximately 15.5 m (50 ft) wide and 1.8 km (1 mi) long.

A vastly different situation prevails in the central Pacific Ocean, 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. Likewise, for two scouting cruises around the Hawaiian Islands during the spring of 1953, Royce and Otsu (1955) reported that every one of 253 fish schools sighted was accompanied by birds. Undoubtedly, this dependence on bird flocks for finding tuna schools in the central Pacific Ocean arises from the prevalence of birds in the area and partly from the prevailing sea state, which is

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[12] Matsumoto, W. M. Purse seining around payao in the Philippines. Manuscr. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.

[13] Kazama, T. H. 1976. Report on observations made aboard one of three purse seiners chartered by Pacific Tuna Development Foundation to fish in the western equatorial Pacific. Admin. Rep. 8H, 7 p. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.

commonly choppy, with numerous white caps. The latter condition makes it extremely difficult to see the wake of a school or jumping fish at any appreciable distance from a vessel. Schools associated with sharks, whales, or logs were not mentioned in either report. The absence of such schools is as expected since one of the 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 other, the whale shark, in Hawaiian waters (Gosline and Brock 1960). Drifting logs also are encountered only sporadically (personal observation by the senior author) in Hawaiian waters.

A report by Waldron (1964) summarized skipjack tuna schools and bird flocks observed in an area of the central Pacific Ocean bounded by lat. 30°N-20°S and long. 110°W-180° during 128 cruises by vessels of the U.S. National Marine Fisheries Service, Honolulu Laboratory, between 1950 and 1961. The results (Fig. 46) indicate that 1) high rates of sightings 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, and 3) the rate of sightings in the Marquesas Islands area was much higher than for other areas of similar size.

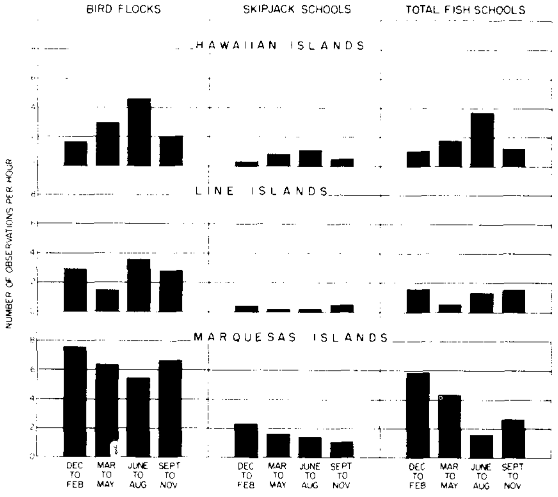


Figure 46.—Seasonal variation in rate of bird flock, skipjack tuna schools, and total fish school sightings for three major island groups (from Waldron 1964).

(4) Length distribution of schools

Brock (1954) noted a comparatively small range of lengths within individual schools in the Hawaiian fishery, in contrast to the range of lengths in the landings as a whole. The mean range of lengths for single school samples was 11.3 cm, with 5 and 21 cm being the least and greatest, whereas the range for the seasonal landing was 47 cm. He thus concluded that the skipjack tuna school was highly size-selective and hypothesized that the segregation by size was likely due to the maximum swimming speed attainable by fish of the same size.

Based on observations from the eastern Pacific tuna fishery, Schaefer (1948) suggested that the tendency of tunas to aggregate by size might, in some cases, be stronger than the tendency to aggregate by species. In addition, Broadhead and Orange (1960) observed that the frequency distributions of the lengths of skipjack tuna in pure and mixed species schools were similar, whereas those of yellowfin tuna differed noticeably (Fig. 47).

Kawasaki (1964) compared 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, i.e., the less mobile the object of association, the greater the size range of fish associated with it. This observation is, thus, consistent with Brock's (1954) hypothesis, since schooling under slow moving objects does not require uniform maximum swimming ability.

Catches of tunas from under stationary floating objects further support Brock's hypothesis. Matsumoto (footnote 12) observed that purse seine catches beneath anchored bamboo rafts in the Philippines included tunas (skipjack, yellowfin, and bigeye tunas, kawakawa, and frigate and bullet tunas) ranging widely in sizes from 24 to 63 cm. One or two large yellowfin tuna or bigeye tuna, 30 to 70 kg or more, were also taken occasionally.

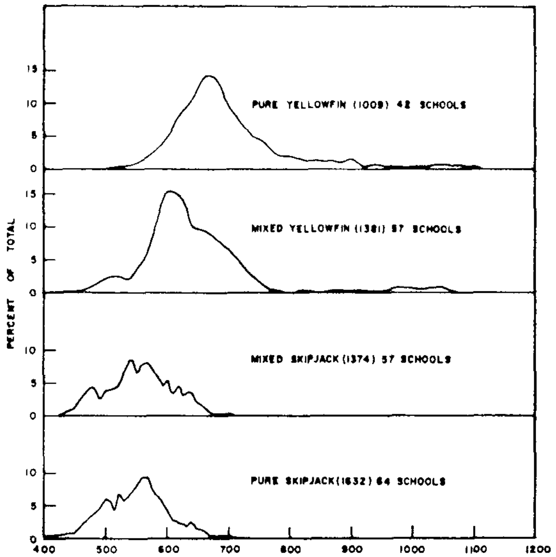


Figure 47.—Frequency distributions of lengths of yellowfin tuna and skipjack tuna from schools of pure and mixed-species composition sampled from bait vessel catches (from Broadhead and Orange 1960).

(5) Size of school

Estimation of school size has been attempted in the eastern Pacific Ocean by Orange et al. (1957), based on the catch-per-set by purse seine vessels, and by Broadhead and Orange (1960), based on the catch-per-school by bait boats. Estimates based on purse seine catches were considered more reliable than those based on bait boat catches because it is assumed a greater percentage of a school is taken by seining than by baitfishing. However, actual school sizes would still be greatly underestimated, since entire schools are not always caught by the purse seine (Orange et al. 1957).

The frequency distribution of catch-per-successful set by species composition categories plotted by Orange et al. (1957) showed that the distributions of pure skipjack tuna schools were skewed very strongly toward small catches (Fig. 48), with more than 50% of the sets falling in the two smallest size classes, i.e., 0.25-4.9 and 5.0-9.9 tons. (Note: Orange et al. used short tons.) The average catch-per-set of pure skipjack tuna schools in the eastern Pacific for the 4-yr period studied was 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 seine vessels were 6.3 and 8.6 tons, respectively (Inoue 1959). Either the schools in the eastern Pacific were larger than those in waters off Japan, or the fishing environment and technique were more conducive to greater catches from similar-sized schools in the eastern Pacific. It is also possible that seiners in the eastern Pacific are less apt to set on small schools than seiners off Japan. On the basis of Figure 48, one can say that the occurrence of small schools (<20 short tons) was the rule and that large schools over 50 short tons occurred less frequently.

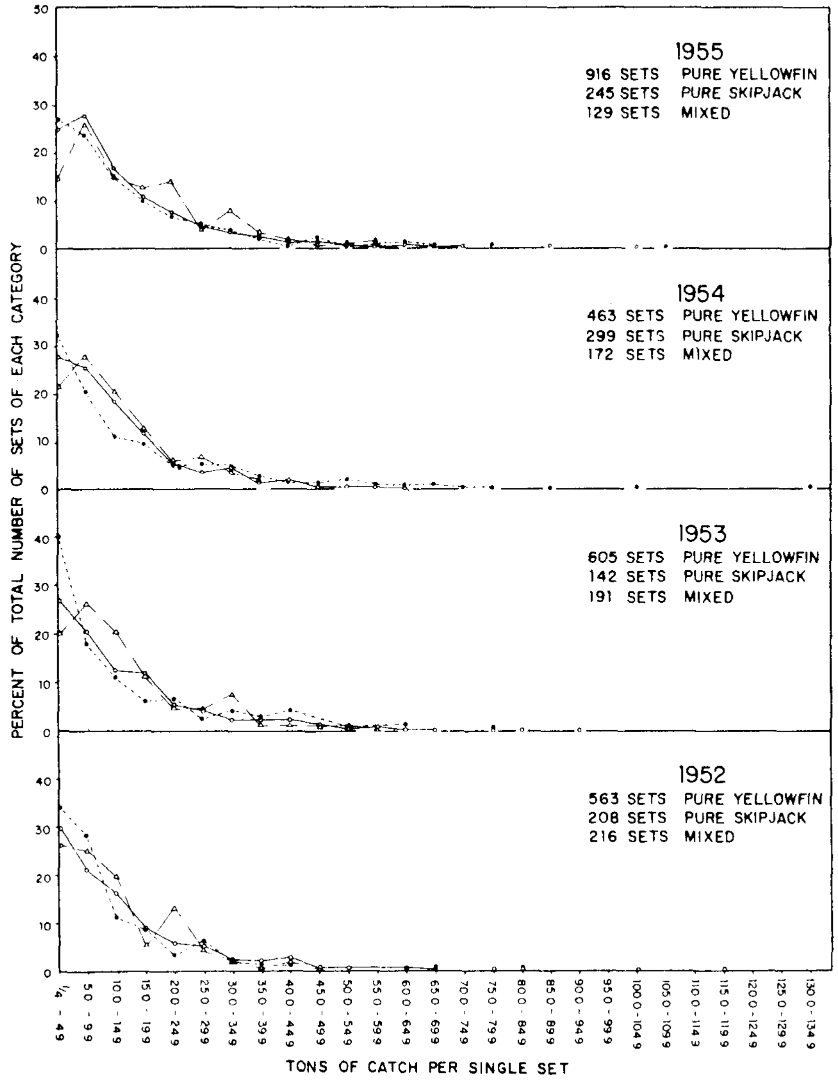


Figure 48.—Percentage frequency distributions of catch-per-set in the eight principal fishing areas of the eastern Pacific tuna fishery, for each year 1952 through 1955, by species-composition categories. Open circles represent catches of pure yellowfin tuna. Solid circles represent catches of pure skipjack tuna. Triangles represent catches of mixed species (from Orange et al. 1957).

The frequency distribution of catch-per-school from pole-and-line fishing (Broadhead and Orange 1960), was similarly skewed strongly toward the small catches (Fig. 49). The majority of the catches (about 65%) from pure schools fell into the two smallest size categories, 0.5 and 1.5 tons (note: Broadhead and Orange used short tons), and the mean catch for all schools was 2.8 tons. The difference in the mean catches by bait boats (2.8 tons) as compared with that of purse seine vessels (13.5 tons) probably reflects lower efficiency of pole-and-line fishing and the likelihood that the purse seine vessels may shun small schools more often than pole-and-line boats.

Broadhead and Orange (1960) compared the sizes of schools fished in the eastern Pacific and Hawaiian fisheries by plotting the distribution of catches from the two areas. Data from the Hawaiian bait boat catches yielded a J-shaped curve similar to that of the eastern Pacific catches but the points fell well below that of the latter. The mean catch-per-school was about 1 ton compared with 2.8 tons from schools fished in the eastern Pacific Ocean. On the basis of this comparison, they stated, "It appears that the skipjack tuna schools fished in the Eastern Tropical Pacific area are, on the average, somewhat larger than those fished in the vicinity of the Hawaiian Islands (assuming that the bait vessels capture the same percentage, on the average, of each school encountered in the two regions)." Such a comparison, however, is dubious since their assumption is incorrect. Both vessel size and number of men fishing per boat differ greatly between the two fisheries, thus resulting in disproportionate catches.

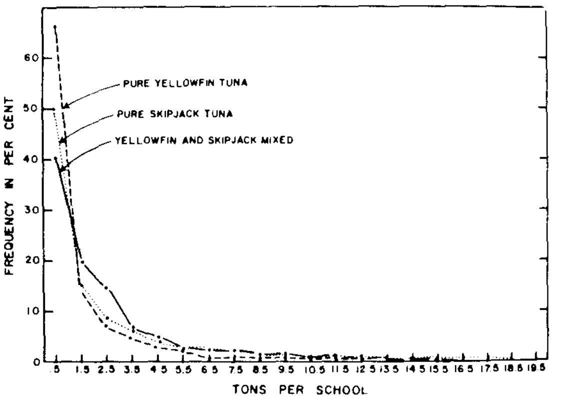


Figure 49.—Percentage frequency distributions of catch-per-school (tons) by bait vessels, by category of school, 1956-58 (from Broadhead and Orange 1960).

(6) Schooling at night

Some evidence for skipjack tuna schooling at night is 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), the fish remained in a school and swam slowly around the pool. Other evidence of schooling at night comes from Yuen (1970). While tracking skipjack tuna fitted with ultrasonic tags, 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 tagged fish.

(7) Activity of schools

That schooling occurs at depths in excess of 100 m was shown by Kimura et al. (1952) and Iwasaki and Suzuki (1972). From vessels equipped with echo sounders, Kimura et al. (1952) located fish schools between depths of 20 and 150 m. They identified them as skipjack tuna by tracking them on the echo sounder and 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 sec, a speed of 2.2 m/s (4.3 kn).

Underwater observations of skipjack tuna schools by Strasburg and Yuen (1960), Strasburg (1961), and Yuen (1970) provide further insight into the behavior of skipjack tuna schools. Strasburg and Yuen (1960) observed that the activity of schools varied with fish size. First, small skipjack tuna (ca. 20 cm) schooled in large numbers (in the thousands), and in spite of their size, the schools seemed to respond instantaneously to stimuli. The fish were closely spaced and maneuvered with precision. Even during feeding, these schools never entirely lost their integrity. Second, in schools of medium-sized fish (45-65 cm), feeding activity was frenzied and most semblance of schooling was lost. The fish made rapid dashes to the surface at speeds of about 12.9 m/s (25 kn), either singly or in pods of half a dozen or so; hence, their swimming was seldom horizontal but oscillated vertically in patterns resembling a series of sine curves. Third, schools of large skipjack tuna (70-80 cm) appeared lethargic in comparison with schools of smaller fish. There were no signs of schooling during feeding, and the individual fish never appeared to swim faster than about 5.1 m/s (10 kn). More often the fish cruised at 1.0 to 2.1 m/s (2 to 4 kn), swimming nearly horizontally, with surface dashes being relatively unhurried.

Strasburg and Yuen (1960) also noted that 1) water sprayed on the surface while chumming increased feeding frenzy, resulting in increased catches, 2) fast chumming (twice normal) resulted in decreased catches, 3) slow chumming or insufficient bait caused the fish to scatter and reform into schools away from the vessel, resulting in decreased catches, 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 fishes in the stomachs was significantly related to diving frequency. Observations on the 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 (Fig. 50) with a mean of 2.7. The schools were away from the surface as briefly as 3 s or as long as 28 min. In a later study (Strasburg et al. 1968) reef-type fishes, such as those found in the stomachs above, were observed from a small submarine at depths of 107 to

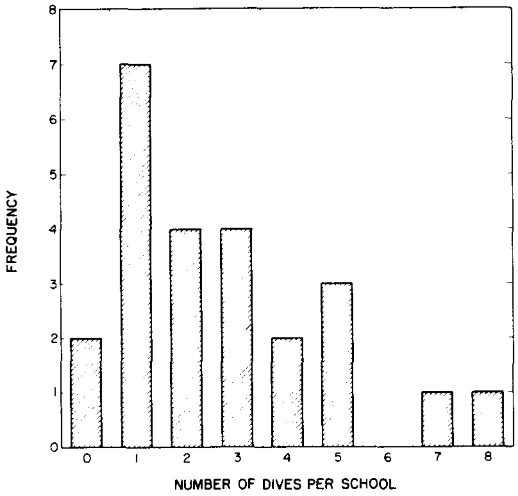


Figure 50.—Frequency of diving in Hawaiian skipjack tuna schools (from Strasburg 1961).

192 m, suggesting that skipjack tuna schools may have descended to these depths to feed.

(8) Biting response of schools

The factors influencing the biting response of skipjack tuna schools have been studied by a number of scientists. These factors include (a) state of hunger, (b) behavior of prey, (c) condition of gonads, (d) distance from land, (e) time of day, and (f) weather.

(a) 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 (1933) further observed that skipjack tuna with stomachs between the extremes of fullness and emptiness tended to respond more poorly than when their stomachs were emptier. This statement, however, is contrary to Yuen's (1959) observation that skipjack tuna schools responded to bait longer when the major food items in the stomachs were in the earlier stages of digestion and that the response became greater as the stomachs emptied. Similarly Uda's (1933) statement is contrary to Magnuson's (1969) observation that attacks by captive skipjack tuna on food particles decreased rapidly only after the stomach contents exceeded 50% of the stomach's capacity.

(b) Behavior of prey

Skipjack tuna feeding on fast-swimming fishes such as tunas, carangids, and gempylids, exhibit a more favorable biting behavior than skipjack tuna feeding on slower swimming chaetodontids, scorpaenids, molids, and acanthurids (Yuen 1959).

(c) Condition of gonads

Brock (1954) commented 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. He suggested that fish with ova larger than 0.7 mm in diameter become progressively less available to the fishery. This suggests that female skipjack tuna may abstain from feeding, immediately prior to and during the spawning period. Yuen (1959) found that maturation of the ovary did not appear to affect biting response, except in fish with ripe eggs. That skipjack tuna likely undergo a period of fasting is borne out by fishermen's remarks (see Section 3.41(4)) concerning the futility of fishing such schools.

(d) Distance from land

Suyehiro (1938) measured biting quality by catch rate (number of fish per man per 100 min), designating a catch of 16 or less fish as poor biting and 17 or more fish as good biting. Applying this criteria to schools fished in Japanese waters by 17 vessels, he found that skipjack tuna schools around islands bit poorly, whereas schools in the open sea generally bit well. Yuen (1959) reported a similar relationship; however, this was true only for large (>60 cm) fish.

(e) Time of day

Uda (1940) reported that there is a relation between time (hour of catch) and total catch, as well as between time and catch-per-school. He observed that catches peaked three times during the day, a primary peak between 0500 and 0900, a secondary peak between 1200 and 1300, and a tertiary peak between 1600 and 1800; and that about half of the day's catch was made between 0500 and 0900, and about two-thirds of the day's catch prior to noon. He explained the pattern of catch thusly: "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 believed that the decrease and increase in appetite occurred again 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 Section 3.41(4)), similar peaks were not reflected in the catch rates shown in 2 of the 4 yr he 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 variables, they used number of schools sighted and number of schools fished successfully. These variables plotted against time of day (Fig. 51) resulted in curves not unlike that obtained by Uda (1940); 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 was 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

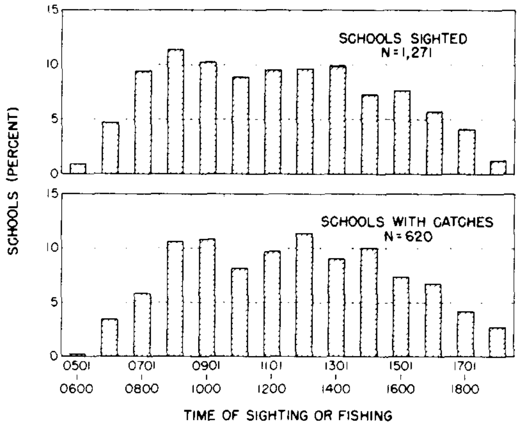


Figure 51.—Frequencies of school sightings and schools with catches, by time of day for seven Hawaiian skipjack tuna fishing vessels, June-August 1967 (from Uchida and Sumida 1971).

reduced sightings and 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 14).

Table 14.—Percentage of the day's total catch aboard the vessels in the first (by 0900), second (0901-1200), third (1201-1500), and fourth (after 1501) quarters of the fishing day for seven Hawaiian skipjack tuna fishing vessels, June-August 1967 (from Uchida and Sumida 1971).

	Quarters of the fishing day			
Vessels	First	Second	Third	Fourth
A	3.3	31.5	42.4	22.8
B	15.5	15.3	35.4	33.8
C	17.0	20.2	23.7	39.1
D	9.2	24.9	35.2	30.7
E	7.1	41.6	28.5	22.8
F	7.2	40.9	33.3	18.6
G	16.4	10.3	21.0	52.3
All	10.8	26.4	31.4	31.4
Cumulative	10.8	37.2	68.6	100.6

(f) 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 Ocean 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 Ocean, Yuen (1959) observed that weather conditions were predominantly uniform and biting behavior did not change by much. On a few days darker than usual, the weather affected fishing only in decreasing the chances of sighting schools.

(g) Other aspects of biting behavior

In the western Pacific Ocean, Uda (1940) indicated that in most of the schools fished, catches generally occurred between 10 and 40 min of fishing, that the catch rate (catch-per-school) increased in direct proportion to the increase in fishing time up to 80 min, and that when fishing time exceeded 80 min, neither the total catch nor the catch rate showed any increase. Similarly, in the central Pacific Ocean, fishing duration of most schools was between 5 and 40 min (Yuen 1959; Uchida and Sumida 1971) and the catch-per-school increased proportionally with fishing duration (Fig. 52).

Yuen (1959) also measured other factors that seemed to influence catch. Of these, 1) fishing duration, 2) peak catch rate, 3) postpeak duration, 4) rate of increase of prepeak catch rates, and 5) mean number of hooks per minute were all found to be related significantly to total catch (Table 15). Of these, 2) and 3) were subsequently used as measures of skipjack tuna response, on the premise that peak catch rate would measure the degree of interest or intensity in feeding and postpeak duration would measure the duration of interest.

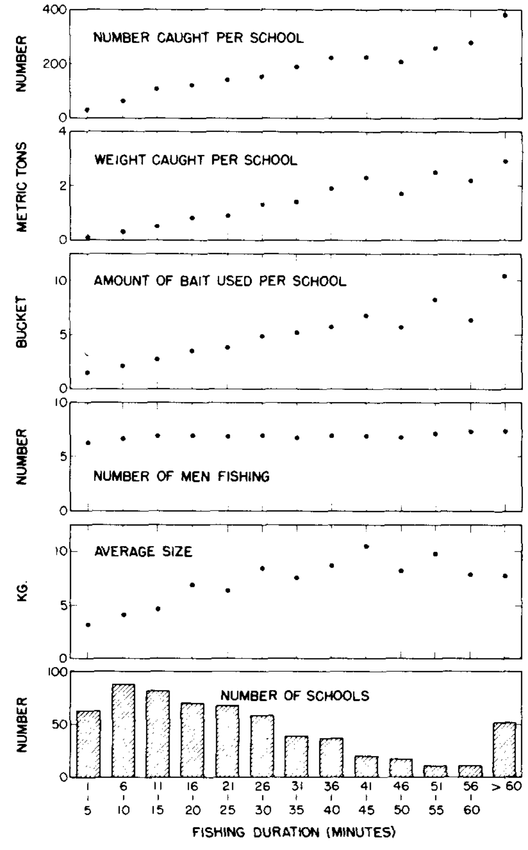


Figure 52.—Relation between fishing duration and average values of catch per school, amount of bait used per school, number of men fishing per school, and size of fish per school, June-August 1967 (from Uchida and Sumida 1971).

Table 15.—Correlation coefficients of total catch of skipjack tuna with various measures of fishing (from Yuen 1959).

Measure	df	r
Fishing duration	84	0.772
Peak catch rate	84	[1]0.614
Prepeak duration	84	0.201
Postpeak duration	84	[1]0.868
Rate of prepeak increase	71	[2]0.274
Rate of postpeak decrease	73	−0.120
Mean number of hooks	84	[1]0.289
Number of passes	81	−0.06
Time from start of pass to start of fishing	79	0.01

[1] Values beyond the 1% level of significance.
[2] Values beyond the 5% level of significance.

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:

1) Fish were attracted in large numbers immediately upon chumming and there was a sudden initial increase in catch,
2) the number of fish increased beyond the fishermen's capacity to catch them,
3) the duration of fishing above a minimum catch rate was long,
4) catch per school was large, and
5) maximum catch was attained quickly.

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

$$W = N\left(1 - (1 - \lambda t)e^{-\lambda t}\right)$$

where W is the number of fish caught, t is fishing duration, N is number of fish in school, and λ is the biting coefficient expressed as the reciprocal of the length of time until the catch rate reached 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 was the same. Ignoring school size, he found no statistical differences in the mean biting coefficient among schools judged as good, average, and poor by the fishermen.

Yao (1962) also observed that the mean biting coefficient, 0.135, for small schools ($<1{,}000$ fish) was extremely high, as compared with the mean coefficient, 0.085, of large schools ($>2{,}000$ fish). He suggested that the high mean coefficient for small schools was due to selective fishing of only good biting schools, whereas fishing was done on both good and slow biting schools when the schools were large.

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 min, depending on school size and state of hunger; and that weather may not be a factor in influencing feeding behavior.

3.6 Physiology

3.61 Energy transfer (metabolism)

Rapid and efficient energy turnover, more than any other single biological factor, characterizes the skipjack tuna's physiological ecology. Life in the warm and relatively unproductive tropical waters necessitates elaborate adaptations for locating and efficiently utilizing the patchily distributed food resources. Studies of these adaptations and estimates of energetic rate processes have provided information and insights for modeling of important management parameters (Sharp and Francis 1976). The detailed understanding of the skipjack tuna's energy budget has had its genesis in basic biological information obtained from experiments with captive specimens at the Kewalo Research Facility of the National Marine Fisheries Service in Honolulu. Indeed, this research facility is the source of much of what is known about the basic biology of tropical tunas.

(1) Energy budget

In all animals, energy transfer in and out of the animal is quantified in the energy budget or mass balance equation (Ricker 1968):

$$C = R + U + F + G + B$$

where C = rate of food consumption
R = rate of metabolism
U = rate of excretion
F = rate of egestion
G = rate of gamete production
B = rate of growth.

For our purposes the units in the analysis of this relationship will be given in caloric units (kcal). Skipjack tuna, for instance, contain an average of 1.46 kcal/g of live weight (Kitchell et al. 1977), and the mean caloric value of skipjack tuna forage is assumed to be 1.1 kcal/g wet weight (Kitchell et al. 1978).

The rate of metabolism (R) is lumped by Kitchell et al. (1978) into two components: 1) The energy, or specific dynamic action (SDA), required to process the forage, and 2) the remainder of the metabolic work (M). Table 16 presents the energy budget values of a 1 kg skipjack tuna under six input-output levels (Kitchell et al. 1978). Values for SDA, U, and F are assumed from work on other fish to be 15, 5, and 15% of ingested calories. Thus, the energy available for M and storage as growth or gonadal development is 0.65 of the calories eaten. Input of calories in the table range from starvation, maintenance calories (no growth) of 5.9% of body weight per day, ingestion of necessary calories to produce "normal" growth (0.7% of body weight per day, Uchiyama and Struhsaker 1981) at three arbitrary multiples of activity, and maximum ingestion of 30% of body weight per day. The maximum ingestion rate was determined in laboratory studies.

Growth under these input conditions varied from −3.6% under starvation conditions to a maximum growth rate of 6.9% of body weight per day when fish were feeding at maximum rations (30% of body weight per day while maintaining levels of activity nearly three times those at minimum sus-

Table 16.—Estimated energy budget terms at six bioenergetic regimes for a 1 kg skipjack tuna at 24°C (from Kitchell et al. 1978).[1]

Bioenergetic regime	Requisite ration (% body wt./d)	Process rate (cal/kcal per day)					
		Consumption (*C*)	Net metabolism (*M*)	SDA	Excretion (*U*)	Egestion (*F*)	Growth (Δ*B*)
Starvation	0	0	29	5	2	0	−36
Maintenance	5.9	44	29	7	2	7	0
Observed growth at							
1 Lab M (= Level I)	7.3	57	29	9	3	9	7
2 Lab M (= Level II)	13.1	99	58	15	5	15	7
2 Lab M (= Level III)	19.0	143	87	21	7	21	7
Maximum	30.0	250	87-155	38	12	38	7-69

[1] Daily ration is given as percentage of body weight consumed per day assuming 1.1 kcal/g live food.

tainable cruising speeds). If activity levels include metabolic costs to five times that at minimum cruising speed, growth rates would be only 0.7%/d at maximum rations. Kitchell et al. (1978) reasoned that these levels of activity were unrealistically high and, therefore, the observed growth rates of 0.7%/d indicated limited food availability rather than high levels of activity.

In skipjack tuna, unlike most other animals, the routine metabolic rate per unit of weight does not decrease as size increases (Brill 1979; Gooding et al. 1981). Large fish have approximately the same metabolic rate per unit of mass as small fish. The reasons for this phenomenon are obscure. However, in skipjack tuna, as in most other animals, the relative capacity for feeding does decrease as size increases. In absolute terms, large fish can eat more than small fish but in relative units, the maximum ration per unit of weight decreases as size increases. Ability to acquire energy and the energy costs of metabolism thus converge as skipjack tuna size increases. This interesting relationship can be used to predict the limits of growth. It has been shown that to pursue and capture prey takes a metabolic rate approximately two times the rate required to just swim at minimum speed (speed required to maintain hydrostatic equilibrium, Magnuson 1973). Then the maximum ability to provide surplus energy for growth (0.65 of maximum ration) is equivalent to the minimum activity necessary for feeding by skipjack tuna weighing 25-30 kg.

For yellowfin tuna, unlike skipjack tuna, the metabolic rate per unit weight declines as size increases. The maximum feeding rate also declines but at a slightly more rapid rate than metabolism. As in skipjack tuna, both rates converge but at levels that predict maximum yellowfin tuna sizes of 150-200 kg. The maximum predicted sizes of the two tunas can be compared with maximum sizes in Section 3.31 for skipjack tuna (22-25 kg) and the largest known yellowfin tuna (180-200 kg).

An economic analogy may help make these concepts more understandable. If: 1) feeding rate is taken as income; 2) egestion, excretion, and SDA rates as taxes (proportional to income); and 3) metabolic rate as fixed costs, then growth (somatic and/or gonadal) can be considered net profit. Small animals have the potential for large profits because their fixed costs are low and their income potential is high. As size increases, so too do fixed costs and taxes, but potential profit margin narrows due to a less rapid increase in income potential. Eventually they converge at a point that dictates the maximum size. In yellowfin tuna, in contrast to skipjack tuna, the fixed costs decline slightly (an economy of scale) as size increases, allowing it to become larger before the convergence of costs and profits occur. Obviously, any differences between real income (food availability) and maximum income potential will cause the zero-profit level to develop at a smaller size.

(2) Respiration

Intermediary metabolism is the process whereby energy is made available for biological power, the fixed costs referenced in the preceding section. Intermediary metabolism, sometimes called internal respiration, is measured in units of oxygen consumed, calories transferred, carbon dioxide liberated, or power in watts. All are stoichiometrically related. External respiration is defined as the mechanism which delivers O_2 and expels CO_2.

Since skipjack tuna cannot use buccal or opercular pumping to force water over their gills, they must continually swim or they will suffocate. They are "ram ventilators." A 44 cm skipjack tuna swimming at a basal speed of 66 cm/s, has a gill resistance equal to 7% of its total swimming resistance (Brown and Muir 1970). The cost of this extra resistance is approximately 1 to 3% of its total metabolism when swimming at basal speeds.

Within the gills, O_2 is extracted from and CO_2 delivered to the water. Here, as in other structures dealing with energy transfer in the tuna, there exist modifications for rapid exchange. Within the secondary lamellae of the gills, blood flows obliquely to the long axis rather than with it as in other teleosts (Muir and Brown 1971). This oblique pathway allows a greatly shortened length of the absorbing vessel, reducing the total blood pressure drop across the skipjack tuna's gill by 16 times. The short path length allows for small diameter absorbing vessels as well as thinner, more efficient lamellae. The latter reduces resistance to water flow. Large gill areas result from the increase in total number of lamellae and their length. These adaptations result in a gill, which, while delicately constructed and fine grained, has an area of from 4 to 30 times larger than other teleosts.

Thus with this large gill surface area, the tuna gill's effectiveness in removing oxygen from the water is higher than other teleosts'. Stevens (1972) has estimated that skipjack tuna can extract up to 90% of the oxygen in the water that enters the mouth. Other fish can extract from 10 to 30%.

Four techniques have been employed to estimate oxygen uptake: 1) Whole animal, in which one or more tuna are confined within a sealed tank and the drop in dissolved oxygen is measured as the tunas respire; 2) starvation experiments, where energy consumption is measured by loss of weight and caloric density; 3) in vitro experiments that measure oxygen uptake of various tissue samples; and 4) restrained experiments, where oxygen consumption is measured from a perfused, paralyzed fish.

Of these four techniques, the measurements of oxygen consumption from fish swimming in enclosed chambers is the most common. Gooding et al. (1981) found that skipjack tuna's "standard" metabolic rate (SMR) was two to five times that of similar-sized, active non-tuna species. However, the true SMR for tunas is oxygen consumption rate at zero activity. This true rate must be extrapolated from rates collected from fish swimming at various voluntary speeds. The regression relating consumption rate to size and swim speed is as follows:

$$\log VO_2 = -1.20 + 0.19 \log W + 0.21\, S$$

where VO_2 = oxygen uptake (mg O_2/g per h)
W = fish weight (g)
S = swim speed (body lengths/s).

Of note is the weight exponent of near 0.2 compared with −0.2 of typical fish. Because the swim speed of routinely active skipjack tuna is inversely related to weight, routine metabolic rate is virtually independent of fish weight.

Lacking any caloric input, skipjack tuna lose mass and caloric density from their tissues from metabolic demand. The oxycalorific equivalent relates oxygen uptake values to those of calories transferred, 3.4 cal/mg O_2. A tuna swimming at its weight-dependent characteristic swimming speed (about 1.4 body lengths/s) has an energy demand (from Gooding et al. 1981) of $\log VO_2 = -0.54 + 0.08 \log W$. Thus, a 1,500 g skipjack tuna, swimming at its characteristic respirometer tank speed would consume 64 kcal/d. In a fasting fish, the energy comes from mobilization of body tissues; Kitchell et al. (1978), citing other sources, estimated that 20% overhead must be obtained from the tissues; the overhead pays for the deamination of proteins (15%) and the excretion of nitrogenous waste (5%). This will add an additional requirement of 16 kcal/d: $80 - (80 \times 0.2) = 64$.

The energy content for a whole skipjack tuna is approximately 1.46 kcal/g, which for our 1,500 g example is 2,190 kcal. Thus, a skipjack tuna swimming at 1.4 body lengths/s should lose about 3.7% of its total energy per day.

How does this compare with a real, fasting fish? Work at the Kewalo Research Facility demonstrated that starving skipjack tuna lose weight at 1.8%/d. But weight loss is not the complete story. Fish utilize fat and hydrate as they starve, so weight loss underestimates energy loss (Kitchell et al. 1977). They estimate that skipjack tuna lose about 1.8% of energy content per unit weight per day. This change of caloric density is added to the absolute weight change to yield an independent estimate of energy loss of 3.6%, which compares favorably with the 3.7% figure estimated from respiration measurements.

Gordon (1968) estimated metabolism from still another approach. Metabolic rates of unstimulated, minced muscle from skipjack and bigeye tunas were measured. Both red and white muscle preparations were employed. Values for red muscles averaged 2 mg O_2/g per h, for white muscle, 0.4 mg O_2/g per h. Tuna muscle is obviously a fast respiring muscle comparable with rat thigh muscle at its physiological temperature (Gordon 1968). Another interesting aspect of this work is the lack of much of a temperature effect upon respiration; a Q_{10} of virtually 1 is observed. Dizon et al. (1977) also observed this temperature compensation of swimming speeds. Perhaps this rapid temperature compensation, something observed in other animals whose habitats have rapid temperature changes, is an adaptation for their behavior of fast, continuous, vertical movements from the thermocline to the surface.

One difficulty in determining respiration of tunas is to arrive at a common level of activity which produces a respiration rate which can be compared with other fish. Usually this value is the SMR, which is defined as the energy requirements of a postabsorptive animal completely at rest. Tunas cannot stop swimming so this activity level is meaningless. Gooding et al. (1981) referred to the routine respiration rate, that is, the energy requirement of a tuna swimming at its "characteristic" speed. A standard rate can be determined from the routine measurement by extrapolating the swimming speed to respiration rate relation back to zero activity. Another approach is a direct measurement of respiration on a paralyzed, restrained fish (Brill 1979).

The SMR of 33 restrained fish ranging in size from 0.3 to 4.7 kg was:

$$\log VO_2 = 0.8987 - 0.437 \log W$$

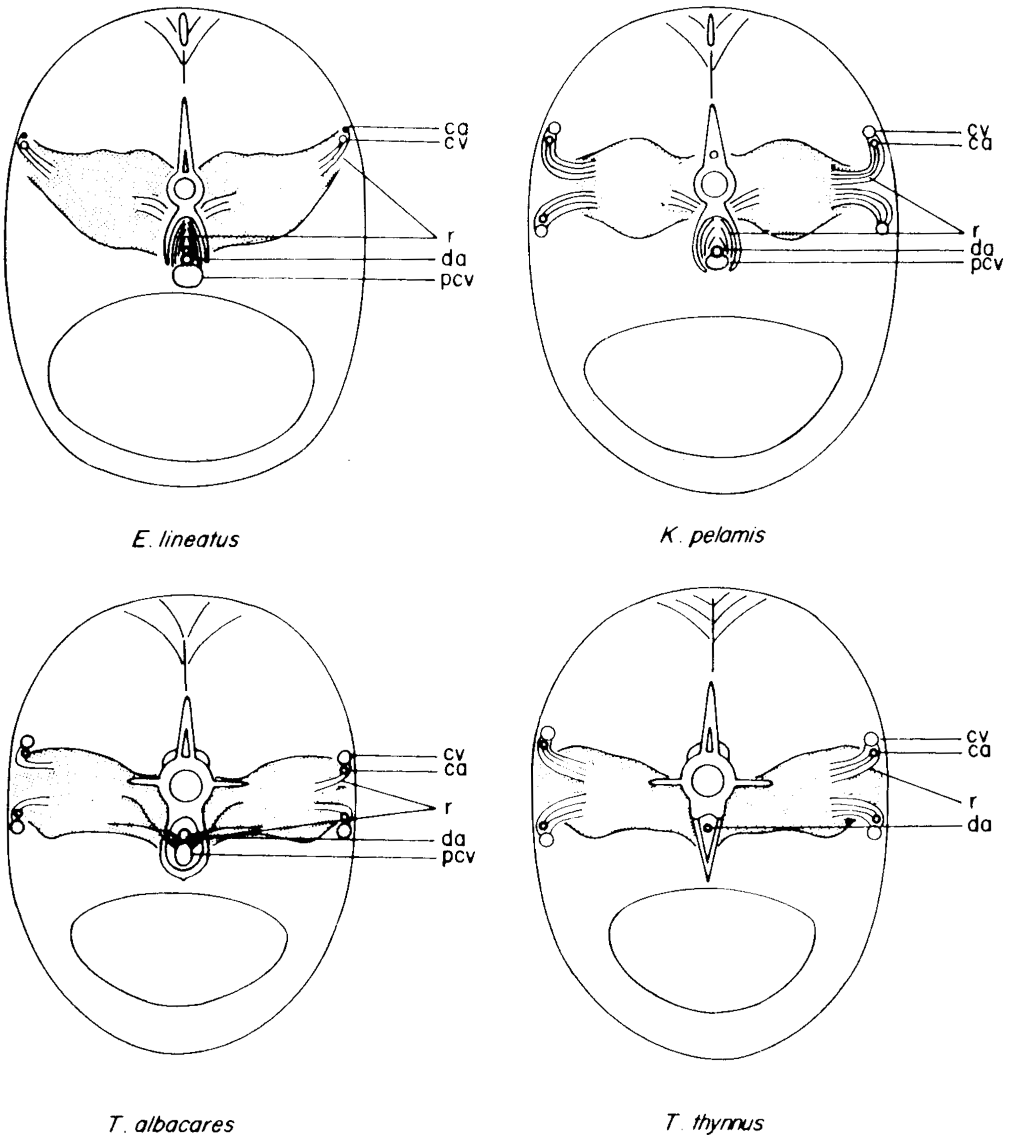
where VO_2 = SMR (mg O_2/g per h)
W = fish weight (g).

How do these values compare for other fish and for other methods of determining tuna respiration? Again the weight exponent is different. Other teleosts range from 0 to about −0.350 (quoted in Brill 1979). The value of −0.437 indicates that as body size increases, the SMR decreases relatively faster than for other teleosts which contradicts Gooding et al. (1981). However, the values predicted for the SMR by Brill's method compares favorably with the extrapolations of speed to zero of Gooding et al.'s regression. Compare 0.253 mg O_2/g per h determined by extrapolation of the regression to 0 and 0.324 mg O_2/g per h determined by Brill (1979). Brill reported that SMR's for tunas by either method exceed those reported for other teleosts by 5 to 10 times.

A logical next step is to inquire if high respiration rates correspond to a sensitivity to low dissolved oxygen (DO) levels in the habitat. Work reported in Dizon (1977) and Gooding et al. (1981) indicate that this is so. Skipjack tuna show definite signs of stress when DO levels fall below 3.5 mg O_2/l. Both investigations report dramatic increases in swim speed around 4.0 mg O_2/l. Dizon (1977) failed to observe any increased swim speed responses in yellowfin tuna at oxygen levels as low as 2.5 mg O_2/l. The swim speed response seems to be an adaptation to remove the animal from stressful habitats. An alternate explanation, increased ram jet ventilation, is not indicated since metabolic O_2 demands rise faster than the O_2 delivery to the gills as swim speed increases. Although these data indicate a great sensitivity to low O_2 environments, skipjack tuna can probably be conditioned to penetrate waters below 2 mg O_2/l for a reward, as was done with kawakawa (Chang and Dizon[14]). Hence the correlation of purse seining success with a shallow, O_2-deficient thermocline (Green 1967) is probably contradicted by the tunas' willingness to penetrate toxic habitats for short periods.

(3) Locomotion

For many years, the biochemistry of the skipjack tunas' unique intermediary metabolism has been researched by P. Hochachka and his students. The following is from Hochachka et al.'s (1978) excellent summary of the skipjack tunas' unique "power plant and furnace." Skipjack tuna, as other tunas, have an unusually large and distinct red muscle mass (8%) (Magnuson 1973), which is distinct and separable from the white (Fig. 53). This fact makes the tuna an excellent



E. lineatus *K. pelamis*

T. albacares *T. thynnus*

Figure 53.—Transverse sections of four tuna species showing the positions of the red muscle (shaded areas), the central and lateral rete mirabile (r), and the major blood vessels supplying the retia; dorsal aorta (da), posterior cardinal vein (pvc), cutaneous arteries (ca), and veins (cv). Note that the position of cutaneous arteries and veins in *Euthynnus lineatus* is reversed compared with that in other species and that only an epaxial pair is present. Also, *Thunnus thynnus* does not have a posterior cardinal vein (from Graham 1975).

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[14] Chang, R. K. C., and A. E. Dizon. Low oxygen levels (and temperature) as a barrier to voluntary movement of tunas. Manuscr. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.

subject for muscle biochemistry studies. Previous data on teleosts supported separation of function for the two types of muscle: red is aerobic and is thus used for basal level swimming; white is anaerobic and is used for high speed and burst swimming. Recent workers suggest that there might be more overlap of function than heretofore suspected (sources cited in Hochachka et al. 1978 and in Brill and Dizon 1979). In general, the red muscle is highly vascularized and contains significant amounts of fat and glycogen, high amounts of enzymes of aerobic metabolism, and tremendous numbers of mitochondria. Red muscle thus appears totally aerobic, burning either carbohydrate, fat, or both. This is the typical teleost pattern. White muscle is, however, unusual. It contains high amounts of glycogen and concomitantly high glycolytic enzyme activities. But the enzymes for aerobic metabolism also occur in large quantities. Mitochondria exist in far greater numbers than in typical teleost white muscle, and fat droplets also occur. While white muscle contributes to burst swimming, supported by the "most intense anaerobic glycolysis thus far known in nature" (Hochachka et al. 1978: 154), most white muscle functioning is aerobic-based. This fact will be important when we later discuss thermoregulation.

The biochemical and physiological adaptations of the skipjack tuna characterize a high performance animal. This is obvious to anyone familiar with the morphology of the tunas. Strong selection pressures have operated to create body and fin configurations, swimming movements, and musculature to minimize drag and maximize thrust production per unit of input energy. Adaptations for reducing drag are more extensive in the tunas than perhaps in any other group. The skipjack tuna has an almost perfect body shape for longitudinal streamlining (Magnuson 1978). Drag reaches a minimum when maximum body thickness is 22% of length (Webb 1975). In contrast, the wahoo has a ratio of 12% (Magnuson 1973).

Turbulence is reduced by the presence of longitudinal, horizontal keels on the caudal peduncle (Webb 1975; Magnuson 1978). Similarly, the midline finlets across the dorsal and ventral portions of the posterior quarter of the body direct the water in a smooth flow as the tail beats in rapid, but low amplitude oscillations. The avoidance of turbulent flow around the fish results in lower drag. The oval peduncle, faired with the lateral bony keels, slips back and forth through the water with a minimum of resistance and yet provides a strong link with the high aspect, lunate tail. Drag producing structures are absent or reduced or can be removed from the water stream. No scales are present, save at the corselet, so the body is smooth. The eyes, nares, and mouth structures are almost perfectly faired into the body surface. The dorsal and pelvic fins are used only during turns so in straight-line swimming, the dorsal fin is slotted into the back and the pelvics are appressed into grooves. The pectoral fins provide lift to the negatively buoyant body and must remain in the water stream. However, when the skipjack tuna turns, the outer fin is appressed into a lateral groove on the body surface and its body pivots. Magnuson (1978) stated that during burst swimming, both pectoral fins are appressed into their respective body depressions, thus presenting a smooth body surface. Tuna fins have high aspect ratios; the length is long with respect to the width. Induced drag is relatively smaller for this fin shape (Magnuson 1978).

Yuen (1966) has recorded swimming speeds from skipjack tuna using cine techniques from a ship's observation chambers at sea. Speeds ranged from 0.5 to 14.4 body lengths/s. Dizon et al. (1978), employing ultrasonic tracking methods, recorded swimming speeds that clustered around 2 body lengths/s—not exceptionally fast, but they observed that sometimes the tuna would maintain speeds above 6 body lengths/s for over 30 min, and over 3 body lengths/s for over 240 min. Trout, in contrast, can only maintain 5 body lengths/s for < 5 min (Brett 1973). But we doubt that tunas are the fastest fish; Fierstine and Walters (1968) compared acceleration times of wahoo and yellowfin tuna and found that wahoo could accelerate around six times faster. While this is not surprising in a "lurking" predator like the wahoo, it provides insight into tuna design criteria. The impression that emerges is that the skipjack tuna should be viewed as a sustained performer, continually swimming at speeds considerably above most other teleosts', but perhaps not capable of the high speed bursts of the lurking predators.

Small tuna species (at least as adults) are totally lacking in a swim bladder and are, as a result, negatively buoyant (Magnuson 1973). Perhaps this is an adaptation to allow them to rapidly forage throughout the water column without danger of embolism. The ultrasonic studies reported by Dizon et al. (1978) showed continuous vertical movement that ranged between the surface and 273 m; these were sometimes completed in less than a minute.

Because the fish are negatively buoyant, lift must be provided to maintain hydrostatic equilibrium. The pectoral fins provide most of this lift (Magnuson 1973). Since lift is generated from the forward motion of the fish, the necessity of maintaining hydrostatic equilibrium imposes a minimum swim speed on the skipjack tuna. If speeds fall below this minimum, insufficient lift is generated and the fish either sinks or must resort to tail-down-head-up swimming behavior or a kind of flapping of the pectoral fins. The minimum swimming speed of skipjack tuna (Fig. 54) falls as size increases, from above 3 body lengths/s for a 12 cm animal to below 1.5 for a 100 cm one (Magnuson 1973). Incidentally, Magnuson (1973) reported that the minimum speeds predicted for skipjack tuna are identical to those predicted by Shuleikin (cited in Magnuson 1973) as most efficient for migration by aquatic species.

Measurements of drag by the various body and fin components can be used to estimate power consumption. Magnuson (1978) and Magnuson and Weininger (1978) provided accurate estimates of body dimensions and drag estimates for the various tunas. Dizon and Brill (1979) and Gooding et al. (1981) have used these to determine power required and heat generated at various swim speeds. An estimate for the 1,500 g example skipjack tuna's theoretical power uptake can be calculated by the following.

1) Total input power to swim is the sum of the power required for caudal thrust divided by the muscle efficiency of the propulsion system (20%) (Webb 1975) and added to the power required for nonswimming processes (Brill 1979; SMR, see Section 3.61(2)).

2) Thrust power must be equal to drag force multiplied by velocity (power equals force times velocity) and is estimated by:

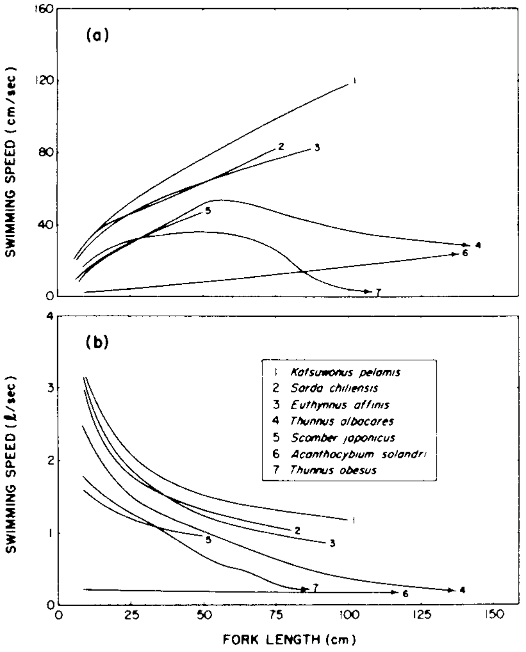

Figure 54.—Estimated minimum swimming speeds of seven scombroid fishes for maintaining hydrostatic equilibrium in (a) cm/sec and (b) body lengths/sec (from Magnuson 1978).

$$P = (0.5 \times \varrho \times S \times V^2 \times \mathrm{Cd} \times 10^{-7}) \times V \times 253$$

where P = required thrust power (mg O_2/h)
ϱ = water density (1.0234)
S = surface area (0.4 L^2, where L = fork length)
V = velocity (centimeters/s)
Cd = coefficient of drag (dimensionless number relating surface area and velocity to drag force)
253 = a multiplier that converts watts to mg O_2/h, assuming an oxycalorific equivalent of 3.4 cal/mg O_2.

3) The coefficients of drag and body surface area have been calculated for skipjack tuna and others by Magnuson and Weininger (1978). For the purposes of this treatment, a simple 0.4 L^2 assumption is sufficient for body surface and an estimate of drag coefficient of:

$$\mathrm{Cd} = 10\left(\frac{\varrho L V}{\mu}\right)^{0.5}$$

where μ = water viscosity (0.0096).

The 1,500 g (43 cm) example skipjack tuna swimming at 1.4 body lengths/s should theoretically have a coefficient of drag of about 0.02, require 0.028 mg O_2/g per h of thrust and thus five times as much input power to the propulsion system to "pay" for the 20% efficiency of the system (80% is lost as heat, some of which warms the body). Input required is thus 0.14 mg O_2/g per h, which must be added to the power required for nonswimming functions such as osmoregulation. Using Brill's (1979) SMR relationship (0.35), the total required power should be 0.49 mg O_2/g per h, which compare well with Gooding et al.'s (1981) measured value of 0.498 mg O_2/g per h.

3.62 Thermoregulation

Stevens and Neill (1978) characterize the life history strategy of the tunas as energy speculators. Tunas gamble relatively large amounts of energy to quickly move through their forage-poor environment and anticipate correspondingly large energy returns. Adaptations for energy speculation have produced many of the unique specializations that we have so far described for fast swimming and rapid energy overturn. It has also presumably brought them to the verge of homeothermy. Tunas, and some pelagic sharks, maintain their body temperature above that of the surrounding water. As indicated in earlier sections, tunas, particularly skipjack tuna, have exceptionally high metabolic rates. Because the propulsion system is only 20% efficient, 80% of the input power to the system is available to heat the tissues. In most teleosts this excess heat is carried from the trunk muscles by the venous system to the gills, where the heat is lost to the water. Thermal equilibrium occurs at a much faster rate than the mass transport of O_2 and CO_2, so the heated venous blood thermally equilibrates with the seawater. As a result, excess temperatures of most teleosts never exceed a few tenths of a degree.

The thermoconserving mechanism taxonomically distinguishes the 13 species of true tunas from the rest of the scombrid family (Klawe 1977; Collette 1978). Heat is transferred from the venous to the arterial sides of the circulatory system in a system of countercurrent parallel arterioles and venules in close contact (Fig. 53). These are the rete mirabile ("wonderful nets"). Tunas have four different types:

1) Cutaneous retia served by cutaneous arteries and veins which are unique among teleosts. This system is very large in bluefin tuna and provides all of the muscle blood flow. In the skipjack tuna, however, it is small and of presumably minor importance (Stevens and Neill 1978).

2) Visceral retia are found within the bluefin tuna, albacore, and bigeye tuna but are absent in the skipjack tuna.

3) Eye and brain retia are found in the bluefin tuna and albacore but unknown in the skipjack tuna, although they exhibit elevated brain temperatures.

4) Central rete are well developed in the skipjack tuna and other small tunas. It is located directly beneath the vertebral column. Stevens et al. (1974) has described the retia in great detail (Fig. 55).

Because of the countercurrent rete, metabolic heat is trapped within the muscle mass of the body with excess temperatures ranging from 1° to 21° above the surrounding water (Barrett and Hester 1964; Carey et al. 1971; Stevens and Fry 1971; Graham 1975; Dizon et al. 1978; Stevens and Neill 1978).

Tunas have several thermoregulatory options (Dizon and Brill 1979):

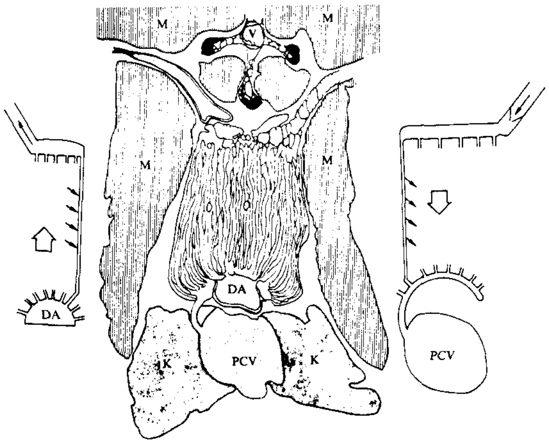

Figure 55.—Schematic drawing illustrating the major features of the vascular heat exchanger of skipjack tuna. DA, dorsal aorta; K, kidney; M, muscle; PCV, post-cardinal vein; V, vertebra. Left inset shows pattern of arterial blood flow; right inset shows patterns of venous blood flow; small arrows indicate heat transfer from venules to arterioles in the exchanger (from Stevens et al. 1974).

1) *Behavorial thermoregulation*

Since tunas are mobile and live in a heterothermal environment, they can behaviorally select optimal thermal habitats. Except for bluefin tuna, the distribution of the others is narrowly circumscribed by temperature (Sund et al. 1981). And because they "store" heat, they can behaviorally regulate activity to alter heat production: less activity means less heat produced.

2) Passive thermoregulation

Any process that stabilizes body temperature without requiring nervous system intervention can be characterized as passive thermoregulation.

Water temperature- and swim velocity-related heat production have been suggested as affecting body temperature. Water temperature affects water viscosity and density and thus influences drag forces which, in turn, alter the energetic requirements of swimming.

Thermal inertia might explain much of what was considered physiological thermoregulation in the past (Carey et al. 1971; Neill and Stevens 1974; Neill et al. 1976; Dizon and Brill 1979). Because of the retia, heat is exchanged with the environment at a much more reduced rate in tunas than in similar-sized teleosts; body temperature changes in tunas thus can significantly lag behind environmental changes.

As swim velocity increases, the surface heat dissipation rate is increased. However, it does not appear that this process is sufficient for stabilizing body temperatures in response to increased heat production as tuna swim faster (Dizon and Brill 1979).

3) *Physiological thermoregulation*

Activity-independent thermoregulation requires that the nervous system has the ability to recognize thermoregulatory needs and alter the effectiveness of thermoconserving structures.

It is difficult to use field data as evidence for physiological thermoregulation. Barrett and Hester (1964) determined a regression between sea surface temperature (*Ta*) and body temperature (*Tb*): $Tb = 0.58\ Ta + 16.39$. Presumably, if *Tb* was constant over a great range of *Ta*'s, one could assume a thermoregulatory ability. In skipjack tuna, the slope is different from unity implying some thermoregulatory process. However, other workers (Carey and Teal 1969; Stevens and Fry 1971) observed muscle temperatures quite different from Barrett and Hester's (1964), although the fish were taken in waters of the same temperature. Still, Stevens and Fry (1971) concluded that skipjack tuna could maintain a fixed *Tb* in waters ranging from 25° to 34°C; that is, that they do regulate. Conclusions drawn from such field evidence, however, are not justified because the thermal histories of the fish prior to capture were unknown. Very cool water is available to the fish within less than a minute before the time it is caught, boated, and measured. Consequently, sea-surface temperature does not necessarily represent the real habitat temperature. Moreover, thermal inertia causes *Tb* to lag behind apparent changes in *Ta*, and activity of the fish is a critical determinant of heat production and presumably *Tb*. All these affect the thermal history of the fish before they are captured.

To differentiate between thermoregulatory options, experiments must be conducted that measure *Tb* and activity at specified, constant *Ta*'s. Dizon et al. (1978) and Dizon and Brill (1979) investigated thermoregulatory performance in skipjack and yellowfin tunas, where *Ta* could be fixed and *Tb* measured by ultrasonic telemetry. Swim speed in an annular tank was constantly monitored with photocells. Under these conditions a simple *Tb* versus *Ta* regression reveals little temperature adjustment. Body temperature is clearly dependent upon *Ta*: $Tb = 3.14 + 0.97\ Ta$. Dizon et al. (1978) estimated heat production (H_p) using the same techniques outlined in the previous section for determining total power input. Heat production is the input power, minus the output power dissipated as thrust, plus the SMR. Use of these relationships allows comparisons to be made between fish of different sizes swimming at different speeds. An index of whole-body thermal conductance can be developed,

$$H_L = k\ (Tb - Ta)$$

where H_L = steady state heat loss.

Since the fish is assumed to be in steady state, that is, *Tb* is constant, then H_L must equal H_p. In contrast to yellowfin tuna, skipjack tuna were found to exhibit a great deal of variability in the whole-body thermal conductance over the temperature range from 20° to 30°C. (If regulation were occurring, increases in *Ta* should be accompanied by increases in H_L so that *Tx* would get smaller where $Tx = Tb - Ta$.) Nevertheless, even though H_p is tightly linked to swim speed, changes in swim speed were not accompanied by changes in body temperature. Clearly, some mechanism existed in skipjack tuna to alter either the pattern of H_p, heat loss, or both.

Dizon and Brill (1979) extended the above experiment by forcing tunas to swim at high speeds in water temperatures approaching their upper lethal limit. Under these conditions, if physiological regulation was possible, the tuna would demonstrate it. Swim speed was increased by force feeding plastic-coated weights to 23 fish. Only three survived the treatment long enough to collect data. Two of the fish were able to significantly increase whole-body thermal conductance and one with no decrease in swim speed. Dizon and Brill (1979) consider this true physiological thermoregulation.

There are two situations in tunas which require some thermoregulatory adjustments: 1) *Tx* should be increased or decreased when ambient temperatures approach lethal limits, and 2) extremely rapid increases in heat production accompanying increases in swim speed must be dissipated to prevent muscle overheating. The tuna could meet these two exigencies with 1) some physiological process that would alter the effectiveness of the heat exchanger, and 2) changes in the relative contribution of the red and white muscle fibers to swimming.

Prevention of overheating presents no problem. There has been much in the literature on the overheating of large, active tunas in warm water, notably Barkley et al. (1978) and Sharp (1978), to define inhabitable regions in the ocean. However, there is no physiological data indicating that tunas can overheat under free-swimming normal conditions. If the notion that the white muscles are only used for high speed swimming is discarded, a way out of the overheating conundrum is apparent. In the section on energetics, the argument was made that white muscle fibers are graded into contributing to swimming propulsion at a relatively low swim speed (Hochachka et al. 1978; Brill and Dizon 1979). White muscle fibers are vascularized by pathways which bypass the vascular heat exchanger (Kishinouye 1923; Godsil and Byers 1944) so the heat or a portion of it is lost at the gills, like other nonthermoconserving fish.

Control of the relative contribution of the two fiber types to swimming might also serve to adjust *Tb* in response to the first exigency. At high environmental temperatures, the tuna might rely more on the white muscles, which add to the body heat burden to a lesser extent than the red. In addition, there might well be some regulation of the effectiveness of the heat exchanger itself.

In summary, tunas have relatively large numbers of processes to deal with thermal challenges. They obviously can employ behavioral responses of seeking new habitat or reducing or increasing swim speed. Thermal inertia helps stabilize body temperatures during periods of rapidly changing environmental temperatures. Physiological mechanisms exist as seen in the observation that heat production and body temperature are not always linked.

As to the question, "Why be warm in the first place?' many ideas have been suggested, but no real answers have emerged. Because of the fast swimming, energy speculative nature of the tuna, most suggestions have centered on swimming. The original assumption (Carey et al. 1971) is that higher temperatures increase muscle power. However, Walters and Fierstine (1964) found that a yellowfin tuna, whose body temperature was twice that of a wahoo, exhibited speeds only slightly greater and acceleration times considerably less. Neill and Stevens (1974) suggested that recovery time from anaerobic activity might be lessened because of the increased temperature. Perhaps energetic efficiency is enhanced, or there are biochemical advantages to the thermoconserving structures. Hochachka et al. (1978) felt that the tuna has greater control over its highly charged metabolsim. Given a Q_{10} of 2, a twentyfold change in metabolic rate can be converted to a fortyfold change, if the change is accompanied by a 10° rise in temperature. Perhaps the retia temperature function is only secondary; its main one may be to retard mass transfer of lactic acid, the byproduct of anaerobic glycolysis. Then lactate from the white muscle would pass to the red muscle, where it would be metabolized by that tissue's liverlike enzymes (Stevens and Neill 1978). But much of the white muscle circulation bypasses the rete mirabile entirely.

There also might be benefits occurring simply from stability of the body temperature. Neill and Stevens (1974) and Neill et al. (1976) suggested also that because of the thermal inertia, perception of very weak horizontal gradients could be accomplished. But because of the skipjack tuna's habit of constantly making vertical migrations (Dizon et al. 1978), we wonder if the horizontal gradients have much meaning to the tuna.

3.63 Hypothetical habitat of skipjack tuna

Barkley (1969) has hypothesized that the habitat of the adult skipjack tuna coincides with the area where a shallow salinity maximum occurs seasonally or permanently, whereas that of larval skipjack tuna coincides with the area having a permanent shallow salinity maximum. Thus, a hypothesized maximum depth and distribution can be mapped (Fig. 56).

Temperature and oxygen data can also be utilized to delimit distributions based upon size (Figs. 57-59). Barkley et al. (1978), based upon information from Neill et al. (1976), considered three environmental conditions that would be likely to operate to determine distribution of skipjack tuna. These are: 1) A lower temperature limit around 18°C, 2) a lower dissolved O_2 level around 3.5 p/m, and 3) a speculative upper temperature limit, ranging from 33°C for the smallest skipjack tuna caught in the fishery to 20°C or less for the largest.

According to the analysis, skipjack tuna larger than 11 kg should find relatively few habitable regions within the eastern tropical Pacific Ocean (Fig. 60). While this agrees with fishery data, the third condition does not seem to hold (see Section 3.62). The authors arrived at this condition by extrapolating from data obtained from restrained fish and by predicting temperatures for a fish swimming with red muscle only. These conditions could then result in thermal runaway; that is, a positive feedback system could be generated with muscle temperature increases causing faster swimming, causing increasing muscle temperatures. But as indicated in the previous section, tunas do not overheat even though they are very active in warm water. Some process intercedes to reduce temperature excess (Dizon and Brill 1979).

3.64 Responses to stimuli

(1) Vision

Nakamura (1968) studied the visual acuity of skipjack tuna and kawakawa using conditioning techniques. Tunas were taught to respond to targets bearing either vertical or horizontal stripes in order to receive food and avoid electric shock. At lower light levels, visual acuity of the two species was similar but at higher levels, the skipjack tuna did better (Fig. 61).

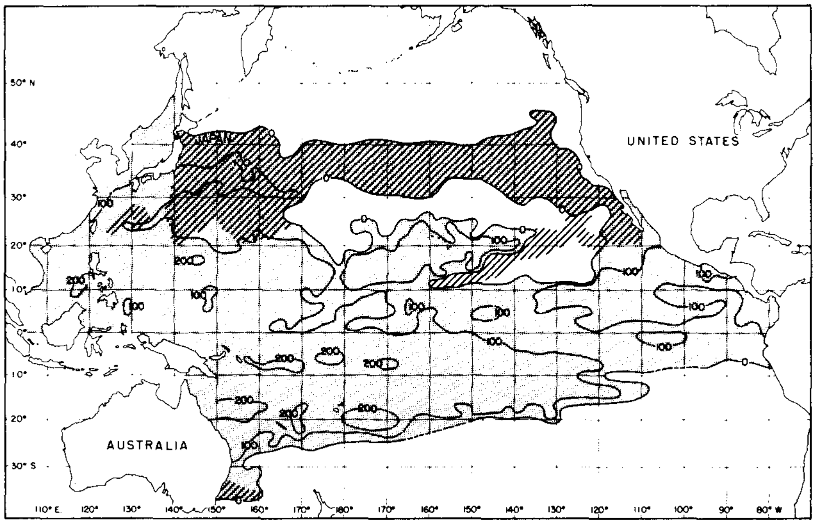

Figure 56.—Depth in meters of the shallow salinity maximum in the Pacific Ocean, based on all available oceanographic station data, averaged within areas of 2° of longitude by 2° of latitude. Regions where a shallow maximum is present during one or more quarters but not all year are indicated by hatching. A region analogous to the hatched area in the North Pacific must also be present in the South Pacific but cannot be shown due to sparsity of data (from Barkley 1969).

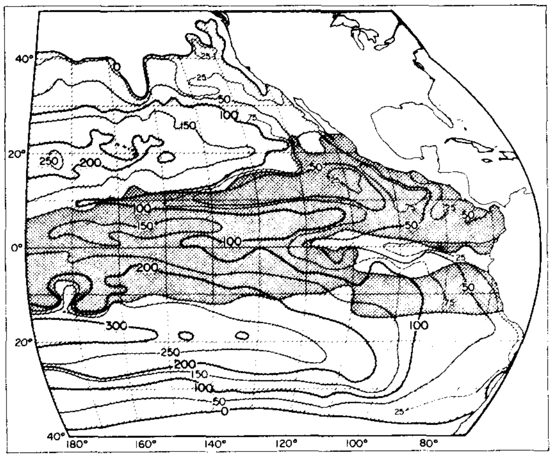

Figure 57.—Hypothetical maximum depth (meters) of the skipjack tuna habitat in the eastern Pacific Ocean, as determined by the depth of the 18°C isotherm (hatched area) or the 3.5 ml/*l* (5 p/m) isopleth of dissolved oxygen (crosshatched area). Contour interval is 50 m except for a few areas near the coast, where a 25 m contour interval is used (from Barkley et al. 1978).

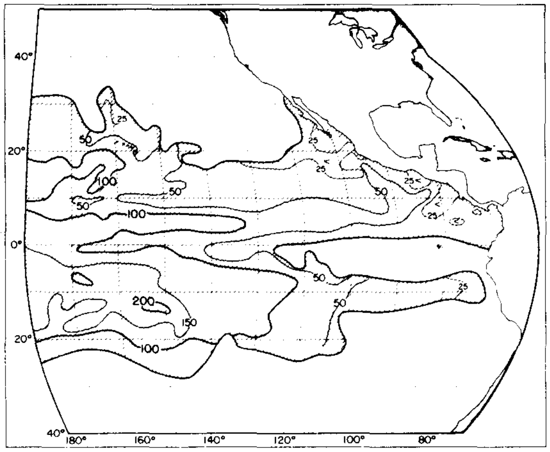

Figure 58.—Hypothetical minimum depth of the skipjack tuna habitat in the Pacific Ocean east of the 180° meridian, for fish weighing about 6.5 kg (14 lb) which are limited to water cooler than 24°C. Contours show the depth, in meters, of the 24°C isotherm (from Barkley et al. 1978).

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 (Strasburg and Marr 1961; Nakamura 1962; Nakamura and Magnuson 1965) or during courtship (Iversen et al. 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 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 re-

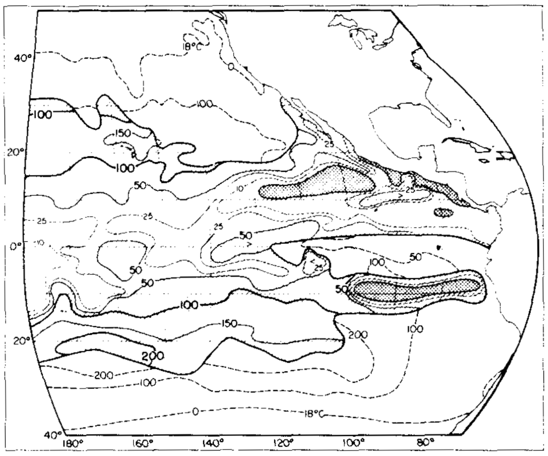

Figure 59.—Thickness of the hypothetical habitat layer (meters), for 6.5 kg skipjack tuna in the eastern and central Pacific Ocean. Contours were obtained by subtracting depths of the upper habitat limit (Fig. 57) from the lower one (Fig. 56). In the crosshatched areas off Mexico and Peru, there should be no habitat suitable for fish of this or larger sizes. In the hatched area, water warmer than 24°C is present above the habitat layer. Immediately beyond this area, the habitat (dashed depth contours) extends to the sea surface. Outside of the 18°C surface isotherm, the water is probably too cold for skipjack tuna (from Barkley et al. 1978).

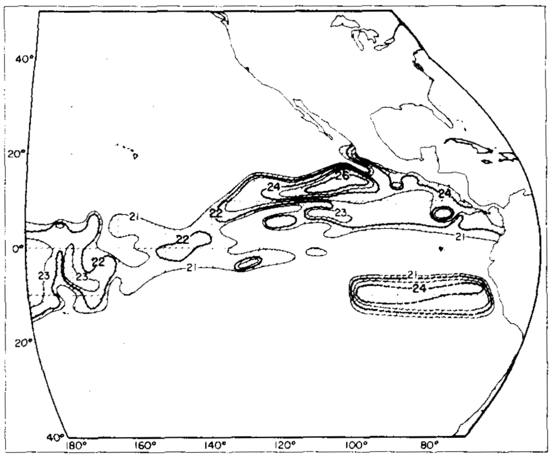

Figure 60.—Water temperature at those depths where the concentration of dissolved oxygen is 3.5 ml/*l*. Deeper water is cooler and lower in oxygen, shallower water is warmer and has more oxygen. Skipjack tuna weighing more than 11 kg require well-oxygenated water cooler than 21°C; they should find all the shaded areas stressful. Similarly, 4 kg skipjack tuna should find the area enclosed by the 26°C contour either too warm or too poor in dissolved oxygen. Smaller skipjack tuna would seldom encounter thermal stress in the eastern tropical Pacific, and can inhabit all areas by staying in the shallower, oxygen-rich layers (from Barkley et al. 1978).

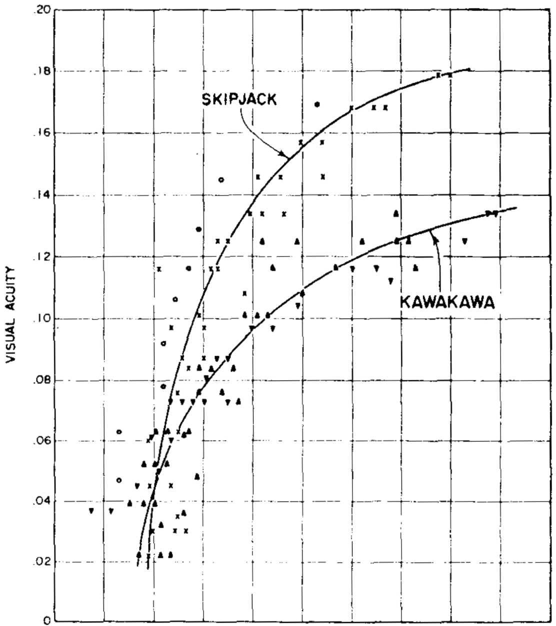

Figure 61.—Visual acuity curves of skipjack tuna and kawakawa, *Euthynnus affinis*, at adaptive illumination of 170 luxes (from Nakamura 1968).

solved at maximum distances of 3.1 m, again in waters having the same visibility conditions as those in the experimental tank. These conditions would be met in pelagic waters typical of the tropical ocean with an unobstructed sun at an altitude of 65°.

The presence of color vision improves perception, but tunas are color blind. Work by Tamura et al. (1972) and Kawamura et al. (1981) failed to find chromaticity-type S-potentials. This is a technique where electrical potentials are measured from the isolated or in situ retina. The chromaticity S-potential is considered by visual physiologists as a definitive test for color vision. The latter authors looked for but failed to find these potentials in yellowfin tuna; bigeye tuna; albacore; striped marlin, *Tetrapturus audax*; blue marlin, *Makaira nigricans*; and black marlin, *M. indica.* Tamura et al. (1972) recorded S-potentials from skipjack tuna, kawakawa, and frigate tuna and failed to find the chromaticity type. That these fish are color blind is consistent with the findings by Tester (1959) that tunas exhibited no color preference in behavior tests. Also, most wavelengths of light are rapidly attenuated with depth, so that the principal habitat of the pelagic fish is a monochromatic one. Munz and McFarland (1977) found only a single visual pigment in retinal extracts of wahoo, yellowfin tuna, kawakawa, black marlin, and blue marlin. This is also a strong indicator of the lack of color vision.

(2) Temperature

Skipjack tuna have thermal receptors and can make behavioral decisions based on temperature stimuli. Dizon et al.

(1974, 1976), using heart-rate conditioning techniques, demonstrated temperature perception in skipjack tuna. Steffel et al. (1976) demonstrated that free-swimming, captive kawakawa could discriminate temperature thresholds of 0.10° to 0.15 °C. We suspect that skipjack tuna can do as well because this degree of sensitivity has been demonstrated in other teleost species. Even though this seems like a high degree of sensitivity, horizontal gradients in the ocean are never likely to exceed 0.0001 ° to 0.001 °C/m. This fact, and the tunas' habit of making continuous vertical movements through gradients of several degrees, makes it unlikely that they use the weak horizontal temperature changes as orienting cues.

(3) Mechanical

Sound does not seem to affect the behavior of skipjack tuna at sea (Strasburg and Yuen 1960). Noise produced by hammering on the hull failed to alter the behavior of the tuna being fished. However, it is doubtful that skipjack tuna are deaf. Iversen (1969) determined threshold curves (thresholds versus frequency) for kawakawa and yellowfin tuna. Thresholds were not remarkable when compared with other teleosts.

York (1974), on the other hand, found that sudden or irregular noise, as caused by worn bearings, a bent propeller shaft, a slack rudder, or changes in throttle with a "high revving" engine, caused schools of skipjack tuna as well as yellowfin tuna and albacore to sound. In addition, York reported some success in attracting skipjack tuna schools by playing back recordings of anchovies "breezing" and gannets diving.

(4) Chemical

Tests at sea to attract skipjack tuna using extracts from skipjack tuna, yellowfin tuna, and anchovy were either negative or inconclusive (Tester et al. 1954). Other substances, such as skipjack tuna blood sprayed in the water or skipjack tuna blood and body slime allowed to drain from the scuppers into the water failed to affect the behavior of the skipjack tuna (Strasburg and Yuen 1960).

4 POPULATION

4.1 Structure

4.11 Sex ratio

Most of the sex ratios reported in the literature are byproducts of studies on maturation and fecundity. No real use was made of the sex ratio information including attempts to relate changes in sex ratio with maturation, size of fish, spawning season, or changes of availability or migration associated with attainment of maturity. The discussion below will proceed by ocean and all ratios are presented as number of males to number of females.

For the Atlantic Ocean, Batts (1972c) presented data obtained from recreational catches off two locations in North Carolina, U.S.A., in 1964-66. Over all years and both areas, the sex ratio favored females in all but one case and ranged from 1.06:1 to 0.58:1, averaging 0.86:1. Cayre (1979) found a ratio of 0.95:1 for a small sample collected in Dakar from Senegalese purse seiners fishing in the Gulf of Guinea. Chur et al. (1980) likewise reported that the sex ratio of fish captured by purse seiners in the eastern tropical Atlantic from 1969 to 1977 did not differ from 1:1.

For the Indian Ocean, Raju (1964a) found males predominating in most months, especially for older age groups in samples collected in the Minicoy Islands. Marcille and Stequert (1976) and Stequert (1976) presented monthly data on the sex ratio of fish collected from Japanese bait boats fishing off the northwest coast of Madagascar from February 1974 to March 1975. There was no apparent trend in the monthly data and all but one of the values favored females. For the entire period, the sex ratio was 0.83:1 and ranged from 1.01:1 to 0.72:1.

For the Pacific Ocean, Schaefer and Orange (1956) found that more females (0.73:1) occurred in the samples from the young fish taken in the eastern tropical Pacific fishery; however, sex could not be determined for a large proportion of the samples. Yoshida (1960) reported that the sex ratio was 1.05:1 for samples collected in the central South Pacific. In Hawaii, Brock (1954) showed that males predominated in the catches during most time periods (1.16:1 overall) and differed significantly from 1:1 in the September-December period in 1949 and 1950 (1.64:1 and 1.32:1, respectively). Also, catches from experimental trolling in inshore Hawaiian waters (Tester and Nakamura 1957) showed a predominance of males (1.57:1). For the northern Marshall Islands area (Marr 1948), males again predominated (1.60:1). For fish taken off Taiwan, Hu and Yang (1972) reported a preponderance of males (1.31:1) in the 50-59 cm FL interval, while the ratio was 1:1 in the adjacent 10 cm FL intervals. Monthly data showed considerable variability, for example, from 3.01:1 to 0.64:1, but there was no apparent trend. Off Japan, the ratio was reported to be 1.09:1 (Waldron 1963). Wade (1950) reported that females dominated in the Philippine catch with a ratio of 0.86:1. Likewise in New Zealand, females are reported to dominate the catch, with the ratio being 0.76:1 for fish caught by purse seine over the period December 1976-March 1978 (Habib 1978).

These statistics suggest that those fisheries known to depend on young, immature fish have sex ratios favoring females while those fisheries harvesting predominately older, spawning age fish exhibit sex ratios favoring males.

4.12 Age composition

Few tables of age composition have been presented in the literature because of the inherent difficulties in aging skipjack tuna as pointed out in a previous section. For the most part, age composition has been determined from tables of size composition using various growth equations. Until skipjack tuna can be aged with certainty and with greater ease than is currently possible using otoliths or other hard parts, little use is likely to be made of tables of age composition.

4.13 Size composition

Since all fisheries capture skipjack tuna over a restricted size (age) range and most over a limited geographical range, the size-frequency distributions and other measures of size composition given below are in all likelihood not representative of any complete stock or population. Length-frequency distributions have been published most commonly to simply describe the size composition of the catch and document seasonal changes in a fishery. They have been used less frequently to study recruitment, relationships among areas or fisheries, growth, and gear selectivity. From another perspective, Sharp (1976, 1978, 1979) and Barkley et al. (1978) proposed that the temperature and oxygen structure of the oceans in interaction with the physiological properties of skipjack tuna limits the distribution of larger individuals. This subject is discussed more fully in Section 3.63.

(1) Length composition

All length measurements are fork length unless otherwise stated. Modes were determined by visually inspecting the distributions in all but one case.

(a) Pacific Ocean

For the eastern tropical Pacific Ocean, Broadhead and Barrett (1964) presented quarterly length-frequency distributions for four northern areas of the fishery in 1954-60. While there was considerable variability among years, the distributions for 1956 (Fig. 62) show that the four areas generally had a single mode, though of different size. The Baja California area tended to have consistently smaller fish (40-50 cm), while the Gulf of California, the Mexican coast, and the Revillagigedo Islands tended to have more fish between 60 and 70 cm. Data presented for more recent periods, for example, 1967-79 for the entire Commission's Yellowfin Regulatory Area (IATTC 1980), likewise show considerable variability among years and, probably because several areas were combined, the distributions tended to show multiple modes. Diaz[15] showed that the length-frequency distribution from purse seine catches frequently shows more large fish than do those for bait boats. His data also indicated that fish off Ecuador were mostly between 50 and 60 cm. While the skipjack tuna taken in the northern area of the fishery are generally considered to comprise a single stock, the variability shown here as well as the morphometric and genetic findings of Sharp (footnote 4) suggest that a considerable amount of heterogeneity may exist.

For Hawaiian waters, Rothschild (1965) compared the third quarter length-frequency distributions for Baja California (taken from Broadhead and Barrett 1964) with those from Hawaii (Fig. 63) and found a remarkable similarity for the small modal group in 1954 and 1960. In 1959, however, the two distributions differed considerably. Rothschild (1965) inferred from this figure and other evidence that the small fish in the Hawaiian and eastern Pacific (at least Baja California) fisheries have a common origin and that the origin is in the central equatorial Pacific Ocean. However, from Figure 63 and other evidence, it is apparent that there are differences in size distributions between the eastern tropical Pacific and Hawaiian fisheries. The Hawaii size frequency is bimodal or trimodal, including small fish as in the east but large fish in addition. Summarizing over years for the winter months in the Hawaiian fishery, modal groups are found at approximately 35, 50, and 75 cm, while in the summer months they are found at approximately 45 and 70 cm. Whereas Brock (1954) found progression of modal groups and based a growth model on them, Rothschild (1965) found the progression to be irregular with instances of regression.

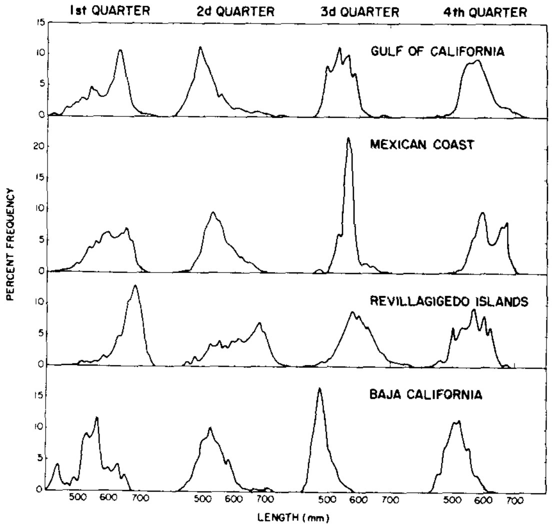

Figure 62.—Length distribution of skipjack tuna for 1956 by quarter of the year for the Gulf of California, Mexican waters, the Revillagigedo Islands, and coastal areas of Baja California (modified from Broadhead and Barrett 1964).

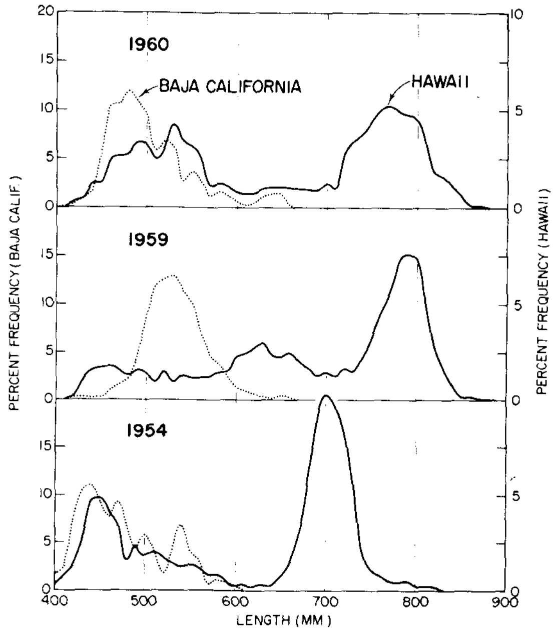

Figure 63.—Length-frequency distributions for skipjack tuna taken during the third quarter of the year from fisheries off Baja California and the Hawaiian Islands (from Rothschild 1965).

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[15] Diaz, E. L. 1966. Growth of skipjack tuna, *Katsuwonus pelamis*, in the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm., Internal Rep. 2, 18 p. Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92037.

For the equatorial region in the central Pacific Ocean, experimental longline catches showed the presence of fish from 47 to 84 cm (Shomura and Murphy 1955). While most of the fish were between 70 and 80 cm, longline catches are commonly believed to be biased toward larger individuals.

For the South Pacific, most data have resulted from exploratory fishing rather than from commercial or subsistence fisheries. Rothschild and Uchida (1968) found that experimental catches in the Marquesas Islands showed a trimodal distribution with modes at 47 (dominant), 67, and 75 cm. Bayliff and Hunt[16] presented data assembled from various sources for the Marquesas and Tuamotu Islands by various months from 1957 to 1959 and 1977 to 1980. In most cases, there were one or two size modes with the major one at approximately 50 cm and a lesser mode sometimes occurring around 70 cm. For the Society Islands, Bayliff and Hunt (footnote 16) again presented data assembled from various sources by various months from 1973 to 1978. Some of these data were collected from the subsistence fishery in Tahiti. There appeared to be three modes, which in many cases fell roughly in the 40-50, 60-70, and 80-90 cm intervals; the total range was 32-91 cm. They also found some evidence of progression of modes which they felt indicated growth, but Josse et al. (1979) concluded otherwise. Moving slightly to the east, a single mode was found at 45-50 cm for samples taken at Pitcairn and Gambier Islands in 1980. For American Samoa, Kearney and Hallier (1978c) presented data for May-June 1978 showing a range of 39-64 cm with modes at about 45 and 60 cm. The sizes of fish collected in West Samoa in July 1978 were somewhat smaller, 36-58 cm, and showed only one mode around 49 cm (Kearney and Hallier 1978b). Moving slightly westward into Tuvalu, the length frequency of fish collected in June-July 1978 had a range of 35-66 cm and exhibited three modes at around 38, 52, and 61 cm (Kearney, Hallier, and Kleiber 1978). Slightly to the north in the Gilbert Islands (Kiribati), the range of fish taken by exploratory bait boat in July 1978 was 38-62 cm, with modes around 40 and 47 cm (Kearney and Gillett 1978). In Fiji the FAO bait boat development project obtained fish ranging in size from 29 to 84 cm in 1972, 1973, 1974 (FAO 1974a). Two modes were apparent at approximately 46 and 54 cm. Length-frequency distributions from the developing purse seine fishery in New Zealand (Vooren 1976; Habib 1978; Habib et al. 1980a, b, c) indicated a size range of 30-70 cm, but generally there was only one strong mode at 45-50 cm with minor modes around 35 and 55-60 cm appearing in some month/area strata. At Norfolk Island, exploratory bait boat catches in March 1980 showed a size range of 42-68 cm and a mode at around 64 cm (Kearney and Hallier 1980a).

For the southwestern Pacific, Kearney and Gillett (1979) reported that off Queensland, Australia, the size range of fish taken by exploratory bait boats was 35-70 cm with modes at 48 and 62 cm; off New South Wales, the range was 39-66 cm with modes at 46, 51, and 60 cm. In New Caledonia, data from experimental trolling in 1956-60 showed a range of 40-75 cm standard length (SL) with a strong mode at 50 cm SL and possibly minor modes at 54, 60, 65, and 72 cm SL (Legand 1971); whereas exploratory bait boat catches in December 1977-January 1978 showed a range of 38-74 cm, with modes around 43, 50, and possibly 55 cm (Kearney and Hallier 1978a). In New Hebrides data from exploratory bait boat catches in December 1977-January 1978 indicated a size range of 41-78 cm with modes near 45 and 51 cm (Kearney Lewis, and Hallier 1978). In Papua New Guinea, exploratory bait boat catches showed a range of 36-66 cm with a mode at 56 cm (Kearney and Hallier 1979), whereas the size range for commercial bait boat catches was 46-69 cm (Wankowski 1980). For the Japanese purse seine fishery to the northeast of Papua New Guinea, Honma and Suzuki (1978) presented data showing catches ranging from 29-30 to 73-74 cm in 1970-74 with a single mode ranging from 44 to 53 cm. There was no indication of a progression of modes with time. For Indonesia, Simpson (1979) presented information on the size composition of the bait boat fishery in Ambon, Bitung, Sorong, and Ternate. In February 1977 and January-May 1978, the size range was 30-72 cm with a single mode at around 50 cm. A more ambitious sampling project is now being conducted by Indonesia (and Philippines) in cooperation with the U.N. South China Sea Fisheries Development and Coordinating Programme and a report on the first year's sampling (1979-80) will be available shortly.

For the northwestern Pacific, we will first discuss the Trust Territory of the Pacific Islands, then Philippines, Taiwan, and Japan. Within the Trust Territory for exploratory Japanese longline operations south of lat. 10°N in 1950-51, the size range was from 47 to 82 cm with a single mode at 57 cm (Murphy and Otsu 1954). For exploratory bait boat catches along a cruise track from the northern Mariana Islands through Truk and Ponape to Kosrae in November 1979, the size range was 27-60 cm with modes at 30 and 52 cm (Kearney and Hallier 1980b). For the northern Marshall Islands, experimental trolling catches had a size range of 34-74 cm with modes at 45, 55, and 65 cm (Marr 1948). The size composition of the catches made by the Japanese distant water bait boat fleet in an area encompassing the northern Mariana Islands and Palau Islands during June 1964-April 1966 showed a range of 35-75 cm (Kasahara and Tanaka 1968). The distributions were multimodal in most months with modes falling in the 40-50, 50-60, and 60-70 cm intervals. Progression of the smallest mode was quite apparent. Data collected during 1965 from the bait boat fishery based in Palau Islands indicated a range of 30-74 cm, and a prominent mode at 50 cm in June and 58 cm in October (Higgins 1966); whereas data collected in 1967 and 1968 showed evidence of at least two modes, one between 45 and 50 cm, and the other around 60 cm (Uchida 1970). Since 1964 the Tohoku RFRL, Japan, has been issuing reports on the Japanesse southern water fishery (Tanaka undated a, b, c, 1978, 1979, 1980; Tohoku Regional Fisheries Research Laboratory undated a, b, c, d), which was initially limited to the area within the Equator and lat. 24°N, and long. 125° and 150°E. Initially, the data were obtained only from bait boats; the season usually started in June and was over by April of the following year, and the area fished was from the northern Mariana Islands to Palau Islands. Now, purse seiners have entered the fishery and the fishing area has expanded to well below the Equator and east to long. 150°W. A few generalizations can be gleaned from these reports. First, it is apparent that catches from shoal-associated schools generally had a single mode around 45 cm,

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[16] Bayliff, W. H., and G. A. Hunt. Undated. Exploratory fishing for tunas and tuna tagging in the Marquesas, Tuamotu, Society, Pitcairn, and Gambier Islands. Inter-Am. Trop. Tuna Comm., Spec. Rep. 3, var. pag. Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92037.

whereas open ocean catches were multimodal. Second, purse seine catches generally exhibited only two modes around 40 and 50 cm whereas bait boat catches exhibited several modes. Third, there were great variations in the frequency distributions among months, years, and areas as well as variations in the amount of fishing effort expended in these time/area strata that make interpretations difficult.

For the Philippines, length-frequency distributions appearing in the literature have been derived primarily from experimental fishing operations. The troll-caught fish from October 1947 to November 1948 had a range of 34-65 cm with a single mode at 50 cm (Wade 1950). Chikuni (1978) presented length-frequency distributions for fish caught by exploratory purse seine fishing primarily at night in association with rafts ("payao" or "payaw") from November 1974 to June 1977. In Moro Gulf, nearly all of the fish taken were between 40 and 55 cm from January through July. Small fish, 25-35 cm, entered the fishery in May and became more prominent in October and December. In the Sulu Sea, the size range was 30-70 cm in July and a broad mode was centered at 52 cm. The size range was much smaller in May and September, with modes at 62 and 52 cm, respectively. Evans et al.[17] reported length-frequency distributions for both small-scale and commercial fisheries based on Camiguin Island in the Bohol Sea. For handline and various sustenance gear, the size range in March-November 1977 was 37-84 cm TL, with possibly two modes at 66 and 72 cm TL. For commercial ring net boats during the same period, the size range was 18-63 cm TL, but the sample size was too small to determine modes.

For Taiwan, Hu and Yang (1972) collected samples in fresh fish markets from skipjack tuna caught by trolling off the southwest coast between August 1970 and November 1971. The samples ranged from 23 to 71 cm and exhibited modes at 30 and 49 cm.

For Japan, Kawasaki (1952, 1955a, b, 1964, 1965b) used length-frequency distributions for skipjack tuna from various areas in the coastal fishery to separate hypothesized nonmigratory and migratory stocks. The distribution varied considerably among months and areas with respect to both the size range and the number of modes. The total range was from 25 to nearly 80 cm and a distinct mode appeared in every 10 cm interval in at least one time or area stratum. Modes within the 40-60 cm range occurred commonly and often showed a monthly progression in average size. Iwasaki (1976, 1980) determined that the size of fish varied with the means of capture and whether the school was associated with banks, floating debris, birds, and sharks or whales. For fish caught in Japanese waters by bait boats, schools associated with birds had a size range of 20-80 cm with modes at 32, 45, 58, 67, and 75 cm; those associated with banks had a range of 42-62 cm and a single mode at 49 cm; those associated with floating debris had a range of 25-61 cm and modes at 34 and 52 cm; and those with sharks and whales had a range of 33-61 cm and a mode at 50 and possibly 40 cm. For purse seine-caught fish, schools associated with birds had a range of 41-54 cm and a single mode at 45 cm while those associated with floating debris, sharks, or whales had a range of 40-78 cm with modes at 45, 62, and 70 cm.

(b) Indian Ocean

Just as the fisheries are relatively underdeveloped in this ocean compared with the Pacific and Atlantic Oceans, there is likewise less information available on the length composition of the stocks. Marcille and Suzuki (1974) summarized length statistics obtained from Japanese longline operations during the period 1967-71. The size range and modes for each area in the Indian Ocean were as follows: South of Indonesia, 36-86 cm with a single mode at about 50 cm or less; eastern central area, 36-88 cm with two modes at 55 and 64 cm; western central area, 44-78 cm with a mode at 50 cm in the first and second quarters and at 60 cm in the fourth quarter; Bay of Bengal area, 38-84 cm with a single mode generally above 60 cm; and northwestern area, 42-84 cm also with a single, but strong mode usually above 60 cm. Generally there was no indication of a progression of modes with time. With the data combined over all areas, two modes at 55 and 68 cm were apparent.

For the waters of Sri Lanka, Sivasubramaniam (1965) presented figures showing the size composition by coastal area and gear type. For the west coast, troll-caught fish had a range of 20 to 70 cm, with a single mode centered at the 50-55 cm size class. On the east coast, catches by bait boats and trollers had a range of 16 to 70 cm, while for gill net catches, the range was 26 to 70 cm. A single mode occurred in the 51-55 cm interval for all gear types. On the south coast, which is the primary tuna fishing area, the size range was 21 to 80 cm for all gear types, and a single broad mode generally occurred in the 41-45 to 46-50 cm interval. For fish taken in several areas and by various gear types, Sivasubramaniam (1972) found five modal groups at 34-36, 42-44, 52-55, 62-64, and 72-74 cm intervals by using the probability paper method of Harding (1949) and Cassie (1954). For experimental Japanese bait boat fishing, the size range was 28 to 72 cm with modes occurring at 32-34, 44-46, and 58-60 cm intervals (Sivasubramaniam 1975).

For the Indian fishery in the Laccadive Islands from 1958 to 1961, Jones and Silas (1963) reported a size range of 32-72 cm. During the December-April period, two modes at about 48 and 60 cm were observed, while during other months, only the 48 cm mode was apparent. The authors stated that the samples indicate size specific recruitment to the fishery.

For the waters off Madagascar, samples collected during August 1973-March 1975 had a size range of 32-71 cm and a single prominent mode at 49 cm, as well as a less well-defined mode in the 50-55 cm range in some months (Marcille and Stequert 1976). The authors noted that the smaller mode progressed from < 45 cm to just over 50 cm from September 1973 to May 1974, but no progression of modes was evident in the remainder of the time period.

(c) Atlantic Ocean

With the ICCAT emphasizing the description of tuna fisheries and the assessment of the tuna stocks in the Atlantic, a number of papers are now available describing size composition of skipjack tuna. For catches by U.S. purse seiners in the eastern tropical Atlantic during 1968-74, the size range

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[17] Evans, L. C., A. D. Uy, and D. D. Tandog. 1978. The abundance, biology and distribution of tuna (Family Thunnidae) in Camiguin and nearby waters. Philippines Dep. Nat. Resour., Bur. Fish. Aquatic Resour., Preliminary Rep., 55 p. Bureau of Fisheries and Aquatic Resources, 860 Quezon Avenue, Quezon City, Metro Manila, Philippines.

was 25-70 cm (Sakagawa et al. 1976), and a single mode usually occurred at 45-50 cm, though at times two modes at 45 and 50 cm were indicated. For catches by Korean bait boats in the same area in 1975, Choo (1977) presented data showing the ranges of 33-65, 32-62, 31-75, and 36-54 cm in each of the four quarters, or 31-75 cm overall. Quarterly average sizes were stated as 49.8, 48.5, 45.6, and 44.1, or 47.6 cm overall. The size ranges of fish taken by Japanese longline boats in the Northern and Southern Hemispheres were 44-84 and 48-86 cm, respectively, while the only obvious mode occurred at 72 cm in both hemispheres (Kume 1977). For Japanese bait boat catches in the Gulf of Guinea during 1974 and 1975, the size range was found to be 37-62 cm, and few fish below 40 cm were captured (Kikawa and Higashi 1979). Then for Japanese purse seiner catches in the same area during 1967-74, the size range was greater, 22-75 cm, and fish below 40 cm were well represented. The authors indicated that recruitment of 30 cm fish occurred continuously throughout the year. Modal groups were not clearly defined nor was any modal progression apparent. Experimental U.S.S.R. purse seine catches in the eastern Atlantic from 1969 to 1977 consisted of fish with a size range of 28-63 cm and modes occurring in the intervals 36-37, 44-45, and 52-53 cm (Chur et al. 1980). In waters off Brazil, Zavala Camin (1978) reported a size range of 54-78 cm with a mode at about 66 cm for fish taken on tuna longline gear in May-August 1977.

Coan (1976) constructed composite length-frequency distributions for fish caught by longline and surface fleets of the participating states over the period 1968-73 (Fig. 64). These distributions were all unimodal with a peak at approximately 50 cm. Sakagawa and Murphy (1976) produced length-frequency distributions comparing the United States purse seine, French-Ivory Coast-Senegalese bait boat, French-Ivory Coast-Senegalese purse seine, and Japanese purse seine fleets. In 1969-71, the distributions for all of these fleets were unimodal with a peak at about 50 cm. In 1972-73, each individual distribution was still unimodal, but the fleets were fishing different sized fish, thus giving the overall distribution a bimodal character with modes at approximately 40 and 55 cm. Length-frequency distributions for specific fleets may be found in Pianet (1974), Bour (1976), Sakagawa et al. (1976), and Ansa-Emmim (1977). For the northwestern Atlantic, Batts (1972a) reported a size range of 26-76 cm for fish taken by charter sportfishing boats off North Carolina, U.S.A., in the summers of 1964 and 1965. He presented length frequencies by age groups (up to five) based on examination of growth rings in the dorsal fin spines, a method generally considered least reliable by recent investigators (see Section 3.43).

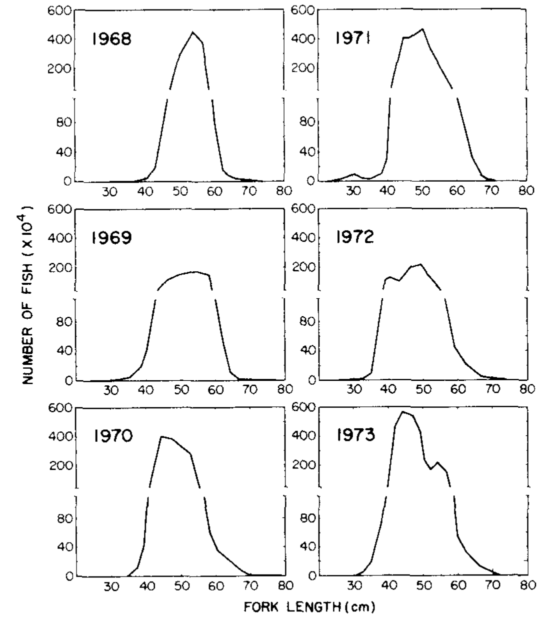

Figure 64.—Length composition of the skipjack tuna catch from the eastern Atlantic Ocean (from Coan 1976).

(2) Size at first capture

The size at first capture of fish amounting to significant numbers in most years in most fisheries, is about 40 cm. Recruitment into the fishable stocks generally takes place at a smaller size, around 30 or even 25 cm for many fisheries (Kawasaki 1955a, 1964; Sivasubramaniam 1965, 1972; Hu and Yang 1972; Iwasaki 1976, 1980; Marcille and Stequert 1976; Sakagawa et al. 1976; Choo 1977; Habib 1978; Honma and Suzuki 1978; Kikawa and Higashi 1979; Habib et al. 1980a, b, c; Tanaka undated a, b, c, 1978, 1979, 1980; Tohoku Regional Fisheries Research Laboratory undated a, b, c, d). For the ring net and purse seine fisheries in the Philippines, the size at first capture is around 25 cm and the size at recruitment is around 15 cm (Evans et al. footnote 17; Choo[18]).

(3) Size at maturity

See Section 3.12.

(4) Length-weight relationships

Length-weight relationships have now been published for all oceans (Table 17), but they are not available for all fisheries. Neither have the papers cited below included studies of sexual, seasonal, or long-term variations.

All of the studies cited in Table 17 fitted the allometric growth equation $W = bL^a$ where W is weight in grams, kilograms, or pounds, L is usually fork length in centimeters or millimeters, a is the coefficient of allometry, and b is another constant. In all but one of the cited studies, the log-linear transformation of the equation,

$$\log_e W = \log_e b + a \log_e L$$

was used to estimate the parameters using predictive (linear) regression analysis. Today it is generally believed that the length-weight relationship is intrinsically nonlinear, meaning

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[18] Choo, Woo-Il. Undated. Interim report on tuna sampling project in the Philippines and Indonesia, November 1979-February 1980. Unpubl. rep. U.N. South China Sea Fish. Develop. Coord. Prog., no pag. Korea Rural Economics Institute, Fishery Development and Research Division, 4-102 Hoigi-dong, Dongdaemoo-ku, Seoul, Korea.

Table 17.—Length-weight relationships of skipjack tuna.

Source	Locality	No. of fish	Size range (cm)	Constant *b*	Coefficient of allometry *a*	Weight unit	Length unit	Calculated weight of 55 cm fish (kg)	Comments
Uda (1941)	Bonin Is. W. Pacific	268	27-69	0.205	3.67	g	cm FL	449.9	Columns 4 and 9 estimated from Uda's fig. 6. Regression statistics suspect.
Kawasaki (1952)	NE of Japan	20	30-60	0.0113	3.16	g	cm FL	3.57	Bait boat catches.
Tester and Nakamura (1957)	Hawaii	268	39-83	1.878×10^{-5}	3.2164	lb	cm FL	3.37	Size range calculated.
Chatwin (1959)	E. Pacific	924	39-71	3.652×10^{-9}	3.403	lb	mm FL	3.50	Bait boat and purse seine catches.
Hennemuth (1959)	E. Pacific	1,282	39-71	3.763×10^{-9}	3.265	lb	mm FL	3.58	Includes data from Chatwin (1959).
Ronquillo (1963)	Philippines	189	34-66	3.267×10^{-5}	3.09569	lb	cm TL	3.40	Males only. Data from Ronquillo's fig. 25 and regression equations.
Ronquillo (1963)	Philippines	151	34-63	1.976×10^{-5}	2.96482	lb	cm TL	3.33	Females only. Data from Ronquillo's fig. 25 and regression equations.
Nakamura and Uchiyama (1966)	Hawaii	1,298	33-88	4.546×10^{-9}	3.36836	lb	mm FL	3.50	Bait boat catches.
Batts (1972a)	W. Atlantic	644	26-76	2.560×10^{-9}	3.3533	kg	mm FL	3.33	Troll catches.
Lenarz (1974)	E. Atlantic	2,554	36-64	5.611×10^{-6}	3.31497	kg	cm FL	3.30	Log linear regression analysis.
Pianet (1974)	E. Atlantic	520	40-73	4.115×10^{-6}	3.409	kg	cm FL	3.35	Linear regression analysis.
Marcille and Stequert (1976)	Madagascar	848	41-62	1.131×10^{-5}	3.158	kg	cm FL	3.54	Bait boat catches.
Vooren (1976)	New Zealand	100	35-54	6.206×10^{-6}	3.19	g	mm FL	3.35	Purse seine catches.
Evans et al. (text footnote 17)	Philippines	200	48-85	5.500×10^{-4}	2.20	kg	cm TL	3.71	Handline catches.
Evans et al. (text footnote 17)	Philippines	44	17-62	3.727×10^{-3}	1.70	kg	cm TL	3.39	Artisanal fishing gears.
Habib (1978)	New Zealand	120	38-71	3.475×10^{-6}	3.29	g	mm FL	3.60	Purse seine catches.

that parameters estimated from a log-linearized relationship are biased. Corrective procedures are available, but none were employed in the papers cited. In addition, Ricker (1973) has pointed out that the predictive regression method (which assumes a dependent-independent variable situation) tends to produce inflated estimates of *a*, especially when the sample range truncates that of the true population; a geometric mean functional (reduced major axis) regression (which does not assume a dependent-independent variable situation) produces less biased results. Pianet (1974) used the latter procedure but performed it on log-transformed data.

A summary of these studies is presented in Table 17, and a typical curve describing the relationship is given in Figure 65. The table is an updated version of a similar table presented by Nakamura and Uchiyama (1966), and the figure, based on data from the central Pacific containing the largest sample size and widest size range of all studies cited, was taken from the same reference. The calculated weights of fish of a common size, based on the regression statistics of the various authors, show close agreement except for that obtained by Uda (1941). The estimates of the coefficients of allometry are amazingly similar, except for those published by Evans et al. (footnote 17), and no effect of ocean or gear type is apparent.

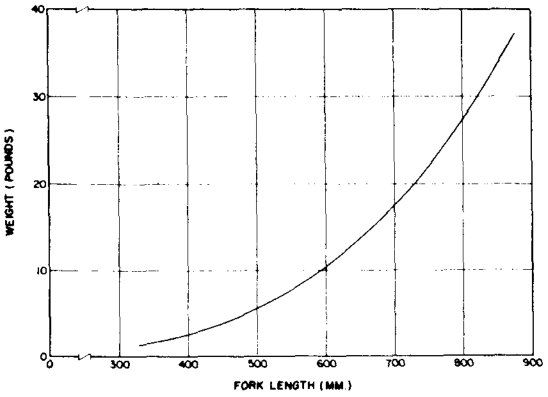

Figure 65.—Length-weight relation of skipjack tuna: log weight = −8.34241 + 3.36836 log length (parameters not corrected for transformation bias); number of observations, 1,298; size range, 327-877 mm; data collection period February 1948-December 1960; from files of Southwest Fisheries Center (from Nakamura and Uchiyama 1966).

4.2 Abundance and density (of population)

(1) Pacific Ocean

Forsbergh (1980) has recently reviewed the history of the measurement of apparent abundance of skipjack tuna in the eastern tropical Pacific. Shimada and Schaefer (1956) produced the first measure of relative density by comparing the daily catch rates of bait boats standardized by vessel class. They concluded from the trends shown in Figure 66 that the fishery was having no measurable effect on the stock. Since purse seine vessels have almost entirely replaced bait boats in the fishery, the measure used today is reported catch divided by reported fishing effort standardized to class 3 purse seine vessels (101-200 short tons or 94-181 t of carrying capacity). For a later period, 1960-79 (Fig. 67), the index in terms of purse seine units shows considerable annual variation but again no discernible trend.

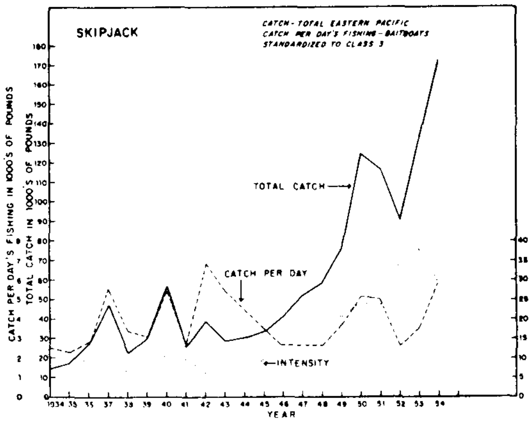

Figure 66.—Catch per standardized-day fished, total catch, and calculated relative fishing intensity for skipjack tuna in the eastern Pacific Ocean, 1934-54 (from Shimada and Schaefer 1956).

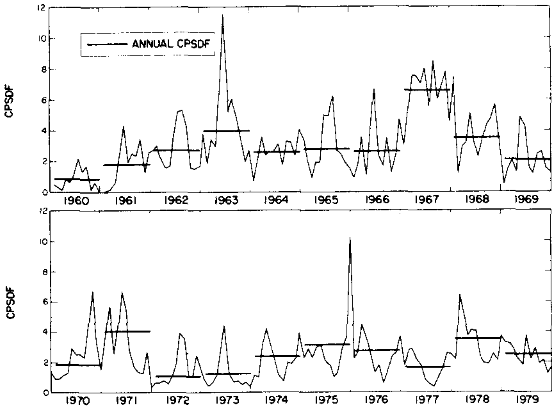

Figure 67.—Monthly and annual catch per standard day's fishing (CPSDF) for skipjack tuna, in class 3 purse seine units, in the eastern tropical Pacific during 1960-79 (from Forsbergh 1980).

Since some fishing effort directed primarily at yellowfin tuna is included in the calculation, this index is biased. Several attempts have been made to improve the index. Calkins (1961) and then Joseph and Calkins (1969) calculated relative density after eliminating those areas of low skipjack tuna catch where the fishing effort was directed primarily at yellowfin tuna. The resultant index of relative abundance again did not show a long-term trend over the 1951-65 period. Relative density was highest in the third quarter, and there appeared to be no relationship between the indices in the areas north and south of lat. 15°N. Subsequently, Pella and Psaropulos (1975) adjusted the fishing effort statistics by simulating the effect of the following factors on the fishing power of vessels: Vessel speed, probability of capturing sighted tuna schools, time spent in a set, and portions of schools retained that are set upon successfully. Using a new standardized fishing effort statistic based on their simulation, they found a different history of relative stock abundance over the years of the fishery (Fig. 68). There seems to be some indication of a decrease in abundance of skipjack tuna in the northern grounds and a definite decrease in the southern grounds. It is not known at this time which index of abundance is the better descriptor of the stock(s). Later, the IATTC computed relative abundance using only those 5° latitude by 5° longitude areas and 3-mo periods where 200 short tons (181 t) or more of skipjack tuna were caught and 100 or more standardized fishing days were expended. This procedure retained 89% of the catch and eliminated 43% of the purse seine fishing effort in 1961-79. The resulting indices of fish density for the years 1951-79 (Fig. 69) show no clear trend in the areas north of lat. 15°N and between lat. 15° and 5°N, whereas south of lat. 5°N the trend has a convex shape (Forsbergh 1980).

For the bait boat fishery in Hawaii, a number of estimates of relative abundance have been made. These indices, measured in catch per trip or per effective trip (as in Fig. 70), are highly correlated with catch and show no long-term trend (Yamashita 1958; Shippen 1961; Uchida 1967, 1976). A

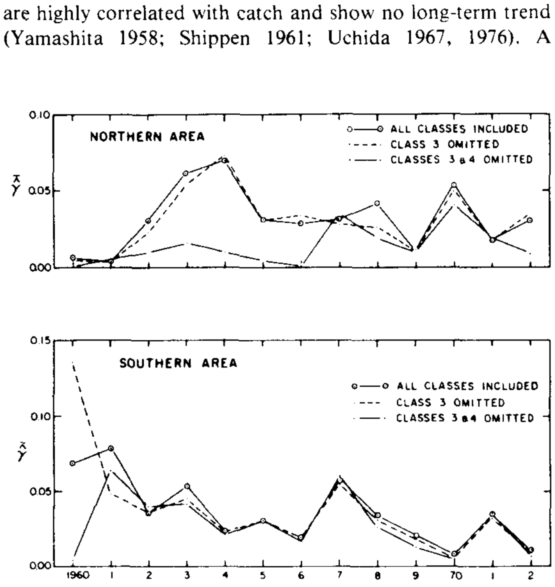

Figure 68.—Annual biomass indices of skipjack tuna in the traditional fishing areas of the eastern Pacific Ocean using different combinations of vessel classes, 1960-72 (from Pella and Psaropulos 1975).

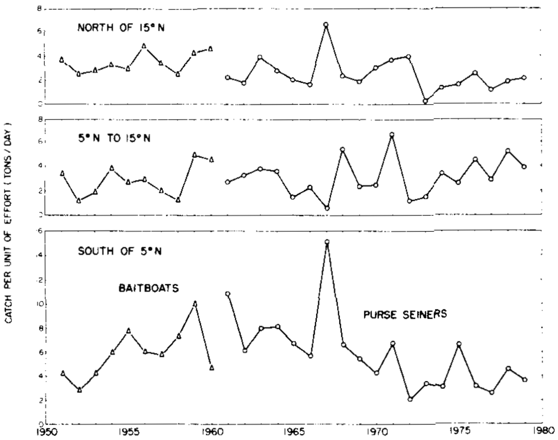

Figure 69.—Indices of abundance of skipjack tuna (in tons per day's fishing standardized to class 4 bait boats and class 3 purse seiners) for three areas of the eastern Pacific Ocean (from Forsbergh 1980).

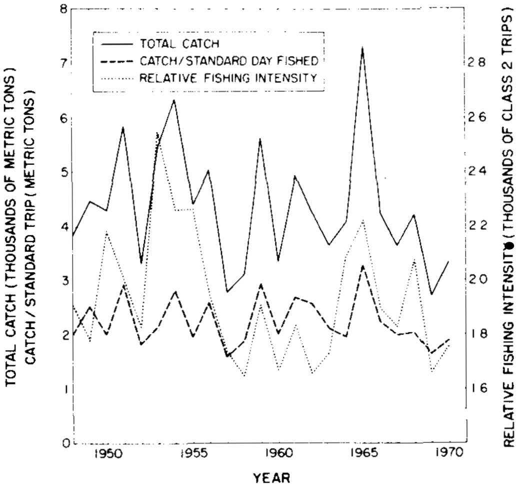

Figure 70.—Total catch, catch per standard day fished, and the relative fishing intensity of skipjack tuna taken in the Hawaiian fishery, 1948-70 (from Uchida 1976).

marked seasonal trend is quite apparent with the highest values occurring in May-September (Shippen 1961).

For the purse seine fishery in New Zealand, relative abundance in terms of catch per set, catch per effective set, catch per day, and catch per season-day shows no long-term trend over the 1975-76 through 1979-80 seasons (Habib 1976, 1978; Habib et al. 1980a, b, c). As in Hawaii, there is a marked seasonal trend, but with the highest density occurring in the January-February period.

In Papua New Guinea for the locally based bait boat fishery, Wankowski (1980) presented relative abundance indices showing the highest values occurring in May-September and the lowest values occurring in December-February. No long-term trend for the period 1970-79 was apparent.

In the Japanese southern water fishery (south of lat. 24°N and from long. 125°E to 150°W), catch per vessel increased both for the 1958-68 period in the Bonin-northern Mariana Islands area (Iwasaki 1970) and for 1964-75 over the entire fishery (Kasahara 1977). However, this trend probably reflects the evolution to larger boats in the fleet rather than changes in relative population density. While catch per day for some areas in the southern water bait boat fishery (Fig. 71) has shown a declining trend (Kasahara 1971), a similar index derived from Japanese purse seine operations in tropical waters shows no such trend (Honma and Suzuki 1978).

For the bait boat fishery off the northeast coast of Japan in 1951-62 (Kawasaki 1964) and off the south and southwest coast in 1957-69 (Kasahara 1971), no trend in relative abundance was evident. The same was true for the purse seine fishery in coastal waters from 1971 to 1974 (Honma and Suzuki 1978). However, Kasahara (1975) showed that the relative density has declined with increasing fishing effort in the Japanese coastal fishery during the period 1958-72. There is a regular seasonal cycle in relative abundance with the highest values occurring in June-August (Anraku and Kawasaki 1966). Lastly, Ishida (1975) showed that there was no

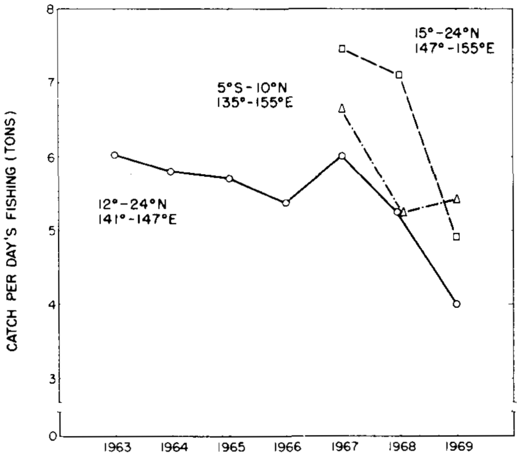

Figure 71.—Indices of relative abundance for the fishing season May-October of skipjack tuna in the Japanese southern water fishery, 1963-69 (from Kasahara 1971).

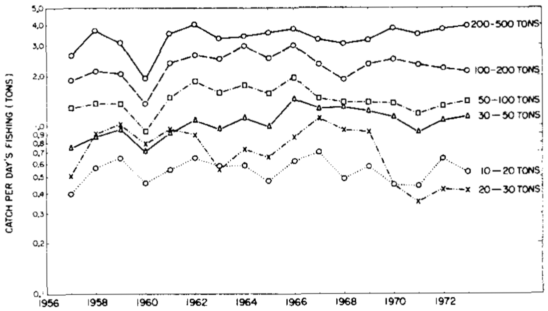

Figure 72.—Catch per day for Japanese bait boats of various size classes in the western Pacific (from Ishida 1975).

trend in the catch per day of Japanese bait boats from 1957 to 1973, apparently over all western Pacific fishery grounds (Fig. 72).

(2) Atlantic Ocean

A number of estimates of relative abundance have been determined using data from the surface fishery in the eastern tropical Atlantic. As is the case with the eastern tropical Pacific fishery, this is a two-species fishery and similar problems exist in separating fishing effort directed at skipjack and yellowfin tunas. For the local bait boat fishery in Angola, de Campos Rosado (1971) presented data showing a steady index of relative abundance for both species combined, while the index for yellowfin tuna has declined proportionally to the increase in the index for skipjack tuna. The relative density derived from purse seine fishing showed an increase in the last half of the year for both United States and Japanese vessels (Sakagawa 1974; Kikawa and Higashi 1979). However, no consistent seasonality in the catch per day statistics for Japanese bait boats was apparent (Kume 1978; Kikawa and Higashi 1979). None of these studies, nor Fonteneau and Cayre's (1980) study on the French-Ivory Coast-Senegalese purse seine fleets, found a long-term trend in relative abundance. However, a study by Pianet (1980) utilizing data from French-Ivory Coast-Senegalese, United States, and Japanese bait boat and purse seine fleets did find a slight decline in relative density over the 1969-78 period (Fig. 73).

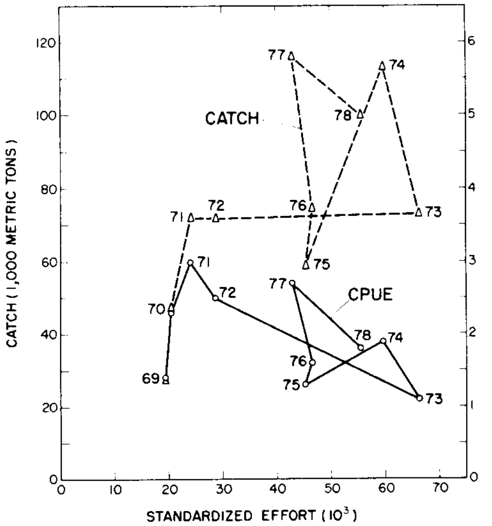

Figure 73.—Relation between catch and CPUE versus standardized effort in the eastern Atlantic (m = 2, K = 1) (from Pianet 1980).

4.3 Natality and recruitment

Various factors relating to natality were discussed in Section 3.1. Reproduction, and more specifically fecundity, was covered in Section 3.15. Recruitment into a fishery, in terms of migration, was discussed in Section 3.51.

Since recruitment into the established and major fisheries around the world is extremely variable, much speculation has been voiced about recruitment into the population(s), but little actual research has been reported in the literature. Recently Forsbergh (1980) described work carried out on this subject by the IATTC in the eastern tropical Pacific. An index of relative abundance of young skipjack tuna in the fishery was tested against three factors: Sea surface temperature in an hypothesized spawning area in the central tropical Pacific (long. 130°W-180°) approximately 1.5 yr earlier, barometric pressure differences at stations in the Indian and Pacific Oceans, and a mixing index in the spawning area. While a significant relationship was found between relative abundance of skipjack tuna in the fishery and temperature in the central tropical Pacific (IATTC 1972, 1973), no obvious biological explanation for this relationship was apparent. Subsequently it was found that the temperature variations in the spawning area were correlated with the southern oscillation index. This index, which is defined as the difference between sea-level atmospheric pressure at sites located in the Indonesian equatorial low region and those in the South Pacific subtropical high region, has been used to study large-scale variations in meteorological and oceanographic conditions occurring over the equatorial Pacific, including the El Niño phenomenon off the northwest coast of South America (Quinn 1976, 1977). In turn, the southern oscillation index has been found to be related to wind conditions in the central equatorial Pacific. During the same period Lasker (1975, 1978, 1981) showed that the survival of anchovy larvae in the California Current was dependent in part on the availability of sufficiently concentrated food and that this occurred with stable structuring of the upper mixed layer of inshore waters. During periods of high wind or strong upwelling, this stable structuring is destroyed and food organisms are dispersed throughout the upper mixed layer resulting in too low a concentration for survival of anchovy larvae. Hypothesizing a similar phenomenon with respect to the survival of skipjack tuna larvae in the central equatorial Pacific spawning area, a significant correlation was found between the index of abundance of fish between 12 and 24 mo of age in the eastern tropical Pacific fishery and an index of mixing (the curl or cube of the wind speed) in the central Pacific approximately 1.5 yr earlier. While the relationship is statistically significant, it accounts for only 47% of the variation and is thus a poor predictor of catch.

4.4 Mortality and morbidity

Most estimates of mortality coefficients appearing in the literature have been calculated for the stock in the eastern tropical Pacific. Using tagging data from 1957, Fink (1965) estimated the total mortality coefficient *Z* to be 6.98, the fishing mortality coefficient *F* to be 2.10, and, using a value of 1.06 for mortality due to tagging from work on yellowfin tuna, the coefficient of natural mortality *M* to be 3.82, all on an annual basis. Joseph and Calkins (1969), using tagging data from a later period, estimated *M* on an annual basis as 1.68. Again utilizing more tagging data for the eastern tropical Pacific, Bayliff[19] estimated *Z* to be 0.58, *F* to be 0.35,

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[19] Bayliff, W. H. 1977. Estimates of the rates of mortality of skipjack tuna in the eastern Pacific Ocean derived from tagging experiments. Inter-Am. Trop. Tuna Comm., Internal Rep. 10, 59 p. Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92037.

and *M* to be 0.23, but in this case, on a monthly basis. Using a completely different approach, Silliman (1966) simulated a catch history for the eastern tropical Pacific fishery by allowing *M* to vary from 0.2 to 0.7 and holding *Z* constant at 0.8. The best fit was obtained with *M* at 0.3, but this method does not provide a unique solution. Most authors indicated that their estimates should be considered as preliminary and acknowledged that the estimates of *M* included emigration and losses due to tagging. Considering the lifespan of skipjack tuna to be about 5 yr, Murphy and Sakagawa (1977) stated that the published estimates of *M* were either too low (0.3) or too high (1.68 and 3.82).

Using tagging data for 1973-74 in Papua New Guinea, Lewis (1980) estimated *Z* on a monthly basis as being equal to 0.257 overall and 1.285 when the stock was exposed to the fishery. Lewis also pointed out that the estimates of *Z* included emigration.

4.5 Dynamics of population (as a whole)

Assessments of the state of the stocks are currently available for the Atlantic and the eastern Pacific, while estimates of potential production are available for the western Pacific and the Indian Oceans. Most of the results must be viewed as preliminary because of the highly variable relationship between catch per unit effort and effort, as well as the low reliability of estimates of population parameters.

(1) Atlantic Ocean

Two estimates of the potential yield are available. First, Shomura (1966b) argued that since the Atlantic Ocean is half the size of the Pacific Ocean, the potential yield for the Atlantic should be half that for the more well-developed fisheries in the Pacific Ocean. Using a catch of 234,100 t in 1962 for the Pacific, he estimated the potential yield for the Atlantic to be 117,000 t, whereas using the largest reported catch for the Pacific, 662,000 t in 1978 (FAO 1980), results in an estimate of 331,000 t for the Atlantic. The harvest reported for the entire Atlantic Ocean was 87,714 t in 1979 (FAO 1980). [Japan.] Fisheries Agency[20] estimated a total production of 100,000 t for the North Atlantic and 100,000-150,000 t for the South Atlantic. The method was based on the abundance of skipjack tuna larvae compared with that for other commercial tuna species.

A yield-per-recruit analysis of the eastern tropical Atlantic fishery by Hayasi (1974) indicated an optimum size at first capture of 0.6-1.3 kg (about 33-40 cm). Hayasi concluded that there was no evidence that skipjack tuna in the Atlantic Ocean was fully exploited. Sakagawa and Murphy (1976) examined the relationship between total catch and normalized catch per unit effort for several gear types in the eastern tropical Atlantic. They concluded also that the stocks were not being fully exploited since there was no consistent trend in the data. Recently, Pianet (1980) found a slight but apparently significant decline in catch per unit effort versus effort for standardized French-Ivory Coast-Senegalese, United States, and Japanese bait boat and purse seiner data from 1969 to 1978 (Fig. 73). A production model fitted to these data resulted in an estimate for maximum sustainable yield of 92,500 t for the eastern tropical Atlantic.

(2) Pacific Ocean

In the eastern tropical Pacific, Joseph and Calkins (1969) estimated yield per recruit, using the Ricker (1958) model, for both the northern and southern skipjack tuna fisheries (Fig. 74). Their model assumed that all individuals in the stock make two passes through the fisheries, and it included von Bertalanffy growth parameters and mortality estimates derived in the same paper. From Figure 74, it can be seen that the yield per recruit for the northern fishery could be increased only slightly by a doubling of the fishing effort (a multiplier equal to 1.0 represents the level of fishing mortality in 1963), while that for the southern fishery could be increased 1 to 1.5 times by increasing fishing effort 2 to 2.5 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. Using the Beverton and Holt (1957) yield per recruit model and lengths of time exposed to the existing coastal fishery of 2 and 6 mo (Fig. 75), Rothschild estimated the yield could be increased between 2 and 17 times the then existing catch. Silliman (1966) estimated the potential yield using a population simulation model which held the total mortality coeffi-

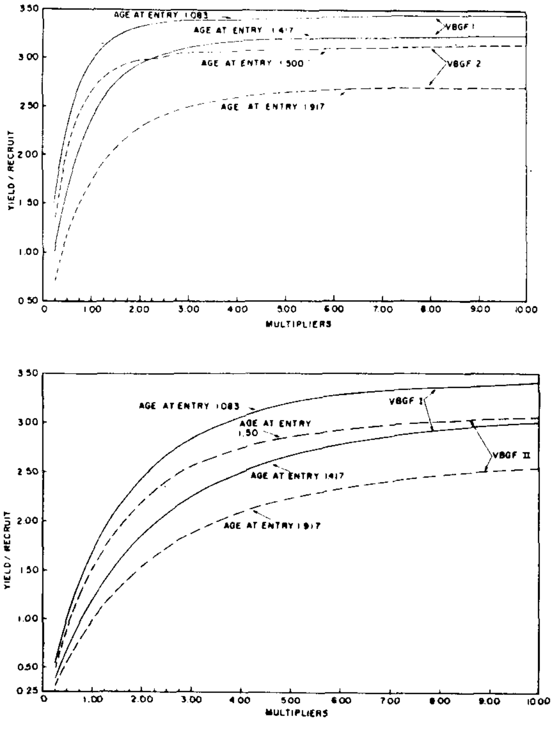

Figure 74.—Yield per recruit of skipjack tuna at age of entry into the northern fishery (top) and southern fishery (bottom), eastern Pacific Ocean, using von Bertalanffy growth parameters from ungrouped data (VBGF 1) and grouped data (VBGF 2) (from Joseph and Calkins 1969).

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[20] [Japan.] Fisheries Agency. 1968. On the possibility of developing marine fishery resources. Information, cited in Kawasaki 1972.

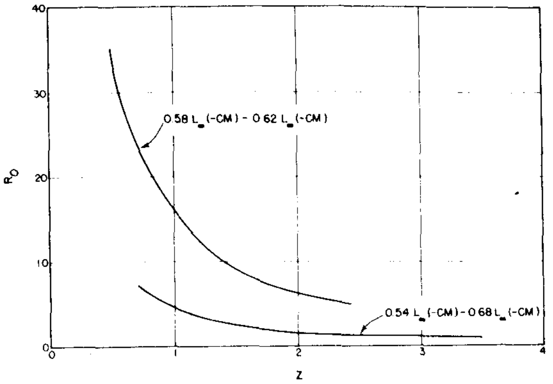

Figure 75.—Values of R_0 (ratio of yields under whole-life exploitation to yield under limited-life exploitation) for skipjack tuna, as a function of Z between 1 and 2. ***Upper curve is for assumed sojourn time of 2 mo, lower curve for 6 mo*** **(from Rothschild 1966).**

cient Z constant at 0.8 and allowed the natural mortality coefficient M to vary from 0.2 to 0.7. Maximum sustainable yield was estimated as 225,000 t with M equal to 0.3 (Table 18). If Rothschild's (1966) 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, both of which are likely, then both Rothschild and Silliman underestimated the potential yield from the central Pacific. While the results from both these authors suggest that yield could be increased by harvesting the escapement stock from the coastal fishery, Joseph and Calkins (1969) observed that yield per recruit could be increased by harvesting fish younger than were then available to the fleet in the eastern tropical Pacific.

Table 18.—Estimates of sustainable yield for the eastern-central Pacific stock of skipjack tuna at M of 0.03 and at selected values of F (from Silliman 1966).

F	Average sustainable yield (1,000 t)	Effort[1] 1,000 boat-days from $f = \frac{F}{q}$	Tons/boat-day
0.5	180	33	5.5
0.6	200	40	5.0
0.8	220	53	4.2
0.9	220	60	3.7
1.0	225	67	3.4
1.1	215	73	2.9

[1] q = 0.01501 from F = 0.5 and f = 33.3, for 1952-56.

[Japan.] Fisheries Agency (footnote 20) estimated potential yields for various oceans and subareas based on the abundance of skipjack tuna larvae and juveniles and their occurrence in the stomachs of predators. These estimates are:

Japanese coastal area	Increase of 200,000-400,000 t
Entire Pacific Ocean	Increase to 800,000-1,000,000 t
Indian Ocean	200,000-300,000 t.

Suda (1972) elaborated on the above procedure by saying that since about twice the number of skipjack tuna larvae were taken in plankton tows as larvae of all other commercial tunas, the spawning stock of skipjack tuna was also roughly two times that of other commercial tunas. Therefore, the potential production of skipjack tuna should be at least two times more than that of all other commercial tunas. Both Kawasaki (1972) and Matsumoto (1974) noted that Suda's projections of adult skipjack tuna catch from larval abundance was oversimplified. By citing differences in fecundity and average body sizes between skipjack tuna and other tunas, Matsumoto showed that the conversion ratio of 2:1 in favor of the skipjack tuna was not logical. One other important factor not taken into account by Suda was the difference in the efficiency of the different types of fishing gear used in taking the various species of tunas and the effect this would have on the conversion ratio.

4.6 *The population in the community and the ecosystem*

4.61 Physical features of the biotope of the community

Skipjack tuna inhabit the epipelagic zone of the world's major oceans and apparently only make forages into deeper zones. As such, they generally live in the upper mixed layer where temperature and salinity variations are small and where oxygen is at or near saturation. Latitudinal and longitudinal variations in temperature and depth of the mixed layer determine to a great extent the distribution of the several races of skipjack tuna. The greatest concentrations of fishery vulnerable skipjack tuna are limited to the temperature range 17°-28°C. The major water masses and their associated currents also influence the distribution of the species, not only through drift of the larvae and possibly the adults as well, but also through the availability of food associated with current boundaries and areas of upwelling. Except for these latter areas of higher productivity, the epipelagic zone is characterized by low productivity.

4.62 *Species composition of the community*

The most important or obvious members of the community are the permanent members of the nekton that feed and reproduce in the epipelagic zone. These include some sharks, *Lamna nasus*, *L. ditropis*, *Isurus glaucus*, *Cetorhinus maximus*, *Prionace glauca*, *Pterolamiops longimanus*, and others; many flying fishes, *Exocoetus volitans*, *E. obtusirostris*, *E. monocirrhus*, *Hirundichthys speculiger*, *H. rondeletii*, *H. albimaculatus*, *Prognichthys gibbifrons*, *P. sealei*, and others; all the Scomberesocidae; several Scombridae, *Gasterochisma melampus*, *Allothunnus fallai*, *Thunnus alalunga*, *T. albacares*, *T. obesus*; marlins, *Tetrapturus audax*, *T. albidus*, *T. angustirostris*, *Makaira nigricans*; swordfish, *Xiphias gladius*; the dolphin, *Coryphaena equiselis*; opah, *Lampris regius*; all the Bramidae; many Nomeidae and Centrolophidae, *Nomeus albula*; species of genera *Psenes*, *Cubiceps*, *Schedophilus*, *Centrolophus*, and *Ichichthys*; Molidae; and some others. A second group of nekton includes those fish that spend their adult stages in the epipelagic zone but whose egg and juvenile stages are found elsewhere. These include the whale shark, *Rhincodon typus*; the dolphin; bluefin tuna, *Thunnus thynnus*; some halfbeaks (Family Hemiramphidae) of the genus *Euleptorhamphus*; needlefishes (Family Belonidae) of the genera *Platybelone* and *Ablennes*; and flyingfishes (Exocoetidae) of the genera *Cypselurus* and *Cheilopogon*. A third group includes the eggs, larvae, and juvenile stages of fishes that inhabit the neritic (pelagic and littoral zones) and the abyssal zones. Among these are some Atherinidae, Scombridae, Carangidae, Gonorhynchidae, Synodontidae, Holocentridae, Stichaeidae, Mullidae, Scorpaenidae, Hexagrammidae, Cottidae (Hemilepidotinae), Nototheniidae, Chaenichthyidae, Acanthuridae, Bothidae, Cynoglossidae, Pleuronectidae, Gonostomidae (*Cyclothone, Vinciguerria*), anglerfishes (Ceratioidei), and apparently some lanternfishes (Myctophidae). Also present are some mesopelagic species that migrate into the epipelagic zone during the night. These include the sharks, *Euprotomicrus bispinatus* and probably *Isistius brasiliensis*; the snake mackerel, *Gempylus serpens*; subsurface lanternfishes of the genera *Myctophum*, *Symbolophorus*, *Centrobranchus, Gonichthys*, *Tarletonbeania*, *Hygophum*, *Loweina*; a few members of Families Melanostomiatidae (*Photonectes, Echiostoma*); and Astronesthidae (*Astronesthes*); and others (Parin 1968).

4.63 Interrelations of the population of the species in the community and ecosystem

Waldron (1963) has adequately described the position of the skipjack tuna as follows: "Within the marine community the skipjack may be listed both as prey and predator, although as a large adult it may be only one step removed from a climax predator. In its larval and juvenile stages it serves as food for larger fish, including adult skipjack. As an adult it serves as food for larger tunas and spearfishes, and at the same time preys upon small to moderate-sized pelagic crustaceans, molluscs, and fish. Skipjack compete for food with tunas and other fish of similar size and habits. They might even be considered as competing with sea birds, for the food organisms are often apparently driven to the surface of the water, where they are preyed upon by both skipjack and various sea birds."

4.64 Hypothetical habitat of skipjack tuna

Metabolic and physiological properties of skipjack tuna in relation to the environment have been discussed in Section 3.63.

5 EXPLOITATION

5.1 Fishing equipment

The two most productive means of catching skipjack tuna on a worldwide basis have been pole-and-line and purse seine fishing. Other methods include gill netting, trolling, trap fishing, harpooning, and beach seining. Recently the importance of flotsam or man-made aggregation devices has increased greatly. Likewise, aerial spotting has become common in some fisheries, and the application of remote sensing is being investigated.

The pole-and-line, bait boat, or live bait fishing method is or has been employed by Japanese fishermen throughout the Pacific and off both coasts of Africa, and by the United States, Ecuadorian, Maldivian, Korean, and Indonesian fishermen, to name only the most obvious instances. Generally, the gear consists of a bamboo pole varying from 3 to 6 m although fiberglass is sometimes used now. The length of the line varies depending on the distance of the fishing location from the sea surface. Generally, a barbless, artificial lure is used which is designed to imitate either a baitfish or a squid. The design of the bait boats varies considerably depending on the nationality and much effort has been expended in recent years, particularly by the Japanese, in modernizing the boats. Cleaver and Shimada (1950) and Yoshida (1966) provided descriptions of the boats that were in use a number of years ago in Japan and the United States. Descriptions of 200 and 250 gross tons (GT) Japanese bait boats appear in Kearney and Hallier (1980b). More modern bait boats are equipped with baitwells with recirculating or even refrigerated water, automatic fishing poles, and fish finders.

Because the Japanese style bait boat carries more fishermen than other types (over 35 compared with as few as 6) and, thus, experiences problems in obtaining enough qualified fishermen, the Japanese have been experimenting with automatic gear, such as a continuous circulating mainline with hooks on short droppers (Inoue 1966; Igeta et al. 1978) and mechanical pole machines (Iwashita et al. 1967; Suzuki Tekkojo Kabushiki Kaisha[21]). The automatic pole machines are now used on 80% of the Japanese bait boats larger than 200 GT, but not on the narrow but highly productive bow area (Maruyama 1980). These machines have also been tried in Australia, as well as in Hawaii and the west coast of the United States.

As the name implies, bait boat fishing includes the chumming of live bait to attract and hold tuna schools close to the vessel. Thus, bait boat fishing is essentially a double fishery, where suitable baitfish resources must be found, captured, hardened for future use, and transported to the fishing grounds in baitwells of the fishing boats. In addition to these technical aspects of baitfishing, the ability of baitfish stocks to withstand harvesting pressure has been investigated by Bayliff (1967) for the eastern tropical Pacific, Wetherall (1977) for Hawaii, and Dalzell and Wankowski (1980) for Papua New Guinea. Because of the limited availability of natural baitfish supplies in small island areas, some interest has been shown in raising or culturing baitfish (Baldwin 1975, 1977; Gopalakrishnan 1979). A workshop on baitfish has covered many of these subjects (Shomura 1977).

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 labor. The major disadvantage is that it is a double fishery. Other disadvantages include the size of the fishing crew, dependence on the biting behavior of the tuna schools, and dependence on good weather conditions to find and fish tuna schools.

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[21] Suzuki Tekkojo Kabushiki Kaisha. 1970. Report on the development of an automatic skipjack fishing machine. From a mimeographed report by the Suzuki Tekkojo Kabushiki Kaisha (Suzuki Ironworks Co., Ltd.), Ishinomaki, Miyagi, Japan, Sept. 30, 1970. [Engl. transl. by T. Otsu, 1970. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.]

Purse seine fishing for tunas began in the eastern tropical Pacific in the 1950's when many of the bait boat clippers began converting to purse seine gear (McNeely 1961). The development of the Puretic power block, which lifts the net with its float line and purse rings, thus enabling the net to be stacked on the deck for the next set, made this possible. Technical aspects of the purse seine are described in McNeely (1961) and Green et al. (1971). Newer developments include lighter fabrication of the net to allow for greater length and depth and other modifications to increase the survival of porpoise (Coe and Vergne 1977). The purse seine net is basically a long net that is set around a school. The ends are brought together and the purse line is drawn until the bottom of the net is pursed or closed. While the first U.S. purse seiners in the eastern tropical Pacific were as small as 130 GT, they now are much larger, commonly around 1,000 GT and as large as 2,000 GT. Modern purse seiners carry a full complement of electronic gear including fish finders and satellite navigation equipment. Similar vessels are now being built in several American countries (e.g., United States, Mexico, and Peru), Spain, France, Poland, and Japan. Fishing operations have expanded from the eastern tropical Pacific to the western Pacific including off Japan, Trust Territory of the Pacific Islands, Philippines, Papua New Guinea, and New Zealand. The more successful boats in the open ocean or small island areas of the western Pacific tend to be smaller, averaging around 500 GT, than in the eastern tropical Pacific. A substantial purse seine fishery takes place in the eastern tropical Atlantic, and the principal countries in the fishery are France, Spain, United States, Japan, and U.S.S.R. Exploratory fishing has taken place in the Indian Ocean.

Both bait boats and purse seine operations have traditionally depended on the spotting of free-swimming, bird-associated, or flotsam-associated tuna schools from the bridge or crow's nest of the fishing boats. Many large purse seine boats now carry helicopters to search for fish schools, and land-based airplanes are commonly used in some fisheries, e.g., in New Zealand (Bell 1976; Habib[22]). Attempts are now underway to use remote sensing of sea surface temperature gradients from satellites or aircraft as an indication of likely fishing areas (Evans 1977; Stevenson and Miller 1977; Eggleston and Paul 1978; Noel 1978; Petit[23,24]; Petit et al. [25]).

While the association of skipjack tuna schools with flotsam (including whales and large sharks) has been known for some time (Inoue et al. 1963, 1968a, b; Greenblatt 1979) and exploited by both bait boats and purse seiners, the new purse seine fishery in the equatorial western Pacific is very dependent on this association. Most purse seine sets take place either at dusk or dawn. Also, anchored rafts are now employed on a commercial scale in the Philippines (Aprieto 1980, 1981; Matsumoto footnote 12) and in Hawaii (Matsumoto et al. 1981), and they are being deployed experimentally throughout the South Pacific, e.g., in American Samoa, West Samoa, northern Marianas, Guam, Palau Islands, Cook Island, and Tonga (Matsumoto footnote 12); in the eastern Pacific (Guillen and Bratten[26]); and in the Indian Ocean, for example, in the Maldives; and probably in other areas as well. In the Philippines, small scouting boats or canoes are used to determine whether tuna have been attracted to the rafts. If so, a light skiff ties up to the raft (or payao) to concentrate the fish for seining. The lights used vary from gasoline lanterns to powerful electrical lights, either submerged or above the surface, depending on the size of the operation. When it is determined that the fish are sufficiently concentrated around the light boat and the raft, the light boat is allowed to slowly drift away until there is room to set the purse seine around the light boat without becoming entangled in the raft. A given purse seiner, which can be anything from a converted tuna longliner to a 2,000 GT purse seiner, will use 15 or more rafts, setting up to 3 times a night and averaging a little over 1 set per night. Tuna are caught on over 90% of the sets.

Advantages of purse seine fishing are independence from baitfish resources, lower requirements for shipboard manpower, and highly efficient catch rate per man per vessel. Disadvantages include the size of the capital investment, inability to fish in rough waters, inability (currently) to fish during the day in waters with a deep thermocline, the requirement for sophisticated unloading and support facilities, and large fuel consumption except when using anchored rafts.

Gill nets are the primary gear used to catch tuna in Sri Lanka and Somalia. The gear used in Sri Lanka is described in de Bruin (1970) and Pajot (1978). Skipjack tuna are quite commonly caught in traps and drive-in nets in the Philippines ([Philippines.] Bureau of Fisheries and Aquatic Resources 1980).

5.2 Fishing areas

The major fisheries have developed adjacent to continents or large islands where upwelling or other oceanographic features lead to a concentration of skipjack tuna near the surface (Fig. 10). The shaded areas around various islands have been exaggerated while subsistence fisheries in the South Pacific Ocean and the small but developing fishery off Australia have not been indicated. Generally, the surface fisheries extend from the neritic-pelagic environment into the adjacent, oceanic-pelagic environment. Reports of skipjack tuna being taken in estuarine environments (river plumes primarily) have been received from the southwestern Pacific Ocean. Open oceanic surface catches are generally associated with upwelling zones between opposing currents, such as along the equatorial currents, the Kuroshio, and the North Pacific subtropical countercurrent.

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[22] G. Habib, *Forum Fisheries Agency*, P.O. Box 627, Honiara, Solomon Islands, pers. commun. 26 June 1981.

[23] Petit, M. 1979. Compte-rendu succinct des travaux accomplis lors de la premiere, periode de l'operation radiometrie aerienene et prospection thoniere (06 fevrier 1979-11 avril 1979). Ref. Article 3 - paragraphe 3-2 du contract No. 1 DOM-TOM-ORSTOM. O.R.S.T.O.M., Centre de Noumea, no pag. O.R.S.T.O.M., B. P. A5, Noumea-Cedex, New Caledonia.

[24] Petit, M. 1979. Compte-rendu des travaux accomplis lors de la deuxieme periode de l'operation radiometrie aerienne et prospection thoniere (16 juin 1979-14 juillet 1979). Ref. Article 3-2 du contract No. 1. DOM-TOM-ORSTOM. O.R.S.T.O.M., Centre de Noumea, no pag. O.R.S.T.O.M., B. P. A5, Noumea-Cedex, New Caledonia.

[25] Petit, M., J. Muyard, and F. Marsac. 1980. Compte-rendu des travaux accomplis lors de la troisieme periode de l'operation radiometrie aerienne et prospection thoniere (25 septembre 1979-11 febvier 1980). Ref. Article 3-2 du contract No. 1. DOM-TOM-ORSTOM. O.R.S.T.O.M., Centre de Noumea, 77 p. O.R.S.T.O.M., B. P. A5, Noumea-Cedex, New Caledonia.

[26] Guillen, R., and D. A. Bratten. 1981. Anchored raft experiment to aggregate tunas in the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm., Internal Rep. 14, 10 p. Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92037.

5.3 Fishing seasons

Generally, fisheries existing in the equatorial, tropical areas do not show much seasonal variation except possibly a slight increase in catches during both the northern and southern summers. Fisheries situated more poleward in the subtropics or bordering on the temperate zone show more seasonality with the peak catches occurring in the summer months for the respective hemispheres.

Specific details on seasonality in various fisheries for the western Pacific and the Indian Oceans may be found in Uchida (1975), for New Zealand in Habib (1976, 1978) and Habib et al. (1980a, b, c), for Papua New Guinea in Wankowski (1980), for the eastern tropical Atlantic Ocean in Sakagawa and Murphy (1976), and for French Polynesia and the eastern tropical Pacific in Forsbergh (1980).

5.4 Fishing operations and results

5.41 Effort and intensity

Various means of measuring fishing effort directed at skipjack tuna were discussed in Section 4.2. Changes in the efficiency of the gear were discussed in Section 5.1.

In the eastern tropical Pacific, reported effort is 22 to 26% less than the total effort; however, there is no apparent trend in the rate of reporting (Forsbergh 1980). The amount of fishing effort increased from 1934 to the 1950's, remained fairly constant during the 1960's, and then increased again through most of the 1970's.

In Hawaii, estimates of relative fishing intensity (Fig. 70) fluctuated substantially from year to year and were at a somewhat higher level during the 1948-56 period than in subsequent years (Uchida 1976).

In the Papua New Guinea bait boat fishery, the amount of fishing effort has increased from some 500 d in 1970 to 8,000-9,000 d by 1979 (Wankowski 1980). In the New Zealand purse seine fishery, about 400 d of effort have been expended in each fishing season starting in 1976-77 (Habib 1976, 1978; Habib et al. 1980a, b).

For the Japanese bait boat fishery, there has been a slight increase in the number of trips from around 7,000 in 1970 to 10,000 in 1976 by all size classes of boats in the coastal fishery (north of lat. 15°N), while for boats between 50 and 100 gross metric tons (GMT), the number of trips increased from about 1,400 to 8,000 (Bour and Galenon 1979). For the southern water fishery, Kasahara (1977) showed that the total number of fishing days for all size classes of bait boats increased from nearly 9,000 in 1970 to over 21,000 in 1975, while the increase for 250 GMT boats was from around 2,600 to nearly 20,000 d during the same period. Honma and Suzuki (1978), in their preliminary description of the Japanese purse seine fishery, showed that the number of single-boat purse seiners increased from 16 in 1969 to 52 in 1974, whereas the number of double-boat purse seiners declined from 55 to 12 over the same period. The number of trips for the single-boat purse seiners varied from some 390 to 940 and for the double-boat purse seiners from 1,500 to about 340 over the same period. In the period 1971-74 the number of sets for single-boat seiners in the coastal fishery fluctuated between 1,000 and 2,000 sets, whereas for double-boat seiners the number of sets declined from around 1,300 to 400. In the southern water fishery, the number of sets by single-boat seiners increased from 60 in 1968 to 428 in 1974.

5.42 Selectivity

Pole-and-line gear (as used on bait boats) tends to take smaller and fewer size classes of skipjack tuna than does purse seine gear. The selectivity of pole-and-line gear can be modified by changing hook size, weight of the pole, or bait size, but most significantly by merely selecting for size of fish in a school. Likewise, the size selectivity of purse seine gear can be varied by selecting schools and by adjusting mesh size to retain fish only of the desired size or larger. Longline gear, which catches skipjack tuna only incidentally, is known to take mostly large individuals as discussed in Section 4.13.

5.43 Catches

(1) Total annual catches

From 1961 through 1979, the nominal catches of skipjack tuna from all oceans have more than tripled, reaching 698.5 t in 1979 (Table 19). While the catch of all tunas has increased varying amounts over this period, that for skipjack tuna has increased more rapidly than the other principal market species of tunas (yellowfin tuna, albacore, bigeye tuna, and bluefin tuna). More specifically, the proportion of skipjack tuna catches has increased steadily from 24.5% in 1961 to around 40% in the late 1970's (Fig. 76). Catches of skipjack tuna first surpassed those of the traditionally dominant yellowfin tuna in 1965, fell below in 1968 and 1969, and then remained above after 1970. Clearly the Pacific Ocean is the most important area for skipjack tuna fishing with catches there accounting for 80 to 90% of the world catch. Also, the fisheries of the western Pacific alone accounted for 67.1% of the world skipjack tuna catch in 1979 (Fig. 77). The developing fisheries in the Atlantic and the Indian Oceans accounted for 12.5 and 4.7% of the world skipjack tuna catch in 1979.

(2) Total annual yields from different fishing grounds

A more detailed breakdown of catches is provided in Table 20 for selected countries in the most productive skipjack tuna fishing areas. In the eastern central Atlantic Ocean, Spain and France have traditionally been the major producers but Japan, and more recently Korea, have become significant participants in the fishery. In the Indian Ocean, the production of the two major fishing countries, Maldives and Sri Lanka, has declined. In the northwestern Pacific Ocean, Japan is essentially the only producer, and their fishery reached a maximum of some 107,000 t in 1973. In the central western Pacific Ocean, the Japanese distant water fishery is the major producer and has shown a large increase from around 35,000 t in 1966 to 198,000 t in 1978. Production by the Philippines, Indonesia, Papua New Guinea, and the Solomons has also shown marked increases in the 1970's. In the eastern central Pacific Ocean, the United States has been the leading fishing nation, producing up to around 100,000 t. Ecuador has been the second largest producer, with a maximum of around 17,000 t. Mexico has recently been adding significantly to its purse seiner carrying capacity and should be expected to con-

Table 19.—Annual landings (in 1,000 t) of skipjack tuna from the major oceans by FAO statistical areas (FAO 1968, 1971, 1974b, 1976, 1977, 1978, 1979, 1980).

	Year																		
Area	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979
Atlantic Ocean[1]	0.3	0.3	2.2	14.3	17.9	25.7	22.7	36.2	32.0	51.6	67.9	73.1	71.8	119.0	67.8	73.5	97.6	95.6	87.6
Northwest 21	No breakdown by area			0.5	0.0	0.0	0.0	1.8	0.4	—	0.4	0.0	0.1	—	0.0	0.2	0.0	0.4	0.3
Northeast 27				—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.6
Western central 31				1.1	1.0	1.1	1.2	1.8	1.3	1.6	1.7	1.6	2.1	4.1	2.9	4.7	6.0	1.9	2.1
Eastern central 34				10.8	16.4	24.0	20.0	31.8	29.9	49.5	64.9	70.4	67.0	101.1	63.1	66.5	86.9	88.3	77.5
Southwest 41				0.4	0.5	0.6	1.5	0.8	0.4	0.4	0.8	1.0	0.6	0.5	1.1	0.6	0.6	1.4	1.4
Southeast 47				1.5	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	2.0	13.3	0.7	1.5	4.1	3.6	3.7
Indian Ocean	—	—	—	0	13.2	16.0	18.1	16.6	18.7	29.7	31.4	20.1	24.2	41.3	36.2	38.4	30.3	30.4	32.6
Western 51	No breakdown by area			0	13.2	16.0	18.1	16.5	18.6	27.4	29.0	16.3	20.1	36.7	31.7	32.4	26.2	25.3	27.0
Eastern 57				0	0.0	0.0	0.0	0.1	0.1	2.3	2.4	3.8	4.1	4.6	4.5	6.0	4.1	5.1	5.6
Pacific Ocean	219.0	252.4	200.8	252.4	235.9	308.6	335.9	273.6	269.6	304.0	328.2	330.1	434.3	510.0	436.3	554.3	504.8	665.8	578.3
Northwest 61	No breakdown by area			187.2	145.8	208.4	176.0	147.6	163.1	166.2	119.8	157.1	202.6	127.2	135.5	151.1	130.0	157.3	143.0
Northeast 67				—	0.2	—	0.1	—	0.1	0.2	0.3	0.0	0.1	0.5	0.1	6.7	0.4	5.8	0.5
Western central 71				—	—	35.7	35.2	42.5	41.5	70.0	114.8	119.9	173.0	303.0	205.4	252.9	272.5	359.7	316.9
Eastern central 77				53.4	76.3	54.2	106.9	74.5	51.5	58.9	87.4	50.1	52.0	75.3	84.5	134.2	91.4	130.0	107.7
Southwest 81				1.5	0.0	0.0	0.2	0.1	0.0	0.0	0.2	0.5	1.8	1.7	6.4	6.3	6.4	9.8	8.5
Southeast 87				10.3	13.6	10.3	17.5	8.9	13.4	8.7	5.7	2.5	4.8	2.3	4.4	3.1	4.1	3.2	1.7
Total	219.3	252.7	203.0	266.7	267.0	350.3	376.7	326.4	320.3	385.3	427.3	423.3	530.3	670.3	540.3	662.2	632.7	791.8	698.5

[1] Landings occur in the Mediterranean but in very small amounts.

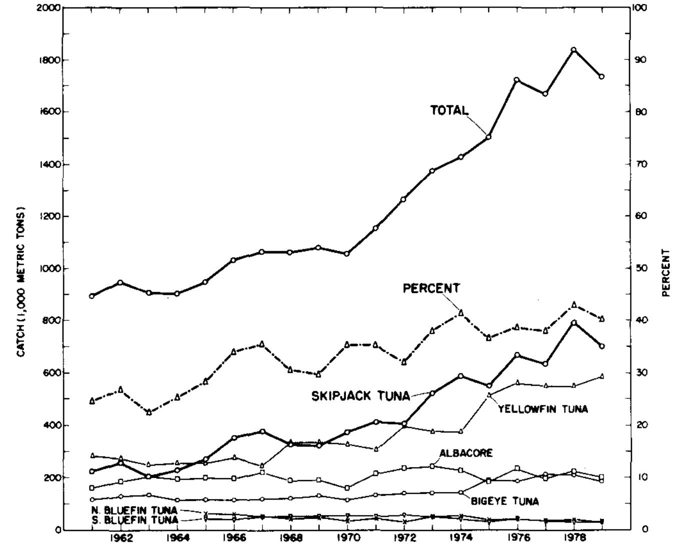

Figure 76.—Annual nominal catches of the principal market species of tunas from all oceans (FAO 1968, 1973, 1975, 1979, 1980) and catches of skipjack tuna as a percent of the total.

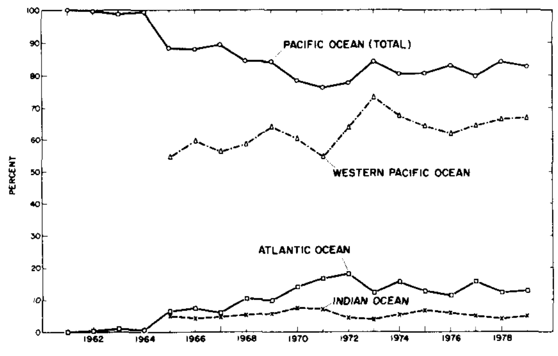

Figure 77.—Percent of skipjack tuna catches by ocean areas.

Table 20.—Annual landings (in 1,000 t) of skipjack tuna by states within key FAO statistical areas (FAO 1968, 1971, 1974b, 1976, 1977, 1978, 1979, 1980).

	Eastern central Atlantic Ocean - 34				Western Indian Ocean - 51		Northwestern Pacific Ocean - 61	Western central Pacific Ocean - 71					Eastern central Pacific Ocean - 77	
Year	Spain	France	Japan	Korea	Maldives	Sri Lanka	Japan	Japan	Philippines	Indonesia	Papua New Guinea	Solomon Islands	United States	Ecuador
1964	2.9	—	3.1	—	—	—	162.6	—	—	—	—	—	41.8	9.3
1965	9.5	—	6.3	—	13.1	—	132.8	—	—	—	—	—	58.1	14.9
1966	18.5	—	4.4	—	15.9	—	191.6	35.7	—	—	—	—	44.1	10.5
1967	13.6	—	3.7	—	17.9	—	154.2	34.7	0.5	—	—	—	93.6	17.3
1968	19.1	—	7.3	—	16.3	—	125.9	40.1	2.4	—	—	—	50.8	12.9
1969	18.3	—	4.9	—	18.4	—	138.8	40.9	0.6	—	—	—	35.1	15.6
1970	22.2	10.6	7.5	—	27.3	—	151.3	53.4	0.3	12.1	2.4	—	39.3	8.8
1971	27.1	9.7	11.7	0.0	28.9	—	99.1	79.3	0.6	12.4	17.0	4.5	77.3	11.9
1972	22.5	15.2	10.2	0.0	16.0	—	156.2	79.7	0.3	19.6	13.1	6.8	22.1	4.5
1973	22.1	12.7	13.1	0.9	20.0	—	200.9	106.9	3.2	22.3	28.5	5.8	27.3	4.4
1974	36.5	18.4	18.7	2.2	24.0	12.3	125.6	196.2	29.5	23.6	40.2	10.0	48.5	7.8
1975	17.8	10.4	3.6	4.7	16.0	15.2	133.3	119.5	31.7	23.3	15.6	7.1	66.2	17.0
1976	18.5	15.5	13.2	1.9	19.9	12.2	149.2	145.3	29.2	25.3	24.4	15.6	87.7	6.2
1977	19.6	24.9	13.2	4.2	14.4	11.4	126.8	148.8	55.1	26.4	19.2	13.0	51.2	10.0
1978	28.9	19.2	14.6	7.4	13.8	11.0	152.3	198.3	49.7	29.4	45.8	17.5	100.5	11.8
1979	19.8	14.7	12.4	12.0	17.9	8.3	139.4	177.4	45.1	30.2	24.0	23.8	72.5	17.6

tribute proportionally more to the total production from the area.

6 PROTECTION AND MANAGEMENT

As yet there are no management regulations for skipjack tuna in any of the world's oceans. From a biological viewpoint, no need for conservation measures has been proven for any fishery, although Kasahara (1977) and others have cautioned that expansion of the fisheries should be done with a knowledge of the limits of the available resources. Kearney (1978, 1979) believed that attempts to optimize socioeconomic returns among participants in the fisheries and states controlling fishing in their extended economic zones will overshadow any conservation needs for many years to come.

As many nations around the world have declared extended economic zones and have begun to regulate fishing activities in their zones, de facto regulation is, in fact, occurring now. However, the goal of the nations promulgating these regulations is to extract economic returns from foreigners fishing in their respective zones or to reserve the resources for domestic harvest. As yet these regulatory measures have been declared unilaterally with no multilateral or international arrangements being effected. Various states in the eastern tropical Pacific, South Pacific, western Pacific, and Indian Oceans are moving toward such international arrangements, but none have been completed.

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LITERATURE CITED

AIKAWA, H.
1937. Notes on the shoal of bonito (skipjack, *Katsuwonus pelamis*) along the Pacific coast of Japan. [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 6:13-21. [Engl. transl. by W. G. Van Campen, 1952. *In* U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 83:32-50.]

AIKAWA, H., and M. KATO.
1938. Age determination of fish (Preliminary Report 1). [In Jpn., Engl. synop.] Bull. Jpn. Soc. Sci. Fish. 7:79-88. [Engl. transl. by W. G. Van Campen, 1950. *In* U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 21, 22 p.]

ALVERSON, F. G.
1963. The food of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 7:293-396.

ANRAKU, M., and T. KAWASAKI.
1966. On the abundance and its fluctuation of the skipjack and albacore migrating to the neighbouring seas of Japan. II. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 26:9-33.

ANSA-EMMIM, M.
1977. Landings and length composition of yellowfin, skipjack and bigeye tunas caught in the eastern tropical Atlantic by the Tema-based tuna fleet, 1975. Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1976) 6:56-61.

APRIETO, V. L.
1980. Philippine tuna fisheries: Resource and industry. Fish. Res. J. Philipp. 5:53-66. (Also as East-West Center, East-West Environ. Policy Inst., Reprint 19.)
1981. Fishery management and extended maritime jurisdiction: The Philippine tuna fishery situation. East-West Center, East-West Environ. Policy Inst., Res. Rep. 4, 78 p.

BAILEY, R. M., J. E. FITCH, E. S. HERALD, E. A. LACHNER, C. C. LINDSAY, C. R. ROBINS, and W. B. SCOTT.
1970. A list of common and scientific names of fishes from the United States and Canada. 3d ed. Am. Fish. Soc., Spec. Publ. 6, 150 p.

BAILEY, R. M., E. A. LACHNER, C. C. LINDSAY, C. R. ROBINS, P. M. ROEDEL, W. B. SCOTT, and L. P. WOODS.
1960. A list of common and scientific names of fishes from the United States and Canada. 2d ed. Am. Fish. Soc., Spec. Publ. 2, 102 p.

BALDWIN, W. J.
1975. Development of skipjack tuna fisheries in the tropical Pacific with cultured baitfishes. Presented at 8th South Pac. Comm. Reg. Tech. Meet. on Fish, Noumea, 20 October 1975. Univ. Hawaii Sea Grant Rep., UNIHI-SEAGRANT-JC-75-14, 8 p.

1977. A review on the use of live baitfishes to capture skipjack tuna, *Katsuwonus pelamis*, in the tropical Pacific Ocean with emphasis on their behavior, survival, and availability. *In* R. S. Shomura (editor), Collection of tuna baitfish papers, p. 8-35. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 408.

BARKLEY, R.A.

1969. Salinity maxima and the skipjack tuna, *Katsuwonus pelamis*. Bull. Jpn. Soc. Fish. Oceanogr., Spec. No. (Prof. Uda's Commemorative Papers), p. 243-248.

1972. Johnston Atoll's wake. J. Mar. Res. 30:201-216.

BARKLEY, R. A., W. H. NEILL, and R. M. GOODING.

1978. Skipjack tuna, *Katsuwonus pelamis*, habitat based on temperature and oxygen requirements. Fish. Bull., U.S. 76:653-662.

BARNARD, K. H.

1925. A monograph of the marine fishes of South Africa. Ann. S. Afr. Mus. 21, 1065 p.

BARNHART, P. S.

1936. Marine fishes of southern California. Univ. Calif. Press, Berkeley, 209 p.

BARRETT, I., and F. J. HESTER.

1964. Body temperature of yellowfin and skipjack tunas in relation to sea surface temperature. Nature (Lond.) 203:96-97.

BARRETT, I., and H. TSUYUKI.

1967. Serum transferrin polymorphism in some scombroid fishes. Copeia 1967:551-557.

BATTS, B. S.

1972a. Age and growth of the skipjack tuna, *Katsuwonus pelamis* (Linnaeus), in North Carolina waters. Chesapeake Sci. 13:237-244.

1972b. Food habits of the skipjack tuna, *Katsuwonus pelamis*, in North Carolina waters. Chesapeake Sci. 13:193-200.

1972c. Sexual maturity, fecundity, and sex ratios of the skipjack tuna, *Katsuwonus pelamis* (Linnaeus), in North Carolina waters. Trans. Am. Fish. Soc. 101:626-637.

BAYLIFF, W. H.

1967. Growth, mortality, and exploitation of the Engraulidae, with special reference to the anchoveta, *Cetengraulis mysticetus*, and the colorado, *Anchoa naso*, in the eastern Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 12:367-432.

BELL, G. R.

1976. Aerial spotting for pelagic fishes. [New Zealand.] Minist. Agric. Fish., Fish. Res. Div., Occas. Publ. 11:47-48.

BELLOC, G.

1955. Les thons de la Méditerranée. Deuxième note: thonine et bonite. Proc. Tech. Pap. Gen. Fish. Counc. Méditerr., FAO 3(52):471-486.

BERG, L. S.

1940. Classification of fishes, both recent and fossil. [In Russ. and Engl.] J. W. Edwards Co., Ann Arbor, Mich., p. 87-517.

BEVERTON, R. J. H., and S. J. HOLT.

1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric., Fish. Food G.B. (Ser. II), 19, 533 p.

BIGELOW, H. B., and W. C. SCHROEDER.

1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BIGELOW, H. B., and W. W. WELSH.

1925. Fishes of the Gulf of Maine. U.S. Bur. Fish., Bull. 40 (part 1), 567 p.

BINI, G., and E. TORTONESE.

1955. Missione sperimentale di pesca nel Cile e nel Perù - Pesci marini Peruviani. Boll. Pesca Piscic. Idrobiol., 1954, 30:151-185.

BLACKBURN, M.

1965. Oceanography and the ecology of tunas. Oceanogr. Mar. Biol., Annu. Rev. 3:299-322.

BLACKBURN, M., and D. L. SERVENTY.

1981. Observations on distribution and life history of skipjack tuna, *Katsuwonus pelamis*, in Australian waters. Fish. Bull., U.S. 79:85-94.

BLEEKER, P.

1856. Beschrijvingen van nieuwe en weinig bekende vischsoorten van Ambonia, versameld op eene reis door den Molukschen Archipel, gedaan in het gevolg van den Gouverneur-Generaal Duymaer van Twist in September en October 1855. Acta Soc. Sci. Indo-Neerl. 1:41-42.

1862. Sixième mémoire sur la faune ichthyologique de l'ile Batjan. Versl. Akad. Amsterdam 14:99-112.

1865. Enumération des espèces de poissons actuellement connues de l'île d'Amboine. Neder. Tijdschr. Dierk. 2:270-293.

BLOCH, M. E., and J. G. SCHNEIDER.

1801. Systema ichthyologiae iconibus ex illustratum. Berolini, 584 p.

BONNATERRE, J. P.

1788. Tableau encyclopédique et mèthodique des trois règnes de la nature. Ichthyologie 6, 215 p.

BOUR, W.

1976. Croissance du listao (*Katsuwonus pelamis*) Est-Atlantique tropical. Note préliminaire. [In Fr., Engl. abstr.] Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1975) 5:142-148.

BOUR, W., and P. GALENON.

1979. The development of tuna fisheries in the western Pacific. South Pac. Comm., Occas. Pap. 12, 34 p.

BREDER, C. M., Jr.

1929. Field book of marine fishes of the Atlantic coast from Labrador to Texas. G. P. Putnam's Sons, N.Y., 332 p.

BREDER, C. M., Jr., and F. HALPERN.

1946. Innate and acquired behavior affecting the aggregation of fishes. Physiol. Zool. 19:154-190.

BRETT, J. R.

1973. Energy expenditure of sockeye salmon, *Oncorhynchus nerka*, during sustained performance. J. Fish. Res. Board Can. 30:1799-1809.

BRIGGS, J. C.

1960. Fishes of worldwide (circumtropical) distribution. Copeia 1960: 171-180.

BRILL, R. W.

1979. The effect of body size on the standard metabolic rate of skipjack tuna, *Katsuwonus pelamis*. Fish. Bull., U.S. 77:494-498.

BRILL, R. W., and A. E. DIZON.

1979. Effect of temperature on isotonic twitch of white muscle and predicted maximum swimming speeds of skipjack tuna, *Katsuwonus pelamis*. Environ. Biol. Fishes 4:199-205.

BROADHEAD, G. C., and I. BARRETT.

1964. Some factors affecting the distribution and apparent abundance of yellowfin and skipjack tuna in the eastern Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 8:419-473.

BROADHEAD, G. C., and C. J. ORANGE.

1960. Species and size relationship within schools of yellowfin and skipjack tuna, as indicated by catches in the eastern tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 4:449-492.

BROCK, V. E.

1949. A preliminary report on *Parathunnus sibi* in Hawaiian waters and a key to the tunas and tuna-like fishes of Hawaii. Pac. Sci. 3:271-277.

1954. Some aspects of the biology of the aku, *Katsuwonus pelamis*, in the Hawaiian Islands. Pac. Sci. 8:94-104.

1959. The tuna resource in relation to oceanographic features. *In* Tuna industry conference papers, May 1959, p. 1-11. U.S. Fish Wildl. Serv., Circ. 65.

BROCK, V. E., and R. H. RIFFENBURGH.

1960. Fish schooling: A possible factor in reducing predation. J. Cons. Cons. Int. Explor. Mer 25:307-317.

BROWN, C. E., and B. S. MUIR.

1970. Analysis of ram ventilation of fish gills with application to skipjack tuna (*Katsuwonus pelamis*). J. Fish. Res. Board Can. 27:1637-1652.

BUÑAG, D. M.

1956. Spawning habits of some Philippine tuna based on diameter measurements of the ovarian ova. Philipp. J. Fish., 1958, 4:145-177.

CALKINS, T. P.

1961. Measures of population density and concentration of fishing effort for yellowfin and skipjack tuna in the eastern tropical Pacific Ocean, 1951-1959. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 6:71-152.

1975. Geographical distribution of yellowfin and skipjack tuna catches in the eastern Pacific Ocean, and fleet and total catch statistics, 1971-1974. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 17:1-116.

CANTOR, T.

1850. Catalogue of Malayan fishes. J. Thomas, Calcutta, xii + 461 p. Rep. J. Asiatic Soc. Bengal, 1849, 18:i-xii, 983-1443.

CAREY, F. G., and J. M. TEAL.

1969. Regulation of body temperature by the bluefin tuna. Comp. Biochem. Physiol. 28:205-213.

CAREY, F. G., J. M. TEAL, J. W. KANWISHER, K. D. LAWSON, and J. S. BECKETT.

1971. Warm-bodied fish. Am. Zool. 11:135-143.

CARUS, J. V.

1893. Prodromus faunae Mediterraneae. Vol. 2, Brachiostomata, Mollusca, Tunicata, Vertebrata. Koch, Stuttgart, 854 p.

CASSIE, R. M.

1954. Some uses of probability paper in the analysis of size frequency distributions. Aust. J. Mar. Freshwater Res. 5:513-522.

CAYRE, P.

1979. Determination de l'age de listao, *Katsuwonus pelamis*, debarques a Dakar; Note préliminaire. [In Fr., Engl. summ.] Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1978) 8:196-200.

CHATWIN, B. M.

1959. The relationships between length and weight of yellowfin tuna (*Neothunnus macropterus*) and skipjack tuna (*Katsuwonus pelamis*) from the eastern tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 3:307-352.

CHEN, C.-J., and R.-T. YANG.

1973. Parasites of yellowfin tuna in the waters southwest off Taiwan. Acta Oceanogr. Taiwan. 3:181-198.

CHEN, S.-C., and T.-H. TAN.

1973. A preliminary report on occurrence of tuna larvae in waters adjacent to Taiwan and South China Sea. Rep. Inst. Fish. Biol. Minist. Econ. Aff. Natl. Taiwan Univ. 3:158-171.

CHI, K.-S., and R.-T. YANG.

1973. Age and growth of skipjack tuna in the waters around the southern part of Taiwan. Acta Oceanogr. Taiwan. 3:199-221.

CHIKUNI, S.

1978. Part I. Report on fishing for tuna in Philippine waters and biological features of the resources. *In* FAO, 1978. Test fishing for tuna and small pelagic species. Reports on the operation of FAO chartered purse seiners in Philippine and South China Sea waters, 1974-1977. FAO, SCS/DEV/78/18, 44 p.

CHOO, W. I.

1977. Report on the Korean baitboat fishery in the Atlantic Ocean, 1975. [In Engl., Fr. and Span. summ.] Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1976) 6:69-71.

CHUR, V. N., V. B. GRUDININ, and V. L. ZHAROV.

1980. Data on length-age composition and gonad maturity stages of skipjack (*Katsuwonus pelamis*) of the eastern tropical Atlantic. Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1979) 9:245-254.

CLARK, F. N.

1934. Maturity of the California sardine (*Sardina caerulea*), determined by ova diameter measurements. Calif. Div. Fish Game, Fish Bull. 42, 49 p.

CLEAVER, F. C., and B. M. SHIMADA.

1950. Japanese skipjack (*Katsuwonus pelamis*) fishing methods. Commer. Fish. Rev. 12(11):1-27.

CLEMENS, W. A., and G. V. WILBY.

1946. Fishes of the Pacific coast of Canada. Fish. Res. Board Can., Bull. 68, 368 p.

COAN, A. L.

1976. Length and age composition of skipjack tuna from the Atlantic Ocean, 1968-73. Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1975) 5:133-141.

COE, J. M., and P. J. VERGNE.

1977. Modified tuna purse seine net achieves record low porpoise kill rate. Mar. Fish. Rev. 39(6):1-4.

COLLETTE, B. B.

1978. Adaptations and systematics of the mackerels and tunas. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 7-39. Acad. Press, N.Y.

COLLETTE, B. B., and L. N. CHAO.

1975. Systematics and morphology of the bonitos (*Sarda*) and their relatives (Scombridae, Sardini). Fish. Bull., U.S. 73:516-625.

COLLETTE, B. B., and R. H. GIBBS, Jr.

1963. A preliminary review of the fishes of the family Scombridae. FAO Fish. Rep. 6(1):23-32.

CONAND, F., and A. W. ARGUE.

1980. Preliminary observations on juvenile skipjack from the stomachs of adult skipjack caught by pole-and-line gear. South Pac. Comm., Reg. Tech. Meet. Fish. 12, 21 p.

CRESSEY, R., and H. B. CRESSEY.

1980. Parasitic copepods of mackerel- and tuna-like fishes (Scombridae) of the world. Smithson. Contrib. Zool. 311, 186 p.

CUNNINGHAM, J. T.

1910. On the marine fishes and invertebrates of St. Helena. Proc. Zool. Soc. Lond., p. 86-131.

CUSHING, J. E., Jr.

1956. Observations on serology of tuna. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 183, 14 p.

CUVIER, G.

1829. Le règne animal. Nouvelle ed. tom. II. Deterville, Paris, 406 p.

CUVIER, G., and A. VALENCIENNES.

1831. Histoire naturelle des poissons, Vol. 8. F. G. Levrault, Paris, 375 p.

DALZELL, P. J., and J. W. J. WANKOWSKI.

1980. The biology, population dynamics, and fisheries dynamics of exploited stocks of three baitfish species, *Stolephorus heterolobus*, *S. devisi*, and *Spratelloides gracilis*, in Ysabel Passage, New Ireland Province, Papua New Guinea. [Papua New Guinea.] Res. Bull. 22, 124 p.

DAY, F.

1878. The fishes of India; being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma, and Ceylon. Vol. 1, 778 p. Dawson and Sons, Lond. (Lithograph reproduction 1958.)

de BEAUFORT, L. F., and W. M. CHAPMAN.

1951. The fishes of the Indo-Australian Archipelago. IX. Percomorphi (concluded), Blennoidea. E. J. Brill, Leiden, 484 p.

de BRUIN, G. H. P.

1970. Drift-net fishing in Ceylon waters. Bull. Fish. Res. Stn. Ceylon 21:17-31.

de BUEN, F.

1926. Catálogo ictiológico del Mediterráneo Español y Marruecos. Result. Camp. Acuerd. Int., Madrid 2, p. 150, 159, 167.

1930. Ictiología española. I. Scombriformes y Thunniformes. Bol. Oceanogr. Pesca, Madrid 15(162):34-53.

1935. Fauna ictiológica. Catálogo de los peces ibéricos, de la planicie continental, aguas dulces, pelágicos y de los abismos próximos. Segunda parte. Notas y resúmenes. Inst. Esp. Oceanogr., Ser. 2, 89:91-149.

1958. Peces del suborden Scombroidei en aguas de Chile. Rev. Biol. Mar., Valparaiso 7:3-38. [Engl. transl. in files of Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

de CAMPOS ROSADO, J. M.

1971. Long-term changes in abundance of yellowfin and skipjack off the coast of Angola. J. Cons. Cons. Int. Explor. Mer 34:65-75.

de MIRANDA RIBEIRO, A.

1915. Fauna Brasiliense. Peixes. Part V. Physoclisti. Arch. Mus. Nac., Rio de Janeiro 17, 600 p. [Pages not continuously numbered.]

DERANIYAGALA, P. E. P.

1933. Names of some fishes from Ceylon. Ceylon J. Sci., Sect. C Fish. 5:79-111.

DIZON, A. E.

1977. Effect of dissolved oxygen concentration and salinity on swimming speed of two species of tunas. Fish. Bull., U.S. 75:649-653.

DIZON, A. E., and R. W. BRILL.

1979. Thermoregulation in tunas. Am. Zool. 19:249-265.

DIZON, A. E., R. W. BRILL, and H. S. H. YUEN.

1978. Correlations between environment, physiology, and activity and the effects on thermoregulation in skipjack tuna. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 233-259. Acad. Press, N.Y.

DIZON, A. E., T. C. BYLES, and E. D. STEVENS.

1976. Perception of abrupt temperature decrease by restrained skipjack tuna, *Katsuwonus pelamis*. J. Therm. Biol. 1:185-187.

DIZON, A. E., W. H. NEILL, and J. J. MAGNUSON.

1977. Rapid temperature compensation of volitional swimming speeds and lethal temperatures in tropical tunas (Scombridae). Environ. Biol. Fishes 2:83-92.

DIZON, A. E., E. D. STEVENS, W. H. NEILL, and J. J. MAGNUSON.

1974. Sensitivity of restrained skipjack tuna (*Katsuwonus pelamis*) to abrupt increases in temperature. Comp. Biochem. Physiol. 49A:291-299.

DONGUY, J. R., W. BOUR, P. GALENON, and J. A. GUERERDRAT.

1978. Les conditions oceanographiques et la pêche de la bonite (*Katsuwonus pelamis*) dans le Pacifique occidental. Cah. O.R.S.T.O.M., Sér. Océanogr. 16(3-4):309-317.

DRAGOVICH, A.

1970. The food of skipjack and yellowfin tunas in the Atlantic Ocean. Fish. Bull., U.S. 68:445-460.

1971. Food of skipjack tuna in the Caribbean Sea and adjacent oceanic waters. *In* Symposium on Investigations and Resources of the Caribbean Sea and Adjacent Regions. FAO Fish. Rep. 71.2:27-40.

DRESSLAR, F. B., and B. FESLER.

1889. A review of the mackerels (Scombrinae) of America and Europe. Bull. U.S. Fish Comm. 7(1887):429-446.

ECKLES, H. H.

1949. Observations on juvenile oceanic skipjack (*Katsuwonus pelamis*) from Hawaiian waters and sierra mackerel (*Scomberomorus sierra*) from the eastern Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 51:245-250.

EGGLESTON, D., and L. J. PAUL.

1978. Satellites, sea temperatures, and skipjack. *In* G. V. Habib and P. E. Roberts (compilers), Proceedings of the Pelagic Fisheries Conference, July 1977, p. 75-84. [New Zealand.] Minist. Agric. Fish., Fish. Res. Div., Occas. Publ. 15.

EHRENBAUM, E.

1936. Naturgeschichte und wirtschaftliche bedeutung der seefische Nordeuropas. *In* H. Lubbert and E. Ehrenbaum (editors), Handbuch der seefischerei Nordeuropas, Band Stuttgart 2, 337 p.

EIGENMANN, C. H., and R. S. EIGENMANN.

1891. Additions to the fauna of San Diego. Proc. Calif. Acad. Sci. Ser. 2, 3:1-24.

EVANS, R. H.

1977. Remote sensing: With applications to the exploitation and management of Atlantic tuna stocks. [In Engl., Fr. and Span. resume.] Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1976) 6:31-49.

EVERMANN, B. W., and A. SEALE.

1907. Fishes of the Philippine Islands. Bull. U.S. Bur. Fish. 26(1906): 49-110.

FAO.

1968. Yearbook of fishery statistics, catches and landings, 1967. FAO Yearb. Fish. Stat. 24:c46-c48.

1971. Yearbook of fishery statistics, catches and landings, 1970. FAO Yearb. Fish. Stat. 30:331-332.

1973. Yearbook of fishery statistics, catches and landings, 1972. FAO Yearb. Fish. Stat. 34:384-406.

1974a. Local tuna fishery, Suva, Fiji. Livebait pole-and-line fishing for tuna (based on work of R. E. K. D. Lee). FAO, Rome, FI:DP/FIJ/70/504, Tech. Rep. 1, 89 p.

1974b. Yearbook of fishery statistics, catches and landings, 1973. FAO Yearb. Fish. Stat. 36:412-434.

1975. Yearbook of fishery statistics, catches and landings, 1974. FAO Yearb. Fish. Stat. 38:130-131.

1976. Yearbook of fishery statistics, catches and landings, 1975. FAO Yearb. Fish. Stat. 40:131-132.

1977. Yearbook of fishery statistics, catches and landings, 1976. FAO Yearb. Fish. Stat. 42:94-95.

1978. Yearbook of fishery statistics, catches and landings, 1977. FAO Yearb. Fish. Stat. 44:102-103.

1979. Yearbook of fishery statistics, catches and landings, 1978. FAO Yearb. Fish. Stat. 46:120-121.

1980. Yearbook of fishery statistics, catches and landings, 1979. FAO Yearb. Fish. Stat. 48:155-156.

FIERSTINE, H. L., and V. WALTERS.

1968. Studies in locomotion and anatomy of scombroid fishes. Mem. South. Calif. Acad. Sci. 6, 31 p.

FINK, B. D.

1965. Estimations, from tagging experiments, of mortality rates and other parameters respecting yellowfin and skipjack tuna. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 10:1-82.

FINK, B. D., and W. H. BAYLIFF.

1970. Migrations of yellowfin and skipjack tuna in the eastern Pacific Ocean as determined by tagging experiments, 1952-1964. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 15:1-227.

FONTENEAU, A., and P. CAYRE.

1980. Analyse de l'état des stocks d'albacore (*Thunnus albacares*) et de listao (*Katsuwonus pelamis*) de l'Atlantique est au 30 septembre 1979. (Analysis of the status of yellowfin and skipjack stocks (*Thunnus albacares* and *Katsuwonus pelamis*) in the eastern Atlantic in September 1979.) [In Fr., Engl. summ.] Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1979) 9:230-244.

FORSBERGH, E. D.

1969. On the climatology, oceanography and fisheries of the Panama Bight. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 14:49-385.

1980. Synopsis of biological data on the skipjack tuna, *Katsuwonus pelamis* (Linnaeus, 1758), in the Pacific Ocean. *In* W. H. Bayliff (editor), Synopsis of biological data on eight species of scombrids, p. 295-360. Inter-Am. Trop. Tuna Comm., Spec. Rep. 2.

FOURMANOIR, P.

1957. Poissons teleosteens des eaux malgaches du Canal de Mozambique. Mém. Inst. Rech. Sci. Madagascar, Ser. F, Oceanogr. 1:1-316.

FOWLER, H. W.

1928. Fishes of Oceania. Mem. Bernice P. Bishop Mus. 10, 540 p.

1938. The fishes of the George Vanderbilt South Pacific Expedition, 1937. Acad. Nat. Sci. Phila. Monogr. 2, 349 p.

1945. Los peces del Peru. [In Span.] Mus. Hist. Nat. "Javier Prado," Lima, 289 p.

1949. The fishes of Oceania—Supplement 3. Mem. Bernice P. Bishop Mus. 12:37-186.

FRADE, F., and F. de BUEN.

1932. Poissons Scombriformes (excepté la Famille *Scombridae*). Clef de classification principalement d'après la morphologie interne. Comm. Int. Explor. Sci. Mer Méditerr., Monaco, Rapp. P.-V. Réun. 7:69-70.

FRADE, F., and E. POSTEL.

1955. Contribution à l'étude de la reproduction des scombridés et thonidés de l'Atlantique tropical. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 137:33-35.

FRASER-BRUNNER, A.

1950. The fishes of the family Scombridae. Ann. Mag. Nat. Hist., Ser. 12, 3:131-163.

FUJINO, K.

1967. Review of subpopulation studies on skipjack tuna. Proc. 47 Annu. Conf. West. Assoc. State Game Fish Comm., Honolulu, Hawaii, July 16-20, 1967, p. 349-371.

1969. Atlantic skipjack tuna genetically distinct from Pacific specimens. Copeia 1969:626-629.

1970a. Immunological and biochemical genetics of tunas. Trans. Am. Fish. Soc. 99:152-178.

1970b. Skipjack tuna subpopulation identified by genetic characteristics in the western Pacific. *In* J. C. Marr (editor), The Kuroshio. A symposium on the Japan Current, p. 385-393. East-West Center Press, Honolulu.

1971. Genetic markers in skipjack tuna from the Pacific and Atlantic *Oceans. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 161:15-18.*

1972. Range of the skipjack tuna subpopulation in the western Pacific Ocean. *In* K. Sugawara (editor), Proceedings of the Second Symposium on the Results of the Cooperative Study of the Kuroshio and Adjacent Regions, The Kuroshio II, Tokyo, Japan, September 28-October 1, 1970, p. 373-384. Saikon Publ. Co., Ltd., Tokyo.

1976. Subpopulation identification of skipjack tuna specimens from the southwestern Pacific Ocean. [In Engl.] Bull. Jpn. Soc. Sci. Fish. 42:1229-1235.

1980. Genetic isolation of skipjack tuna in the western Pacific Ocean. *In* Symposium for the Co-operative Study of the Kuroshio and Adjacent Regions. Proceedings of the Symposium for the Co-operative Study of the Kuroshio and Adjacent Regions, The Kuroshio IV, Tokyo, 14-17 February 1979, p. 732-742. Saikon Publ. Co., Tokyo.

FUJINO, K., and T. KANG.

1968a. Serum esterase groups of Pacific and Atlantic tunas. Copeia 1968:56-63.

1968b. Transferrin groups of tunas. Genetics 59:79-91.

FUJINO, K., and T. K. KAZAMA.

1968. The Y system of skipjack tuna blood groups. Vox Sang. 14:383-395.

GIBBS, R. H., Jr., and B. B. COLLETTE.

1967. Comparative anatomy and systematics of the tunas, genus *Thunnus*. U.S. Fish Wildl. Serv., Fish. Bull. 66:65-130.

GMELIN, J. F.

1788. Pisces. *In* C. Linne, Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis 1(3):1126-1516.

GODSIL, H. C.

1938. The high seas tuna fishery of California. Calif. Div. Fish Game, Fish Bull. 51, 41 p.

1954. A descriptive study of certain tuna-like fishes. Calif. Dep. Fish Game, Fish Bull. 97, 185 p.

GODSIL, H. C., and R. D. BYERS.

1944. A systematic study of the Pacific tunas. Calif. Div. Fish Game, Fish Bull. 60, 131 p.

GOODE, G. B. (editor).

1884. The fisheries and fishery industries of the United States. Sect. 1, Natural history of useful aquatic animals. Part 3: The food fishes of the United States, p. 163-682. U.S. Gov. Print. Off., Wash., D.C.

GOODE, G. B., and T. H. BEAN.

1879. The oceanic bonito on the coast of the United States. Proc. U.S. Natl. Mus. 1:24-26.

GOODING, R. M., and J. J. MAGNUSON.

1967. Ecological significance of a drifting object to pelagic fishes. Pac. Sci. *21*:486-497.

GOODING, R. M., W. H. NEILL, and A. E. DIZON.

1981. Respiration rates and low-oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis*. Fish. Bull., U.S. 79:31-48.

GOPALAKRISHNAN, V.
1979. Status and problems of culture of baitfish for the skipjack fishery in the Pacific region. *In* T. V. R. Pillay and W. A. Dill (editors), Advances in aquaculture, p. 58-62. FAO Technical Conference on Aquaculture, Kyoto, Japan, 26 May—2 June 1976. Fish. News (Books), Farnham, Engl.

GORBUNOVA, N. N.
1963. Larvae of scombroid fishes (Pisces, Scombriformes) from the Indian Ocean. [In Russ., Engl. summ.] Tr. Inst. Okeanol. Akad. Nauk SSSR 62:68-95. [Engl. transl. available, U.S. Dep. Commer., Off. Tech. Serv., Wash., D.C.]
1965a. On the distribution of scombroid larvae (Pisces, Scombroidei) in the eastern part of the Indian Ocean. [In Russ., Engl. summ.] Tr. Inst. Okeanol. Akad. Nauk SSSR 80:32-35.
1965b. Seasons and conditions of spawning of the scombroid fishes (Pisces, Scombroidei). [In Russ., Engl. summ.] Tr. Inst. Okeanol. Akad. Nauk SSSR 80:36-61. [Engl. transl. available, U.S. Dep. Commer., Off. Tech. Serv., Wash., D.C.]

GORBUNOVA, N. N., and D. SALABARRÍA.
1967. Reproduccion de los peces del suborden Scombroidei (Pisces, Scombroidei) en las regiones occidentales del Atlantico. [In Russ., Span. summ.] (Reproduction of scombroids (Pisces, Scombroidei) in western regions of the Atlantic.) *In* Soviet-Cuban Fish. Invest., VNIRO, Moscow 2:120-131. [Engl. transl. by W. L. Klawe, 1968, 24 p.; Inter-Am. Trop. Tuna Comm., La Jolla, Calif.]

GORDON, M. S.
1968. Oxygen consumption of red and white muscles from tuna fishes. Science (Wash., D.C.) 159:87-90.

GOSLINE, W. A., and V. E. BROCK.
1960. Handbook of Hawaiian fishes. Univ. Hawaii Press, Honolulu, 372 p.

GRAHAM, J. B.
1975. Heat exchange in the yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*, and the adaptive significance of elevated body temperatures in scombrid fishes. Fish. Bull., U.S. 73:219-229.

GREEN, R. E.
1967. Relationship of the thermocline to success of purse seining for tuna. Trans. Am. Fish. Soc. 96:126-130.

GREEN, R. E., W. F. PERRIN, and B. P. PETRICH.
1971. The American tuna purse seine fishery. *In* H. Kristjonsson (editor), Modern fishing gear of the world: 3, p. 182-194. Fish. News (Books), Lond.

GREENBLATT, P. R.
1979. Associations of tuna with flotsam in the eastern tropical Pacific. Fish. Bull., U.S. 77:147-155.

GUDGER, E. W.
1941. The food and feeding habits of the whale shark, *Rhinaodon typus*. J. Elisha Mitchell Sci. Soc. 57:57-72.

GÜNTHER, A.
1860. Catalogue of the acanthopterygian fishes in the collection of the British Museum. Vol. 2, 548 p. Taylor and Francis, Lond.
1876. Die Fische der Südsee. J. Mus. Godeffroy 2(11), 257 p.

HABIB, G.
1976. The 1975-76 purse seine skipjack fishery. *In* Proceedings of the Skipjack Tuna Conference, July 1976, p. 40-46. [New Zealand.] Minist. Agric. Fish., Fish. Res. Div., Occas. Publ. 11.
1978. Skipjack biology and the 1976-77 purse-seine fishery. *In* G. V. Habib and P. E. Roberts (compilors), Proceedings of the Pelagic Fisheries Conference, July 1977, p. 17-26. [New Zealand.] Minist. Agric. Fish., Fish. Res. Div., Occas. Publ. 15.

HABIB, G., I. T. CLEMENT, and K. A. FISHER.
1980a. The 1977-78 purse-seine skipjack fishery in New Zealand waters. [New Zealand.] Minist. Agric. Fish., Fish. Res. Div., Occas. Publ. 25, 42 p.
1980b. The 1978-79 purse seine skipjack fishery in New Zealand waters. [New Zealand.] Minist. Agric. Fish., Fish. Res. Div., Occas. Publ. 26, 39 p.
1980c. The 1979-80 purse-seine skipjack fishery in New Zealand waters. [New Zealand.] Minist. Agric. Fish., Fish. Res. Div., Occas. Publ. 29, 42 p.

HARADA, T., K. MIZUNO, O. MURATA, S. MIYASHITA, and H. HURUTANI.
1971. On the artificial fertilization and rearing of larvae in yellowfin tuna. [In Jpn., Engl. synop.] Mem. Fac. Agric. Kinki Univ. 4:145-151.

HARADA, T., O. MURATA, and H. FURUTANI.
1973. On the artificial fertilization and rearing of larvae in marusoda, *Auxis tapeinosoma*. [In Jpn., Engl. synop.] Mem. Fac. Agric. Kinki Univ. 6:113-116.

HARADA, T., O. MURATA, and S. MIYASHITA.
1973. On the artificial fertilization and rearing of larvae in hirasoda, *Auxis thazard*. [In Jpn., Engl. synop.] Mem. Fac. Agric. Kinki Univ. 6:109-112.

HARDENBERG, J. D. F.
1950. Development of pelagic fisheries. Proc. Indo-Pac. Fish. Counc. 1949:138-143.

HARDING, J. P.
1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. Biol. Assoc. U.K. 28:141-153.

HAYASI, S.
1974. A comment on the skipjack stock in the Atlantic Ocean. Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1973) 2:134-140.

HENNEMUTH, R. C.
1959. Additional information on the length-weight relationship of skipjack tuna from the eastern tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 4:25-37.

HERRE, A. W.
1932. A check list of fishes recorded from Tahiti. J. Pan-Pac. Res. Inst. 7(1):2-6.
1933. A check list of fishes from Dumaguete, Oriental Negros, P. I., and its immediate vicinity. J. Pan-Pac. Res. Inst. 8(4):6-11.
1953. Check list of Philippine fishes. U.S. Fish Wildl. Serv., Res. Rep. 20, 977 p.

HERRE, A. W., and A. F. UMALI.
1948. English and local common names of Philippine fishes. U.S. Fish Wildl. Serv., Circ. 14, 128 p.

HIGGINS, B. E.
1966. Sizes of albacore and bigeye, yellowfin, and skipjack tunas in the major fisheries of the Pacific Ocean. *In* T. A. Manar (editor), Proceedings of the Governor's Conference on Central Pacific Fishery Resources, p. 169-195. State of Hawaii, Honolulu.
1967. The distribution of juveniles of four species of tunas in the Pacific Ocean. Proc. Indo-Pac. Fish. Counc. 12(Sect. 2):79-99.
1970. Juvenile tunas collected by midwater trawling in Hawaiian waters, July-September 1967. Trans. Am. Fish. Soc. 99:60-69.

HILDEBRAND, S. F.
1946. A descriptive catalog of the shore fishes of Peru. U.S. Natl. Mus. Bull. 189, 530 p.

HOCHACHKA, P. W., W. C. HULBERT, and M. GUPPY.
1978. The tuna power plant and furnace. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 153-174. Acad. Press, N.Y.

HOEK, P. P. C.
1904. Catalogue des poissons du nord de l'Europe, avec les noms vulgaires dont on se sert dans les langues de cette region. Cons. Explor. Mer, Publ. Circum. 12:1-76.

HONMA, M., and Z. SUZUKI.
1978. Japanese tuna purse seine fishery in the western Pacific. [In Jpn., Engl. summ.] Far Seas Fish. Res. Lab., S Ser. 10, 66 p.

HORNELL, J.
1935. Report on the fisheries of Palestine. Crown Agents Colonies, Lond., 106 p.

HOTTA, H.
1953. On the distribution of young of skipjack, *Katsuwonus pelamis* in the southern seas of Kyushu. [In Jpn., Engl. abstr.] Bull. Tohoku Reg. Fish. Res. Lab. 2:19-21.

HOTTA, H., T. KARIYA, and T. OGAWA.
1959. A study on the "biting" of skipjack in the live-bait fishery. Part 1. Relation between the "biting" and the alimental canal in the Tohoku Sea area. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 13:60-78.

HOTTA, H., and T. OGAWA.
1955. On the stomach contents of the skipjack, *Katsuwonus pelamis*. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 4:62-82.

HU, F., and R.-T. YANG.
1972. A preliminary study on sexual maturity and fecundity of skipjack tuna. [In Engl., Chin. abstr.] J. Fish. Soc. Taiwan 1:88-98.

HUNTER, J. R., and C. T. MITCHELL.
1967. Association of fishes with flotsam in the offshore waters of Central America. U.S. Fish Wildl. Serv., Fish. Bull. 66:13-29.

IGETA, Y., K. YOSHIDA, R. AMANO, M. IWASHITA, and C. MIYAZAKI.
1978. Manufactured and angling test of automatic circulating angling

machine for skipjack. [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 44:331-340.

IMAMURA, Y.

1949. The skipjack fishery. [In Jpn.] *In* Suisan Kōza, The text of the fishery. Jpn. Fish. Assoc. Vol. 6, Fishing Section, p. 17-94. [Engl. transl. by W. G. Van Campen, 1951. The Japanese skipjack fishery. *In* U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 49, 67 p.]

INOUE, M.

1959. On the relation of behaviours of skipjack and tuna shoals to their catch inferred from the data for seine fishery. [In. Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 25:12-16.

1966. Automation of skipjack and tuna fishing by the use of the lift system. [In Jpn.] Tuna Fishing 51:24-25. [Engl. transl. by J. Isa, 1966, 4 p.; U.S. Civil Admin., Ryukyu Is., for Bur. Commer. Fish. Biol. Lab., Honolulu.]

INOUE, M., R. AMANO, and Y. IWASAKI.

1963. Studies on environments alluring skipjack and other tunas—I. On the oceanographical condition of Japan adjacent waters and the drifting substances accompanied by skipjack and other tunas. [In Jpn., Engl. summ.] Rep. Fish. Res. Lab., Tokai Univ. 1:12-23.

INOUE, M., R. AMANO, Y. IWASAKI, and M. YAMAUTI.

1968a. Studies on environments alluring skipjack and other tunas—II. On the driftwoods accompanied by skipjack and tunas. Bull. Jpn. Soc. Sci. Fish. 34:283-287.

1968b. Studies on environments alluring skipjack and other tunas—III. Tagging experiments on the experimental driftwoods as part of ecological study of tunas. Bull. Jpn. Soc. Sci. Fish. 34:288-294.

INTER-AMERICAN TROPICAL TUNA COMMISSION.

1972. Bi-Monthly report, May-June 1972. Inter-Am. Trop. Tuna Comm., La Jolla, Calif., 16 p.

1973. Bi-Monthly report, January-February 1973. Inter-Am. Trop. Tuna Comm., La Jolla, Calif., 22 p.

1980. Annual report of the Inter-American Tropical Tuna Commission 1979. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., La Jolla, Calif., 227 p.

ISHIDA, R.

1975. Skipjack tuna fishery and fishing grounds (Katsuo gyogyō to gyojyō). *From* Reports pertaining to effects of ocean disposal of solid radioactive wastes on living marine resources (Hōshasei kotai haiki butsu no kaiyō shobun ni tomonau kaisan seibutsu tō ni kansuru chosa hokokusho). [In Jpn.] Jpn. Fish. Agency, Tokai Reg. Fish. Res. Lab., Tohoku Reg. Fish. Res. Lab., and Far Seas Fish. Res. Lab., p. 88-92. [Engl. transl. by T. Otsu, 1975, 10 p., transl. no. 12; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

ISHIYAMA, R., and K. OKADA.

1957. Postlarval form of the skipjack (*Katsuwonus pelamis*) from the Phoenix Islands. [In Jpn., Engl. summ.] J. Shimonoseki Coll. Fish. 7:141-146.

IVERSEN, E. S., and H. O. YOSHIDA.

1957. Notes on the biology of the wahoo in the Line Islands. Pac. Sci. 11:370-379.

IVERSEN, R. T. B.

1969. Auditory thresholds of the scombrid fish *Euthynnus affinis*, with comments on the use of sound in tuna fishing. FAO Fish. Rep. 62(3): 849-859.

IVERSEN, R. T. B., E. L. NAKAMURA, and R. M. GOODING.

1970. Courting behavior in skipjack tuna, *Katsuwonus pelamis*. Trans. Am. Fish. Soc. 99:93.

IWASAKI, Y.

1970. Recent status of pole-and-line fishing in southern waters. From abstract II-(1), p. 8-12 of a paper presented at Symp. 1, Japan Tuna Fishery Research Conference, February 1970, compiled by the Far Seas Fish. Res. Lab., Shimizu. [Engl. transl. by T. Otsu, 1970, 8 p.; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

1976. Study on the shoals of skipjack by body size compositions. [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 42:543-548.

1980. A study on the body size composition of yellowfin tuna and skipjack shoals caught by purse seines. [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 46:19-25.

IWASAKI, Y., and T. SUZUKI.

1972. On the distribution of skipjack shoals viewed from fishing vessel reports and echo-sounder records and diurnal change of swimming layer of skipjack in the western tropical Pacific Ocean. [In Jpn., Engl. abstr.] J. Faculty Mar. Sci. Technol., Tokai Univ. 6:95-104.

IWASHITA, M., M. INOUE, Y. IGETA, K. YOSHIDA, R. AMANO, and K. KODAMA.

1967. Mechanization of pole-and-line fishing for skipjack—I. Fabrication and testing of the SFM No. 1. [In Jpn., Engl. summ.] J. Faculty Mar. Sci. Technol., Tokai Univ. 2:211-219.

[JAPAN.] FISHERIES AGENCY OF, RESEARCH DIVISION.

1967a. Annual report of effort and catch statistics by area on Japanese tuna longline fishery, 1964. Fish. Agency Jpn., Res. Div., 379 p.

1967b. Annual report of effort and catch statistics by area on Japanese tuna longline fishery, 1965. Fish. Agency Jpn., Res. Div., 375 p.

1968. Annual report of effort and catch statistics by area on Japanese tuna longline fishery, 1966. Fish. Agency Jpn., Res. Div., 299 p.

1969. Annual report of effort and catch statistics by area on Japanese tuna longline fishery, 1967. Fish. Agency Jpn., Res. Div., 293 p.

1971. Annual report of effort and catch statistics by area on Japanese tuna longline fishery, 1969. Fish. Agency Jpn., Res. Div., 299 p.

1972. Annual report of effort and catch statistics by area on Japanese tuna longline fishery, 1970. Fish Agency Jpn., Res. Div., 326 p.

1973. Annual report of effort and catch statistics by area on Japanese tuna longline fishery, 1971. Fish. Agency Jpn., Res. Div., 319 p.

1979a. Annual report of effort and catch statistics by area on Japanese tuna longline fishery, 1977. Fish. Agency Jpn., Res. Div., 235 p.

1979b. Annual report of effort and catch statistics by area. Japanese skipjack baitboat fishery, 1977. Fish. Agency Jpn., Res. Div., 333 p.

1980a. Annual report of effort and catch statistics by area on Japanese tuna longline fishery, 1978. Fish. Agency Jpn., Res. Div., 241 p.

1980b. Annual report of effort and catch statistics by area. Japanese skipjack baitboat fishery, 1978. Fish. Agency Jpn., Res. Div., 287 p.

1981. Annual report of effort and catch statistics by area on Japanese tuna longline fishery, 1979. Fish. Agency Jpn., Res. Div., 243 p.

JENKINS, O. P.

1904. Report on collections of fishes made in the Hawaiian Islands, with descriptions of new species. Bull. U.S. Fish Comm. 22(1902):417-511.

JONES, S.

1959. Notes on eggs, larvae and juveniles of fishes from Indian waters. III. *Katsuwonus pelamis* (Linnaeus) and IV. *Neothunnus macropterus* (Temminck and Schlegel). Indian J. Fish. 6:360-373.

JONES, S., and M. KUMARAN.

1963. Distribution of larval tuna collected by the Carlsberg Foundation's *Dana* Expedition (1928-30) from the Indian Ocean. [In Engl., Fr. résumé.] FAO Fish. Rep. 6(3):1753-1774.

JONES, S., and E. G. SILAS.

1960. Indian tunas—A preliminary review, with a key for their identification. Indian J. Fish. 7:369-393.

1963. Synopsis of biological data on skipjack *Katsuwonus pelamis* (Linnaeus) 1758 (Indian Ocean). FAO Fish. Rep. 6(2):663-694.

1964. A systematic review of the scombroid fishes of India. *In* Proceedings of the Symposium on Scombroid Fishes, p. 1-105. Mar. Biol. Assoc. India, Symp. Ser. 1.

JORDAN, D. S.

1907. Fishes. Am. Nat. Ser. Gp. I. Holt and Co., N.Y., 789 p., 18 pls., 673 illus.

JORDAN, D. S., and B. W. EVERMANN.

1898. The fishes of north and middle America. Bull. U.S. Natl. Mus. 47:2183-3136.

JORDAN, D. S., B. W. EVERMANN, and H. W. CLARK.

1930. Check list of the fishes and fishlike vertebrates of north and middle America north of the northern boundary of Venezuela and Colombia. Rep. U.S. Comm. Fish. 2(1928), 670 p.

JORDAN, D. S., and C. H. GILBERT.

1882. Synopsis of the fishes of North America. Bull. U.S. Natl. Mus. 16, 1018 p.

JORDAN, D. S., and C. L. HUBBS.

1925. Record of fishes obtained by David Starr Jordan in Japan, 1922. Mem. Carnegie Mus. 10:93-346.

JORDAN, D. S., and E. K. JORDAN.

1922. A list of the fishes of Hawaii, with notes and descriptions of new species. Mem. Carnegie Mus. 10:1-92.

JOSEPH, J.

1963. Fecundity of yellowfin tuna (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) from the Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 7:257-292.

JOSEPH, J., and T. P. CALKINS.

1969. Population dynamics of the skipjack tuna (*Katsuwonus pelamis*) of the eastern Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 13:1-273.

JOSSE, E., J. C. Le GUEN, R. KEARNEY, A. LEWIS, A. SMITH, L. MAREC, and P. K. TOMLINSON.

1979. Growth of skipjack. South Pac. Comm., Occas. Pap. 11, 83 p.

JOUBIN, L., and E. Le DANOIS.

1924. Catalogue illustré des animaux marins comestibles des côtes de France et des mers limitrophes avec leurs noms communs francais et êtrangers. Mém. Off. Sci. Tech. Pech. Marit., Sér. Spéc., Pt. 1, 220 p.

JUÁREZ, M.

1974. ¿Dónde desova el atun? Mar Pesca 106:44-47.

KAMOHARA, T.

1941. Scombroidei (exclusive of Carangiformes). [In Jpn.] Fauna Nipponica 15-2(5), 125 p. + 102 figs.

KASAHARA, K.

1968. A look at the skipjack fishery and its future. [In Jpn.] Bull. Jpn. Soc. Fish. Oceanogr. 13:127-132. [Engl. transl. by T. Otsu, 1969, 9 p.; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

1971. Skipjack tuna resource and fishing grounds. Suisan Sekai 20(10): 30-37. [Engl. transl. by T. Otsu, 1972, 20 p.; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

1975. Nanpo katsuo gyogyo—sono shigen to gijitsu. [Existing state and trend of skipjack resources in the exploited areas.] [In Jpn.] *In* Jpn. Soc. Sci. Fish. (compiler), Skipjack fishery in the southern fishing ground. Its resources and technique. Fish. Sci. Ser., Tokyo 11:7-29.

1977. The trends in the southern water skipjack tuna fishery (Nanpo katsuo gyogyō no dōkō). [In Jpn.] Suisan Sekai 26(3):28-33. [Engl. transl. by T. Otsu, 1977, 15 p., transl. no. 24; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

KASAHARA, K., and T. TANAKA.

1968. On the fishing and the catches of skipjack tuna (*Katsuwonus pelamis*) in the southern waters. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 28:117-136.

KAWAMURA, G., W. NISHIMURA, S. UEDA, and T. NISHI.

1981. Color vision and spectral sensitivity in tunas and marlins. Bull. Jpn. Soc. Sci. Fish. 47:481-485.

KAWASAKI, T.

1952. On the populations of the skipjack, *Katsuwonus pelamis* (Linnaeus), migrating to the north-eastern sea area along the Pacific coast of Japan. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 1:1-14.

1955a. On the migration and the growth of the skipjack, *Katsuwonus pelamis* (Linnaeus), in the south-western sea area of Japan. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 4:83-100.

1955b. On the migration and the growth of the skipjack, *Katsuwonus pelamis* (Linnaeus), in the Izu and Bonin Sea areas and the north-eastern sea area along the Pacific coast of Japan. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 4:101-119.

1958. On the fluctuation of the fisheries conditions in the livebait fishery of skipjack in waters adjacent to Japan. II. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 11:65-81.

1959. On the structure of "fish school" of tunas. [In Jpn., Engl. abstr.] Jpn. J. Ecol. 9:52-54.

1963. The growth of skipjack on the northeastern Sea of Japan. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 23:44-60.

1964. Population structure and dynamics of skipjack in the North Pacific and its adjacent waters. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 24:28-47.

1965a. Ecology and dynamics of the skipjack population. I. Classification, distribution and ecology. [In Jpn.] Jpn. Fish. Resour. Prot. Assoc., Stud. Ser. 8:1-48. [Engl. transl. by M. P. Miyake, 1967, 54 p.; Inter-Am. Trop. Tuna Comm., La Jolla, Calif.]

1965b. Ecology and dynamics of the skipjack population. II. Resources and fishing conditions. [In Jpn.] Jpn. Fish. Resour. Prot. Assoc., Stud. Ser. 8:49-108. [Engl. transl. 1967, 79 p.; U.S. Joint Publ. Res. Serv.]

1972. The skipjack tuna resource (Katsuo no shigen ni tsuite). [In Jpn.] Suisan Shuho (The Fishing and Food Industry Weekly) 660:32-38, July 15, 1972. [Engl. transl. 1973, *In* U.S. Dep. Commer., Mar. Fish. Rev. 35(5-6):1-7.]

KAYA, C. M., A. E. DIZON, S. D. HENDRIX, T. K. KAZAMA, and M. K. K. QUEENTH.

1982. Rapid and spontaneous maturation, ovulation, and spawning of ova by newly captured skipjack tuna, *Katsuwonus pelamis*. Fish. Bull., U.S. 80:393-396.

KEARNEY, R. E.

1975. The stock structure of skipjack resources and the possible implications on the development of skipjack fisheries in the central and western Pacific. *In* Studies on skipjack in the Pacific, p. 59-69. FAO Fish. Tech. Pap. 144.

1978. Some hypotheses on skipjack (*Katsuwonus pelamis*) in the Pacific Ocean. South Pac. Comm., Occas. Pap. 7, 23 p.

1979. An overview of recent changes in the fisheries for highly migratory species in the western Pacific Ocean and projections for future developments. South Pac. Bur. Econ. Co-op., SPEC (79)17, 99 p.

KEARNEY, R. E., and R. D. GILLETT.

1978. Interim report of the activities of the Skipjack Survey and Assessment Programme in the waters of the Gilbert Islands (5 - 25 July 1978). South Pac. Comm., Skipjack Surv. Assess. Programme, Prelim. Country Rep. 11, 11 p.

1979. Interim report of the activities of the Skipjack Survey and Assessment Programme in the waters of Australia (1 April - 13 May 1979). South Pac. Comm., Skipjack Surv. Assess. Programme, Prelim. Country Rep. 17, 15 p.

KEARNEY, R. E., and J.-P. HALLIER.

1978a. Interim report of the activities of the Skipjack Survey and Assessment Programme in the waters of New Caledonia (13 December 1977-19 January 1978). South Pac. Comm., Skipjack Surv. Assess. Programme, Prelim. Country Rep. 3, 20 p.

1978b. Interim report of the activities of the Skipjack Survey and Assessment Programme in the waters of Western Samoa (6 - 14 June 1978). South Pac. Comm., Skipjack Surv. Assess. Programme, Prelim. Country Rep. 8, 10 p.

1978c. Interim report of the activities of the Skipjack Survey and Assessment Programme in the waters of American Samoa (31 May - 5 June, 15 - 21 June 1978). South Pac. Comm., Skipjack Surv. Assess. Programme, Prelim. Country Rep. 9, 9 p.

1979. Second interim report of the activities of the Skipjack Survey and Assessment Programme in the waters of Papua New Guinea (14 May - 2 July 1979). South Pac. Comm., Skipjack Surv. Assess. Programme, Prelim. Country Rep. 18, 14 p.

1980a. Interim report of the activities of the Skipjack Survey and Assessment Programme in the waters of Norfolk Island (26 - 30 March 1980). South Pac. Comm., Skipjack Surv. Assess. Programme, Prelim. Country Rep. 24, 9 p.

1980b. Second interim report of the activities of the Skipjack Survey and Assessment Programme in the waters of the Trust Territory of the Pacific Islands (2-21 November 1979). South Pac. Comm., Skipjack Surv. Assess. Programme, Prelim. Country Rep. 19, 14 p.

KEARNEY, R. E., J.-P. HALLIER, and P. KLEIBER.

1978. Interim report of the activities of the Skipjack Survey and Assessment Programme in the waters of Tuvalu (25 June - 4 July 1978). South Pac. Comm., Skipjack Surv. Assess. Programme, Prelim. Country Rep. 10, 9 p.

KEARNEY, R. E., A. D. LEWIS, and J.-P. HALLIER.

1978. Rapport interimaire sur les activities au titre du programme d'etude et d'evaluation des stocks de bonites dans les eaux des Nouvelles-Hebrides (5-13 décembre 1977 - 20-23 janvier 1978). [In Fr.] South Pac. Comm., Skipjack Surv. Assess. Programme, Prelim. Country Rep. 4, 18 p.

KIKAWA, S.

1953. Observations on the spawning of the big-eyed tuna (*Parathunnus mebachi* Kishinouye) near the southern Marshall Islands. [In Jpn., Engl. summ.] Contrib. Nankai Reg. Fish. Res. Lab. 1(24), 10 p.

KIKAWA, S., and N. HIGASHI.

1979. Distribution, apparent relative abundance and size composition of skipjack tuna in the Gulf of Guinea waters from Japanese surface data. Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1978) 8:189-195.

KIMURA, K.

1954. Analysis of skipjack (*Katsuwonus pelamis*) shoals in the water of "Tohoku Kaiku" by its association with other animals and objects based on the records by fishing boats. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 3, 87 p.

KIMURA, K., M. IWASHITA, and T. HATTORI.

1952. Image of skipjack and tuna recorded on echo sounding machine. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 1:15-19.

KING, J. E., and I. I. IKEHARA.

1956. Comparative study of food of bigeye and yellowfin tuna in the central Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 57:61-85.

KISHINOUYE, K.

1915. A study of the mackerels, cybiids, and tunas. Suisan Gakkai Hō 1(1):1-24. [Engl. transl. by W. G. Van Campen, 1950. *In* U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 24, 14 p.]

1917. A new order of the Teleostomi. Suisan Gakkai Hō 2(2):1-4. [Engl. transl. by W. G. Van Campen, 1951. *In* U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 50:1-3.]

1923. Contributions to the comparative study of the so-called scombroid fishes. J. Coll. Agric., Imp. Univ., Tokyo 8:293-475.

1926. An outline of studies of the Plecostei (tuna and skipjack) in 1925. Suisan Gakkai Hō 4(3):125-137. [Engl. transl. by W. G. Van Campen, 1950. *In* U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 19:1-8.]

KITCHELL, J. F., J. J. MAGNUSON, and W. H. NEILL.

1977. Estimation of caloric content for fish biomass. Environ. Biol. Fishes 2:185-188.

KITCHELL, J. F., W. H. NEILL, A. E. DIZON, and J. J. MAGNUSON.

1978. Bioenergetic spectra of skipjack and yellowfin tunas. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 357-368. Acad. Press, N.Y.

KLAWE, W. L.

1960. Larval tunas from the Florida Current. Bull. Mar. Sci. Gulf Caribb. 10:227-233.

1963. Observations on the spawning of four species of tuna (*Neothunnus macropterus*, *Katsuwonus pelamis*, *Auxis thazard* and *Euthynnus lineatus*) in the eastern Pacific Ocean, based on the distribution of their larvae and juveniles. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 6:449-540.

1977. What is a tuna? Mar. Fish. Rev. 39(11):1-5.

KOGA, S.

1958. On the difference of the stomach contents of tuna and black marlin in the south equatorial Pacific Ocean. [In Jpn., Engl. summ.] Bull. Fac. Fish. Nagasaki Univ. 7:31-39. [Engl. transl. by G. Y. Beard, 1960, 12 p.; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

KOJIMA, S.

1956. Fishing for dolphins in the western part of the Japan Sea—II. Why do the fish take shelter under floating materials? [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 21:1049-1052. [Engl. transl. by W. G. Van Campen, 1962, 7 p.; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

1960. Fishing for dolphins in the western part of the Japan Sea—V. Species of fishes attracted to bamboo rafts. [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 26:379-382. [Engl. transl. by W. G. Van Campen, 1962, 4 p.; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

KUME, S.

1977. Some biological information on skipjack caught by Japanese longline fishery in the Atlantic Ocean. Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1976) 6:75-78.

1978. Change in catch per unit of effort for skipjack and yellowfin tuna caught by Japanese pole-and-line fishery in Gulf of Guinea, 1969-1976. Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1977) 7:21-23.

KURODA, R.

1955. On the water temperature in the fishing grounds of the skipjack, *Katsuwonus pelamis* (Linnaeus), caught in the north-eastern sea area along the Pacific coast of Japan. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 4:47-61.

LACÉPÈDE, B. G. E.

1802. Histoire naturelle des poissons. Paris, Plassan 3, 558 p.

LAEVASTU, T., and H. ROSA, Jr.

1963. Distribution and relative abundance of tunas in relation to their environment. FAO Fish. Rep. 6(3):1835-1851.

La MONTE, F.

1945. North American game fishes. Doubleday, Doran and Co., Garden City, N.Y., 202 p.

LASKER, R.

1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.

1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 173: 212-230.

1981. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: Contrasting years, 1975 through 1978. Rapp. P.-V. Réun. Cons. Int. Eplor. Mer 178:375-388.

Le GALL, J.

1934. *Katsuwonus pelamis.* J. Cons. Cons. Perm. Int. Explor. Mer. *In* Faun. Ichthyol. Atl. Nord. 15.

LEGAND, M.

1971. Données sur la bonite a ventre rayé dans le sud-ouest Pacifique. [In Fr., Engl. abstr.] Cah. O.R.S.T.O.M., Sér. Oceanogr. 9:403-409.

LENARZ, W. H.

1974. Length-weight relations for five eastern tropical Atlantic scombrids. Fish. Bull., U.S. 72:848-851.

LESSON, R. P.

1828. Description du nouveau genre *Ichthyophis* et de plusieurs espèces inédites ou peu connues de poissons, . . . recueillis dans le voyage autour du monde de "La Coquille." Mém. Soc. Hist. Nat. Paris 4:397-412.

1830. Les poissons. *In* L. I. Duperry (editor), Voyage autour du monde exécute sur la corvette "La Coquille," pendant les années 1822-25, chapter 10, vol. 2:66-238.

LEWIS, A. D.

1980. Tagging of skipjack tuna (*Katsuwonus pelamis*) in Papua New Guinea waters, 1973-1974. Papua New Guinea, Dep. Prim. Ind. Res. Bull. 26, 31 p. + 3 append.

LINNAEUS, C.

1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tom. I (Regnum animale), 10th ed. Holmiae. Lithoprinted, 1956. Br. Mus. Nat. Hist., 824 p.

LIVING MARINE RESOURCES.

1977. Pacific Tuna Development Foundation final report. Tuna purse-seine charter to the western Pacific, July-November 1976. Living Marine Resources (San Diego), 14 p. + 17 tables.

LOVE, C. M. (editor).

1970. EASTROPAC Atlas, Vol. 4. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Circ. 330, viii + 12 p. + figs.

1971. EASTROPAC Atlas, Vol. 2. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Circ. 330, vii + figs.

1972. EASTROPAC Atlas, Vol. 6. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Circ. 330, vi + figs.

1974. EASTROPAC Atlas, Vol. 8. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Circ. 330, vii + figs.

LOVE, M. S., and M. MOSER.

1977. Parasites of California, Oregon, and Washington marine and estuarine fishes. Univ. Calif. Santa Barbara, Mar. Sci. Inst., 530 p.

LÜTKEN, C.

1880. Spolia Atlantica. Bidrag til kundskab om formforandringer hos fiske under deres vaext og udvikling, saerligt hos nogle af Atlanterhavets Højsøfiske. K. Dansk. Vid. Selsk. Skrift., Kjobenhavn, Ser. 12:409-613.

MACLEAY, W.

1881. Descriptive catalogue of Australian fishes. Sydney 1:191-192.

MAGNUSON, J. J.

1969. Digestion and food consumption by skipjack tuna (*Katsuwonus pelamis*). Trans. Am. Fish. Soc. 98:379-392.

1973. *Comparative study of adaptations for continuous swimming and* hydrostatic equilibrium of scombroid and xiphoid fishes. Fish. Bull., U.S. 71:337-356.

1978. Locomotion by scombrid fishes: Hydromechanics, morphology, and behavior. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 7, p. 239-313. Acad. Press, N.Y.

MAGNUSON, J. J., and J. G. HEITZ.

1971. Gill raker apparatus and food selectivity among mackerels, tunas, and dolphins. Fish. Bull., U.S. 69:361-370.

MAGNUSON, J. J., and J. H. PRESCOTT.

1966. Courtship, locomotion, feeding, and miscellaneous behaviour of Pacific bonito (*Sarda chiliensis*). Anim. Behav. 14:54-67.

MAGNUSON, J. J., and D. WEININGER.

1978. Estimation of minimum sustained speed and associated body drag of scombrids. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 293-311. Acad. Press, N.Y.

MARCILLE, J., and B. STEQUERT.

1976. Etude préliminaire de la croissance du listao (*Katsuwonus pelamis*) dans l'Océan Indien tropical. (First results of the study of listao (*Katsuwonus pelamis*) in the tropical western Indian Ocean.) [In Fr., Engl. summ.] Cah. O.R.S.T.O.M., Sér. Océanogr. 14(2):139-151.

MARCILLE, J., and Z. SUZUKI.

1974. Distribution of skipjack caught by Japanese tuna longline fishery in the Indian Ocean. [In Jpn., Engl. summ.] Bull. Far Seas Fish. Res. Lab. (Shimizu) 10:87-107.

MARR, J. C.

1948. Observations on the spawning of oceanic skipjack (*Katsuwonus pelamis*) and yellowfin tuna (*Neothunnus macropterus*) in the northern Marshall Islands. U.S. Fish Wildl. Serv., Fish. Bull. 51:201-206.

MARUYAMA, T.

1980. Report on the southern water skipjack tuna fishery (Nanpō katsuo gyogyō ni kansuru repōto). [In Jpn.] Int. Manage. Assoc., Tokyo, August 20, 1980, 12 p. (unnumbered). [Engl. transl. by T. Otsu, 9 p., transl. no. 49; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

MATSUI, K.

1942. The gonads of skipjack from Palao waters. [In Jpn.] South Sea Sci. 5:117-122. [Engl. transl. by W. G. Van Campen, 1950. *In* U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 20, 6 p.]

MATSUMOTO, W. M.

1958. Description and distribution of larvae of four species of tuna in central Pacific waters. U.S. Fish Wildl. Serv., Fish. Bull. 58:31-72.

1961. Collection and descriptions of juvenile tunas from the central Pacific. Deep-Sea Res. 8:279-286.

1974. The skipjack tuna, *Katsuwonus pelamis*, an underutilized resource. Mar. Fish. Rev. 36(8):26-33.

1975. Distribution, relative abundance, and movement of skipjack tuna, *Katsuwonus pelamis*, in the Pacific Ocean based on Japanese tuna longline catches, 1964-67. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-695, 30 p.

MATSUMOTO, W. M., T. K. KAZAMA, and D. C. AASTED.

1981. Anchored fish aggregating devices in Hawaiian waters. Mar. Fish. Rev. 43(9):1-13.

MATSUMOTO, W. M., F. H. TALBOT, B. B. COLLETTE, and R. S. SHOMURA.

1969. Pacific bonito (*Sarda chiliensis*) and skipjack tuna (*Katsuwonus pelamis*) without stripes. Copeia 1969:397-398.

McCABE, M. M., and D. M. DEAN.

1970. Esterase polymorphisms in the skipjack tuna, *Katsuwonus pelamis*. Comp. Biochem. Physiol. 34:671-681.

McCABE, M. M., D. M. DEAN, and C. S. OLSON.

1970. Multiple forms of 6-phosphogluconate dehydrogenase and alpha-glycerophosphate dehydrogenase in the skipjack tuna, *Katsuwonus pelamis*. Comp. Biochem. Physiol. 34:755-757.

McNEELY, R. L.

1961. Purse seine revolution in tuna fishing. Pac. Fisherman 59(7):27-58.

MEAD, G. W.

1951. Postlarval *Neothunnus macropterus*, *Auxis thazard*, and *Euthynnus lineatus* from the Pacific coast of Central America. U.S. Fish Wildl. Serv., Fish. Bull. 52:121-127.

MEEK, S. E., and S. F. HILDEBRAND.

1923. The marine fishes of Panama. Field Mus. Nat. Hist., Publ. 215, Zool. Ser. 15, Part 1, 330 p.

MENDIS, A. S.

1954. Fishes of Ceylon. (A catalogue, key & bibliography.) Bull. Fish. Res. Stn. Ceylon 2, 222 p.

MIYAKE, M. P.

1968. Distribution of skipjack in the Pacific Ocean, based on records of incidental catches by the Japanese longline tuna fishery. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 12:509-608.

MIYAKE, M., and S. HAYASI.

1972. Field manual for statistics and sampling of Atlantic tunas and tuna-like fishes. Int. Comm. Conserv. Atl. Tunas, Madrid, pag. var.

MORELAND, J. M.

1967. Marine fishes of New Zealand. A. H. & A. W. Reed, Wellington, N.Z., 56 p.

MORI, K.

1970. A consideration on the spawning of the tunas, especially of the yellowfin tuna (*Thunnus albacares*) in the adjacent sea of the Pacific coast of Japan. [In Jpn., Engl. synop.] Bull. Far Seas Fish. Res. Lab. (Shimizu) 3:215-228.

1972. Geographical distribution and relative apparent abundance of some scombroid fishes based on the occurrences in the stomachs of apex predators caught on tuna longline-I. Juvenile and young of skipjack tuna (*Katsuwonus pelamis*). [In Jpn., Engl. abstr.] Bull. Far Seas Fish. Res. Lab. (Shimizu) 6:111-157.

MORI, K., S. UEYANAGI, and Y. NISHIKAWA.

1971. The development of artificially fertilized and reared larvae of the yellowfin tuna, *Thunnus albacares*. [In Jpn., Engl. synop.] Bull. Far Seas Fish. Res. Lab. (Shimizu) 5:219-232.

MORICE, J.

1953. Un caractère systématique pouvant servir à séparer les espèces de Thunnidae Atlantiques. Rev. Trav. Inst. Sci. Tech. Pêches Marit. 18:65-74.

MORROW, J. E.

1954. Fishes from East Africa, with new records and descriptions of two new species. Ann. Mag. Nat. Hist., Ser. 12, 7:797-820.

1957. Shore and pelagic fishes from Peru, with new records and the description of a new species of *Sphoeroides*. Bull. Bingham Oceanogr. Collect. Yale Univ. 16(2):5-55.

MUIR, B. S., and C. E. BROWN.

1971. Effects of blood pathway on the blood-pressure drop in fish gills, with special reference to tunas. J. Fish. Res. Board Can. 28:947-955.

MUNRO, I. S. R.

1955. The marine and fresh water fishes of Ceylon. Dep. Ext. Aff., Canberra, 351 p.

1958. The fishes of the New Guinea region. A check-list of the fishes of New Guinea incorporating records of species collected by the Fisheries Survey Vessel "Fairwind" during the years 1948 to 1950. Papua New Guinea Agric. J. 10(4):97-369.

MUNZ, F. W., and W. N. McFARLAND.

1977. Evolutionary adaptations of fishes to the photic environment. *In* F. Crescitelli (editor), The visual system in vertebrates, p. 193-274. Handb. Sens. Physiol. 7(5). Springer-Verlag, N.Y.

MURDY, E. O.

1980. The commercial harvesting of tuna-attracting payaos: A possible boon for small-scale fishermen. Int. Cent. Living Aquat. Resour. Manage Newsl. 3(1):10-13.

MURPHY, G. I., and I. I. IKEHARA.

1955. A summary of sightings of fish schools and bird flocks and of trolling in the central Pacific. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 154, 19 p.

MURPHY, G. I., and T. OTSU.

1954. Analysis of catches of nine Japanese tuna longline expeditions to the western Pacific. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 128, 46 p.

MURPHY, T. C., and G. T. SAKAGAWA.

1977. A review and evaluation of estimates of natural mortality rates of tunas. [In Engl., Fr. and Span. résumé.] Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1976) 6:117-123.

NAGANUMA, A.

1979. On spawning activities of skipjack tuna in the western Pacific Ocean. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 40:1-13.

NAKAMURA, E. L.

1962. Observations on the behavior of skipjack tuna, *Euthynnus pelamis*, in captivity. Copeia 1962:499-505.

1965. Food and feeding habits of skipjack tuna (*Katsuwonus pelamis*) from the Marquesas and Tuamotu Islands. Trans. Am. Fish. Soc. 94:236-242.

1968. Visual acuity of two tunas, *Katsuwonus pelamis* and *Euthynnus affinis*. Copeia 1968:41-49.

NAKAMURA, E. L., and J. J. MAGNUSON.

1965. Coloration of the scombrid fish *Euthynnus affinis* (Cantor). Copeia 1965:234-235.

NAKAMURA, E. L., and, W. M. MATSUMOTO.

1967. Distribution of larval tunas in Marquesan waters. U.S. Fish Wildl. Serv., Fish. Bull. 66:1-12.

NAKAMURA, E. L., and J. H. UCHIYAMA.

1966. Length-weight relations of Pacific tunas. *In* T. A. Manar (editor), Proceedings of the Governor's Conference on Central Pacific Fishery Resources, p. 197-201. State of Hawaii, Honolulu.

NAKAMURA, H.

1935. Uber intersexualitat bei *Katsuwonus pelamis* (Linn.). [In Jpn.] Trans. Nat. Hist. Soc. Formosa 25(141):197-198.

NAKAMURA, I.

1965. Relationships of fishes referable to the subfamily Thunninae on the basis of the axial skeleton. Bull. Misaki Mar. Biol. Inst., Kyoto Univ. 8:7-38.

NEILL, W. H., R. K. C. CHANG, and A. E. DIZON.

1976. Magnitude and ecological implications of thermal inertia in skipjack tuna, *Katsuwonus pelamis* (Linnaeus). Environ. Biol. Fishes 1:61-80.

NEILL, W. H., and E. D. STEVENS.

1974. Thermal inertia versus thermoregulation on "warm" turtles and tuna. Science (Wash., D.C.) 184:1008-1010.

NICHOLS, J. T., and R. C. MURPHY.

1944. A collection of fishes from the Panama Bight, Pacific Ocean. Bull. Am. Mus. Nat. Hist. 83:221-260.

NISHIKAWA, Y., S. KIKAWA, M. HONMA, and S. UEYANAGI.

1978. Distribution atlas of larval tunas, billfishes and related species - Results of larval surveys by R/V *Shunyo Maru* and *Shoyo Maru* (1956-1975). [In Jpn., Engl. summ.] Far Seas Fish. Res. Lab. (Shimizu), S Ser. 9, 99 p.

NOBRE, A.
1935. Fauna marinha de Portugal. Part I-Vertebrados (Mamiferos, Reptis e Peixes). Univ. Porto, Portugal, 574 p.

NOEL, J.
1978. Utilisation des donnes thermiques de télédétection pour l'aide a la pêche. (*Use of remote sensing thermal data for helping fisheries.*) [In Fr.] *In* Utilisation pour l'océanologie des satellites d'observation de la terre, p. 63-65. Centre Nat. d'Études Spatiales, Lannion (France): Publ. CNEXO, Paris, Actes Colloq., No. 5.

OKADA, Y.
1955. Fishes of Japan. Illustrations and descriptions of fishes of Japan. Maruzen Co., Ltd., Tokyo, 462 p.

OKADA, Y., and K. MATSUBARA.
1938. Keys to the fishes and fish-like animals of Japan. [In Jpn.] Sanseido Co., Tokyo, 584 p.

ORANGE, C. J.
1961. Spawning of yellowfin tuna and skipjack in the eastern tropical Pacific, as inferred from studies of gonad development. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 5:459-526.

ORANGE, C. J., M. B. SCHAEFER, and F. M. LARMIE.
1957. Schooling habits of yellowfin tuna (*Neothunnus macropterus*) and skipjack (*Katsuwonus pelamis*) in the eastern Pacific Ocean, as indicated by purse seine catch records, 1946-1955. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 2:83-126.

OSBECK, P.
1765. Reise nach Ostindien und China. . . . Aus dem Schwedischen übersetzt von J. G. Georgi. Johann Christian Koppe, Rostock, xxvi + 552 p.

PAJOT, G.
1978. Fishing gear and methods for off-shore fishing in Sri Lanka. Bull. Fish. Res. Stn., Sri Lanka 28:59-69.

PALMA, F.
1941. Nombres de peces cubanos y floridianos. Carbonell, Habana, 82 p.

PARIN, N. V.
1968. Ichthyofauna of the epipelagic zone. Academy of Sciences of the U.S.S.R. [In Russ.] Institute of Oceanology, Izdatel'stvo "Nauka," Moskva 1968. [Transl. by M. Raveh, edited by H. Mills, 1970, 206 p.; Israel Prog. Sci. Transl., available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va. as TT 69-59020.)

PARONA, C.
1919. Il tonno e la sua pesca. [In Ital.] Mem. R. Com Talassogr. Ital. Venezia 68, 255 p.

PELLA, J. J., and C. T. PSAROPULOS.
1975. Measures of tuna abundance from purse-seine operations in the eastern Pacific Ocean, adjusted for fleet-wide evolution of increased fishing power, 1960-1971. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 16:283-400.

[PHILIPPINES.] BUREAU OF FISHERIES AND AQUATIC RESOURCES.
1980. 1978 Fisheries statistics of the Philippines. Philipp., Minist. Nat. Resour., Bur. Fish. Aquatic Res., Vol. XXVIII, 374 p.

PIANET, R.
1974. Relations poids-longueur des listaos (*Katsuwonus pelamis*) pêches dans le secteur de Pointe-Noire. [In Fr., Engl. summ.] Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1973) 2:126-133.
1980. La pêcherie de listaos (*Katsuwonus pelamis*) dans l'Atlantique tropical est état des stocks au 31 décembre 1978. [In Fr., Engl. summ.] Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1979) 9:275-281.

PLAYFAIR, R. L., and A. C. L. G. GÜNTHER.
1866. The fishes of Zanzibar. John Van Voorst, Lond. *Lithoprinted* (Lim. ed.), 1971, Gregg, Kentfield, 153 p.

POEY, F.
1868. Synopsis piscium Cubensium. Repert. Fish.-Nat. Cuba 2:279-484.
1875. Enumeratio piscium Cubensium. Ann. Soc. Esp. Hist. Nat. 4:76-161.

POSTEL, E.
1955. La bonite à ventre rayé (*Katsuwonus pelamis*) dans la région du Cap Vert. Bull. Inst. Fr. Afr. Noire 17A:1202-1213.
1963. Exposé synoptique des données biologiques sur la bonite à ventre rayé *Katsuwonus pelamis* (Linné) 1758 (Atlantique et Méditerranée). (Synopsis on the biology of the skipjack *Katsuwonus pelamis* (Linné) 1758 (Atlantic and Mediterranean.) [In Fr.] FAO Fish. Rep. 6(2): 515-537.
1964. Les thonidés d'Afrique du Nord. *In* Proceedings of the Symposium of Scombroid Fishes, p. 211-220. Mar. Biol. Assoc. India, Symp. Ser. 1.

POTTHOFF, T., and W. J. RICHARDS.
1970. Juvenile bluefin tuna, *Thunnus thynnus* (Linnaeus), and other scombrids taken by terns in the Dry Tortugas, Florida. Bull. Mar. Sci. 20:389-413.

POWLES, H.
1977. *Island mass effects on the distribution of larvae of two pelagic fish species off Barbados.* FAO Fish. Rep. 200:333-346.

QUINN, W. H.
1976. Use of southern oscillation indices to assess the physical environment of certain tropical Pacific fisheries. *In* Proceedings NMFS/EDS Workshop on Climate and Fisheries, April 26-29, 1976, p. 50-70. Cent. Climatic and Environ. Assess., Columbia, Mo. U.S. Dep. Commer., NOAA, NMFS/EDS, Wash., D.C.
1977. Use of southern oscillation index anomalies for predicting El Niño type activity. [In Engl., Span. résumé.] Cienc. Mar. 4:40-66.

RADOVICH, J.
1963. Effects of water temperature on the distribution of some scombrid fishes along the Pacific coast of North America. [In Engl., Fr. and Span. résumé.] FAO Fish. Rep. 6(3):1459-1475.

RAFINESQUE, C. S.
1810. Indice d'ittiologia siciliana; ossia catalogo metodico dei nomi latini, italiana, e siciliani dei pesci, che si rinvengono in Sicilia: disposti secondo un metodo naturale e seguito da un'appendice che contiene la descrizione di alcuni nuovi pesci siciliana. Messina, 70 p.

RAJU, G.
1960. A case of hermaphroditism and some other gonadal abnormalities in the skipjack *Katsuwonus pelamis* (Linnaeus). J. Mar. Biol. Assoc. India 2:95-102.
1964a. Fecundity of the oceanic skipjack *Katsuwonus pelamis* (Linnaeus) of Minicoy. *In* Proceedings of the Symposium on Scombroid Fishes, p. 725-732. Mar. Biol. Assoc. India, Symp. Ser. 1.
1964b. Observations on the food and feeding habits of the oceanic skipjack, *Katsuwonus pelamis* (Linnaeus) of the Laccadive Sea during the years 1958-59. *In* Proceedings of the Symposium of Scombroid Fishes, p. 607-625. Mar. Biol. Assoc. India, Symp. Ser. 1.
1964c. Studies on the spawning of the oceanic skipjack *Katsuwonus pelamis* (Linnaeus) in Minicoy waters. *In* Proceedings of the Symposium on Scombroid Fishes, p. 744-768. Mar. Biol. Assoc. India, Symp. Ser. 1.

REGAN, C. T.
1909. *XI.—On the anatomy and classification of the scombroid fishes.* Ann. Mag. Nat. Hist., Ser. 8, 3:66-75.

REINTJES, J. W., and J. E. KING.
1953. Food of yellowfin tuna in the central Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 54:91-110.

RICHARD, J.
1905. Campagne scientifique du yacht "Princesse-Alice" en 1904. Bull. Mus. Oceanogr. Monaco 41, 30 p.

RICHARDS, W. J.
1969. Distribution and relative apparent abundance of larval tunas collected in the tropical Atlantic during EQUALANT surveys 1 and 2. *In* Proceedings of the Symposium of the Oceanography and Fisheries Resources of the Tropical Atlantic, p. 289-315. UNESCO, Paris.

RICHARDS, W. J., and G. R. DOVE.
1971. Internal development of young tunas of the genera *Katsuwonus*, *Euthynnus*, *Auxis*, and *Thunnus* (Pisces, Scombridae). Copeia 1971: 72-78.

RICHARDS, W. J., and D. C. SIMMONS.
1971. Distribution of tuna larvae (Pisces, Scombridae) in the northwestern Gulf of Guinea and off Sierra Leone. Fish. Bull., U.S. 69:555-568.

RICKER, W. E.
1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can. Bull. 119, 300 p.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

RICKER, W. E. (editor).
1968. Methods for assessment of fish production in fresh waters. Blackwell Sci. Publ., Lond., 313 p.

RISSO, A.
1810. Ichthyologie de Nice, ou histoire naturelle des poissons du Département des Alpes Maritimes. F. Schoell, Paris, 388 p.
1826. Histoire naturelle des poissons de la Méditerranée qui fréquentent les côtes des Alpes Maritimes, et qui vivent dans le Golfe de Nice. *In* Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes, Vol. 3, p. 97-480. F. G. Levrault, Paris.

RIVAS, L. R.

1949. Check list of the Florida game and commercial marine fishes, including those of the Gulf of Mexico and the West Indies, with approved common names. Univ. Miami Mar. Lab., Fla. State Board Conserv. Educ. Ser. 4, 39 p.

1951. A preliminary review of the western North Atlantic fishes of the family Scombridae. Bull. Mar. Sci. Gulf Caribb. 1:209-230.

RIVERO, L. H., and M. J. FERNANDEZ.

1954. Estados larvales y juveniles del bonito (*Katsuwonus pelamis*). Torreia 22, 14 p.

ROBERTS, P. E.

1972. Selective feeding by albacore and skipjack tuna in the New Zealand region in spring. Proc. Indo-Pac. Fish. Counc., 15(Sect. 3):461-469.

ROBINS, C. R., R. M. BAILEY, C. E. BOND, J. R. BROOKER, E. A. LACHNER, R. N. LEA, and W. B. SCOTT.

1980. A list of common and scientific names of fishes from the United States and Canada. 4th ed. Am. Fish. Soc., Spec. Publ. 12, 174 p.

ROBINS, J. P.

1952. Further observations on the distribution of striped tuna, *Katsuwonus pelamis* L., in eastern Australian waters, and its relation to surface temperature. Aust. J. Mar. Freshwater Res. 3:101-110.

RONQUILLO, I. A.

1953. Food habits of tunas and dolphins based upon the examination of their stomach contents. Philipp. J. Fish. 1954, 2:71-83.

1963. A contribution to the biology of Philippine tunas. FAO Fish. Rep. 6(3):1683-1752.

ROSA, H., Jr.

1950. Scientific and common names applied to tunas, mackerels, and spear fishes of the world with notes on their geographic distribution. FAO, Wash., D.C., 235 p.

ROTHSCHILD, B. J.

1963. Skipjack ecology. *In* W. G. Van Campen (editor), Progress in 1961-62, p. 13-17. U.S. Fish Wildl. Serv., Circ. 163.

1965. Hypotheses on the origin of exploited skipjack tuna (*Katsuwonus pelamis*) in the eastern and central Pacific Ocean. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 512, 20 p.

1966. Preliminary assessment of the yield potential of the skipjack tuna in the central Pacific Ocean. *In* T. A. Manar (editor), Proceedings of the Governor's Conference on Central Pacific Fishery Resources, p. 251-258. State of Hawaii, Honolulu.

1967. Estimates of the growth of skipjack tuna (*Katsuwonus pelamis*) in the Hawaiian Islands. Proc. Indo-Pac. Fish. Counc. 12(Sect. 2):100-111.

ROTHSCHILD, B. J., and R. N. UCHIDA.

1968. The tuna resources of the oceanic regions of the Pacific Ocean. *In* D. Gilbert (editor), The future of the fishing industry of the United States, p. 19-51. Univ. Wash., Publ. Fish., New Ser. 4.

ROUX, C.

1961. Résumé des connaissances actuelles sur *Katsuwonus pelamis* (Linné). [In Fr.] Bull. Inst. Pêches Marit. Maroc 7:33-53.

ROYCE, W. F.

1957. Observations on the spearfishes of the central Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 57:497-554.

ROYCE, W. F., and T. OTSU.

1955. Observation of skipjack schools in Hawaiian waters in 1953. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 147, 31 p.

SAKAGAWA, G. T.

1974. Participation by Panamanian and U.S. seiners in 1972 tuna fishery of the eastern tropical Atlantic. Mar. Fish. Rev. 36(3):10-13.

SAKAGAWA, G. T., A. L. COAN, and E. P. HOLZAPFEL.

1976. Length composition of yellowfin, skipjack, and bigeye tunas caught in the eastern tropical Atlantic by American purse seiners. Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1975) 5:48-63.

SAKAGAWA, G. T., and T. C. MURPHY.

1976. Status of the skipjack tuna stocks of the Atlantic Ocean. Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1975) 5:149-159.

SANTOS, A.

1978. Campaña atunera de 1977 en Canarias: Resultados preliminares. [1977 tuna survey in the Canaries: preliminary results.] Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1977) 7:146-148.

SCACCINI, A., R. SARA, C. PICCINETTI, and G. P. MANFRIN.

1975. Uova e larve di tonno pescate nella Sicilia occidentale e loro allevamento. [In Ital.] Ministero della Marine Mercantile, Memoria 39, 119 p.

SCHAEFER, M. B.

1948. Size composition of catches of yellowfin tuna (*Neothunnus macropterus*) from Central America, and their significance in the determination of growth, age, and schooling habits. U.S. Fish Wildl. Serv., Fish. Bull. 51:197-200.

1960. Report on the investigations of the Inter-American Tropical Tuna Commission for the year 1959. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Annu. Rep. 1959, p. 39-156.

1961a. Appendix A. Report on the investigations of the Inter-American Tropical Tuna Commission for the year 1960. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Annu. Rep. 1960:40-183.

1961b. Tuna oceanography programs in the tropical central and eastern Pacific. Calif. Coop. Oceanic Fish. Invest. Rep. 8:41-44.

SCHAEFER, M. B., B. M. CHATWIN, and G. C. BROADHEAD.

1961. Tagging and recovery of tropical tunas, 1955-1959. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 5:343-455.

SCHAEFER, M. B., and J. C. Marr.

1948. Spawning of yellowfin tuna (*Neothunnus macropterus*) and skipjack (*Katsuwonus pelamis*) in the Pacific Ocean off Central America, with descriptions of juveniles. U.S. Fish Wildl. Serv., Fish. Bull. 51:187-196.

SCHAEFER, M. B., and C. J. ORANGE.

1956. Studies of the sexual development and spawning of yellowfin tuna (*Neothunnus macropterus*) and skipjack (*Katsuwonus pelamis*) in three areas of the eastern Pacific Ocean, by examination of gonads. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 1:283-349.

SCHULTZ, L. P.

1960. Suborder Scombrina. Family Scombridae: Tunas. *In* L. P. Schultz and collaborators: W. M. Chapman, E. A. Lachner, and L. P. Woods, Fishes of the Marshall and Marianas Islands, p. 410-417. Bull. U.S. Natl. Mus. 202(2).

SCHULTZ, L. P., and E. M. STEARN.

1948. The ways of fishes. Van Nostrand Co., N.Y., 264 p.

SEALE, A.

1940. Report on fishes from Allan Hancock expeditions in the California Academy of Sciences. Allan Hancock Found. Pac. Exped. 9:1-46.

SECKEL, G. R.

1972. Hawaiian-caught skipjack tuna and their physical environment. Fish. Bull., U.S. 70:763-787.

SENTA, T.

1966. Experimental studies on the significance of drifting seaweeds for juvenile fishes—III. Experiments on visual stimulations. [In Engl.] Bull. Jpn. Soc. Sci. Fish. 32:693-696.

SERVENTY, D. L.

1941. The Australian tunas. Counc. Sci. Ind. Res., Div. Fish., Rep. 4, 48 p.

SETTE, O. E.

1950. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part II: Migrations and habits. U.S. Fish Wildl. Serv., Fish. Bull. 51:251-358.

SHABOTINIETS, E. I.

1968. Opredelenie vozrasta tuntsov Indiiskogo okeana (Age determination of Indian Ocean tunas). [In Russ.] Tr. VNIRO 64, Tr. AzcherNIRO 28:374-376. [Engl. transl. by W. L. Klawe, 1968, 5 p.; Inter-Am. Trop. Tuna Comm., La Jolla, Calif.]

SHARP, G. D.

1969. Electrophoretic study of tuna hemoglobins. Comp. Biochem. Physiol. 31:749-755.

1973. An electrophoretic study of hemoglobins of some scombroid fishes and related forms. Comp. Biochem. Physiol. 44B:381-388.

1976. Vulnerability of tunas as a function of environmental profiles. [In Engl. and Jpn.] *In* Maguro Gyogyō Kyōgikai Gijiroku, Suisansho-Enyō Suisan Kenkyusho (Proceedings of Tuna Fishery Research Conference, Fisheries Agency, Far Seas Fisheries Research Laboratory, Shimizu, Japan), p. 124-133.

1978. Behavioral and physiological properties of tunas and their effects on vulnerability to fishing gear. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 397-449. Acad. Press, N.Y.

1979. Areas of potentially successful exploitation of tunas in the Indian Ocean with emphasis on surface methods. FAO IOFC/DEV/79/47, 51 p. Dev. Rep. Indian Ocean Prog. Develop. Rep. 47.

SHARP, G. D., and R. C. FRANCIS.

1976. An energetics model for the exploited yellowfin tuna, *Thunnus albacares*, population in the eastern Pacific Ocean. Fish. Bull., U.S. 74:36-51.

SHARP, G. D., and S. PIRAGES.

1978. The distribution of red and white swimming muscles, their biochemistry, and the biochemical phylogeny of selected scombrid fishes. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 41-78. Acad. Press, N.Y.

SHIMADA, B. M.

1951. Contributions to the biology of tunas from the western equatorial

Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 52:111-119.

SHIMADA, B. M., and M. B. SCHAEFER.

1956. A study of changes in fishing effort, abundance, and yield for yellowfin and skipjack tuna in the eastern tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 1:351-469.

SHIPPEN, H. H.

1961. Distribution and abundance of skipjack in the Hawaii fishery, 1952-53. U.S. Fish Wildl. Serv., Fish. Bull. 61:281-300.

SHOMURA, R. S.

1966a. Age and growth studies of four species of tunas in the Pacific Ocean. *In* T. A. Manar (editor), Proceedings of the Governor's Conference on Central Pacific Fishery Resources, p. 203-219. State of Hawaii, Honolulu.

1966b. The Atlantic tuna fisheries, 1963. Commer. Fish. Rev. 28(5):1-11.

SHOMURA, R. S. (editor).

1977. Collection of tuna baitfish papers. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 408, 167 p.

SHOMURA, R. S., and G. I. MURPHY.

1955. Longline fishing for deep-swimming tunas in the central Pacific, 1953. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 157, 70 p.

SILAS, E. G.

1967. Parasites of scombroid fishes. Part I. Monogenetic trematodes, digenetic trematodes, and cestodes. *In* Proceedings of the Symposium on Scombroid Fishes, p. 799-875. Mar. Biol. Assoc. India, Symp. Ser. 1.

SILAS, E. G., and A. N. P. UMMERKUTTY.

1967. Parasites of scombroid fishes. Part II. Parasitic Copepoda. *In* Proceedings of the Symposium on Scombroid Fishes, p. 876-993. Mar. Biol. Assoc. India, Symp. Ser. 1.

SILLIMAN, R. P.

1966. Estimates of yield for Pacific skipjack and bigeye tunas. *In* T. A. Manar (editor), Proceedings of the Governor's Conference on Central Pacific Fishery Resources, p. 243-249. State of Hawaii, Honolulu.

SIMMONS, D. C.

1969. Maturity and spawning of skipjack tuna (*Katsuwonus pelamis*) in the Atlantic Ocean, with comments on nematode infestation of the ovaries. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 580, 17 p.

SIMPSON, A. C. (consultant).

1979. Report of the workshop on the tuna resources of Indonesia and Philippine waters, Jakarta, 20-23 March 1979. South China Seas Fish. Develop. Coord. Prog. Manila. FAO, SCS/GEN/79/21, 35 p.

SIVASUBRAMANIAM, K.

1965. Exploitation of tunas in Ceylon's coastal waters. Bull. Fish. Res. Stn., Ceylon 18:59-72.

1972. Skipjack tuna (*K. pelamis*, L.) resource in the seas around Ceylon. Bull. Fish. Res. Stn., Sri Lanka (Ceylon) 23:19-28.

1975. An analysis of the experimental pole and line fishery conducted around Sri Lanka by Nichiro Fishing Company of Japan. Bull. Fish. Res. Stn., Sri Lanka (Ceylon) 26:61-82.

SMITH, J. L. B.

1949. The sea fishes of southern Africa. Central News Agency, Ltd., Cape Town, South Africa, 550 p.

SMITT, F. A. (editor).

1893. A history of Scandinavian fishes, by B. Fries, C. U. Ekstrom, and C. Sundevall. 2d ed. revised and completed by F. A. Smitt. Part I. P. A. Norstedt and Soner, Stockholm, 566 p.

SNODGRESS, R. E., and E. HELLER.

1905. Shore fishes of the Revillagigedo, Clipperton, Cocos and Galapagos Islands. Proc. Wash. Acad. Sci. 6:333-427.

SOEMARTO.

1960. Fish behaviour with special reference to pelagic shoaling species: Lajang (*Decapterus* spp.). Proc. Indo-Pac. Fish. Counc. 8(Sect.3):89-93.

SOKAL, R. R., and F. J. ROHLF.

1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman, San Franc., 776 p.

SOLDATOV, V. K., and G. J. LINDBERG.

1930. A review of the fishes of the seas of the Far East. Bull. Pac. Sci. Fish. Inst. 5, 576 p.

SOUTH PACIFIC COMMISSION.

1980. Review of preliminary results from genetic analysis of skipjack blood samples collected by the Skipjack Survey and Assessment Programme. South Pac. Comm., Skipjack Surv. Assess. Programme Tech. Rep. 1, 22 p.

1981. Report of the Second Skipjack Survey and Assessment Programme Workshop to review results from genetic analysis of skipjack blood samples. South Pac. Comm., Skipjack Surv. Assess. Programme, Tech. Rep. 6, 39 p.

SPRAGUE, L. M.

1963. Subpopulations. *In* W. G. Van Campen (editor), Progress in 1961-62, p. 10-12. U.S. Fish Wildl. Serv., Circ. 163.

1970. The electrophoretic patterns of skipjack tuna tissue esterases. Hereditas 65:187-190.

SPRAGUE, L. M., and J. R. HOLLOWAY.

1962. Studies of the erythrocyte antigens of the skipjack tuna (*Katsuwonus pelamis*). Am. Nat. 96:233-238.

SPRAGUE, L. M., J. R. HOLLOWAY, and L. I. NAKASHIMA.

1963. Studies of the erythrocyte antigens of albacore, bigeye, skipjack, and yellowfin tunas and their use in subpopulation identification. FAO Fish. Rep. 6(3):1381-1393.

SPRAGUE, L. M., and L. I. NAKASHIMA.

1962. Studies on the erythrocyte antigens of the skipjack tuna (*Katsuwonus pelamis*). [Abstr.] *In* J. C. Marr (editor), Pacific Tuna Biology Conference, Honolulu, Hawaii, August 14-19, 1961, p. 36-37. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 415.

STARKS, E. C.

1910. The osteology and mutual relationships of the fishes belonging to the family Scombridae. J. Morphol. 21:77-99.

STEFFEL, S., A. E. DIZON, J. J. MAGNUSON, and W. H. NEILL.

1976. Temperature discrimination by captive free-swimming tuna, *Euthynnus affinis*. Trans. Am. Fish. Soc. 105:588-591.

STEINDACHNER, F.

1868. Ichthyologischer Bericht uber eine nach Spanien und Portugal unternommene Reise (V and VI). Ubersicht der Meeresfische an den Kusten Spanien's und Portugal's. Sitzber. Akad. Wiss. Wien, p. 351-738.

STEINITZ, H., and A. BEN-TUVIA.

1955. Fishes from Eylath (Gulf of Aquaba), Red Sea. Bull. Sea Fish. Res. Stn., Haifa, Isr. 11, 15 p.

STEQUERT, B.

1976. Étude de la maturité sexuelle, de la ponte et de la fécondité du listao (*Katsuwonus pelamis*) de la côte nord-ouest de Madagascar. [A study of sexual maturity, the fertility and spawning of the skipjack (*Katsuwonus pelamis*) of the north-west coast of Madagascar.] [In Fr., Engl. abstr.] Cah. O.R.S.T.O.M., Sér. Océanogr. 14:227-247.

STEVENS, E. D.

1972. Some aspects of gas exchange in tuna. J. Exp. Biol. 56:809-823.

STEVENS, E. D., and F. E. J. FRY.

1971. Brain and muscle temperatures in ocean caught and captive skipjack tuna. Comp. Biochem. Physiol. 38A:203-211.

STEVENS, E. D., H. M. LAM, and J. KENDALL.

1974. Vascular anatomy of the counter-current heat exchanger of skipjack tuna. J. Exp. Biol. 61:145-153.

STEVENS, E. D., and W. H. NEILL.

1978. Body temperature relations of tunas, especially skipjack. *In* W. D. Hoar and D. J. Randall (editors), Fish physiology, Vol. 7, p. 315-359. Acad. Press, N.Y.

STEVENSON, M., and F. MILLER.

1977. Comparison of infrared satellite data and fish catch data. *In* 5 Congreso Nacional de Oceanografia. Memorias. Guyaymas, Sonora, 22-25 de octobre 1974. F. A. Manrique (editor), Instituto Tech. y de Estudios Super. de Monterrey, Guaymas, Mexico, p. 663-679. Escuela de Ciencias Maritimis y Alimentarias 1977.

STRASBURG, D. W.

1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. U.S. Fish Wildl. Serv., Fish. Bull. 58:335-361.

1960. Estimates of larval tuna abundance in the central Pacific. U.S. Fish. Wildl. Serv., Fish. Bull. 60:231-255.

1961. Diving behaviour of Hawaiian skipjack tuna. J. Cons. Cons. Int. Explor. Mer 26:223-229.

STRASBURG, D. W., E. C. JONES, and R. T. B. IVERSEN.

1968. Use of a small submarine for biological and oceanographic research. J. Cons. Cons. Int. Explor. Mer 31:410-426.

STRASBURG, D. W., and J. C. MARR.

1961. Banded color phases of two pelagic fishes, *Coryphaena hippurus* and *Katsuwonus pelamis*. Copeia 1961:226-228.

STRASBURG, D. W., and H. S. H. YUEN.

1960. Preliminary results of underwater observations of tuna schools and practical applications of these results. Proc. Indo-Pac. Fish. Counc. 8(Sect. 3):84-89.

SUAREZ CAABRO, J. A., and P. P. DUARTE-BELLO.

1961. Biologia pesquera del bonito (*Katsuwonus pelamis*) y la albacora (*Thunnus atlanticus*) en Cuba. I. Inst. Cub. Invest. Technol., Ser. Estud. Trab. Invest. 15, 151 p.

SUDA, A.

1953. Juvenile skipjack from the stomach contents of tunas and marlins. [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 19:319-340.

1972. The skipjack fishery of the future (Shorai no katsuo gyogyō). [In Jpn.] Kansai Shibu Gyosen Kenkyukai, Mie Chiku Kenkyukai. Reprinted from Gyosen 182:44-52. [Engl. transl. of a part of the conference proceedings by T. Otsu, 1973, 16 p.; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

SUND, P. N., M. BLACKBURN, and F. WILLIAMS.

1981. Tunas and their environment in the Pacific Ocean: A review. Oceanogr. Mar. Biol. Annu. Rev. 19:443-512.

SUND, P. N., and W. J. RICHARDS.

1967. Preliminary report on the feeding habits of tunas in the Gulf of Guinea. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 551, 6 p.

SUYEHIRO, Y.

1938. The study of finding the reasons why the bonito does not take to the angling-baits. [In Jpn., Engl. abstr.] J. Imp. Fish. Exp. Stn. Tokyo 9:87-102. [Engl. transl. by G. Y. Beard, 1960, 12 p.; in files of Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

TAKAHASHI, N.

1924. On the order Plecostei established by Dr. Kishinouye. [In Jpn.] Zool. Mag., Tokyo 36(432):397-408. [Engl. transl. by W. G. Van Campen, 1951. *In* U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 50:3-16.]

TALBOT, F. H.

1964. The South African tunas. *In* Proceedings of the Symposium on Scombroid Fishes, p. 187-209. Mar. Biol. Assoc. India, Symp. Ser. 1.

TAMURA, T., I. HANYU, and H. NIWA.

1972. Spectral sensitivity and color vision in skipjack tuna and related species. [In Engl.] Bull. Jpn. Soc. Sci. Fish. 38:799-802.

TANAKA, S.

1912. *Euthynnus pelamis* (Linnaeus). (Scombridae). *In* Figures and descriptions of the fishes of Japan, Vol. 8, p. 140-143.

TANAKA, T.

Undated a. Atlas of skipjack tuna fishing grounds in southern waters, 1974 fishing season (July 1974-May 1975) (Nanpo kaiiki ni okeru katsuo gyojyozu, Showa 49 nendo). Tohoku Reg. Fish. Res. Lab., 4 p. text, 13 charts. [Engl. transl. by T. Otsu, 1976, 24 p., transl. no. 14; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

Undated b. Atlas of skipjack tuna fishing grounds in southern waters, 1975 fishing season (June 1975-May 1976) (Nanpo kaiiki ni okeru katsuo gyojyozu, Showa 50 nendo). Tohoku Reg. Fish. Res. Lab., 5 p. text, 15 charts. [Engl. transl. by T. Otsu, 1976, 25 p., transl. no. 15; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

Undated c. Atlas of skipjack tuna fishing grounds in southern waters, 1976 fishing season (July 1976-April 1977). Tohoku Reg. Fish. Res. Lab., 6 p. text, 14 charts. [Engl. transl. by T. Otsu, 1977, 30 p., transl. no. 23; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

1978. Atlas of skipjack tuna fishing grounds in southern waters, 1977 fishing season (June 1977-April 1978). Tohoku Reg. Fish. Res. Lab., 8 p. text, 16 charts. [Engl. transl. by T. Otsu, 1978, 33 p., transl. no. 30; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

1979. Atlas of skipjack tuna fishing grounds in southern waters, 1978 fishing season (June 1978-May 1979). Tohoku Reg. Fish. Res. Lab., 6 p., 14 charts. [Engl. transl. by T. Otsu, 1979, 39 p., transl. no. 39; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

1980. Atlas of skipjack tuna fishing grounds in southern waters, 1979 fishing season (May 1979-April 1980). Tohoku Reg. Fish. Res. Lab., 12 p. text, 19 charts. [Engl. transl. by T. Otsu, 1980, 48 p., transl. no. 48; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

TEMMINCK, C. J., and H. SCHLEGEL.

1842. Pices (*In* Siebold, P. Fr. von: Fauna Japonica, sive description animalium quae in itinere per Japoniam suscepto annis 1823-1830 collegit, etc.) 2 vols. Lugduni Batavorum, 1842-50, 323 p., 160 pls.

TESTER, A. L.

1959. Summary of experiments on the response of tuna to stimuli. *In* H. Kristjonsson (editor), Modern fishing gear of the world, p. 538-542. Fish. News (Books), Lond.

TESTER, A. L., and E. L. NAKAMURA.

1957. Catch rate, size, sex, and food of tunas and other pelagic fishes taken by trolling off Oahu, Hawaii, 1951-55. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 250, 25 p.

TESTER, A. L., H. YUEN, and M. TAKATA.

1954. Reaction of tuna to stimuli, 1953. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 134, 33 p.

THOMAS, P. T.

1964. Food of *Katsuwonus pelamis* (Linnaeus) and *Neothunnus macropterus* (Temminck and Schlegel) from Minicoy waters during the season 1960-61. *In* Proceedings of the Symposium on Scombroid Fishes, p. 626-630. Mar. Biol. Assoc. India, Symp. Ser. 1.

THOMAS, P. T., and G. RAJU.

1964. Gonadial abnormalities in scombroid fishes. *In* Proceedings of the Symposium on Scombroid Fishes, p. 719-724. Mar. Biol. Assoc. India, Symp. Ser. 1.

THOMPSON, W. W.

1918. Catalogue of fishes of the Cape Province. Mar. Biol. Rep. 4:75-177.

TOHOKU REGIONAL FISHERIES RESEARCH LABORATORY.

Undated a. Atlas of skipjack tuna fishing grounds in southern waters, 1964 and 1965. Tohoku Reg. Fish. Res. Lab., 2 p. text, 28 charts. [Engl. transl. by T. Otsu, 1968, 34 p.; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

Undated b. Atlas of skipjack tuna fishing grounds in southern waters, 1968-69 fishing seasons. Tohoku Reg. Fish. Res. Lab., 2 p. text, 24 charts. [Engl. transl. by T. Otsu, 1971, 30 p.; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

Undated c. Atlas of skipjack tuna fishing grounds in southern waters, 1970-71 fishing seasons. Tohoku Reg. Fish. Res. Lab., 2 p. text, 30 charts. [Engl. transl. by T. Otsu, 1972, 36 p.; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

Undated d. Atlas of skipjack tuna fishing grounds in southern waters, 1973 fishing season (July 1973-May 1974). Tohoku Reg. Fish. Res. Lab., 5 p. text, 14 charts. [Engl. transl. by T. Otsu, 1974, 22 p., transl. no. 7; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

TOMINAGA, S.

1957. Skipjack behavior and fishing methods. [In Jpn.] Ishizaki-Shoten Co., Tokyo, 160 p. + charts. [Translated excerpts, 1958, The skipjack - Its habits and fishing methods. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

UCHIDA, R. N.

1961. Hermaphroditic skipjack. Pac. Sci. 15:294-296.

1967. Catch and estimates of fishing effort and apparent abundance in the fishery for skipjack tuna (*Katsuwonus pelamis*) in Hawaiian waters, 1952-62. U.S. Fish Wildl. Serv., Fish. Bull. 66:181-194.

1970. Distribution of fishing effort and catches of skipjack tuna, *Katsuwonus pelamis*, in Hawaiian waters, by quarters of the year, 1948-65. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 615, 37 p.

1975. Recent development in fisheries for skipjack tuna, *Katsuwonus pelamis*, in the central and western Pacific and the Indian Ocean. *In* Studies on skipjack in the Pacific, p. 1-57. FAO Fish. Tech. Pap. 144.

1976. Reevaluation of fishing effort and apparent abundance in the Hawaiian fishery for skipjack tuna, *Katsuwonus pelamis*, 1948-70. Fish. Bull., U.S. 74:59-69.

UCHIDA, R. N., and R. F. SUMIDA.

1971. Analysis of the operations of seven Hawaiian skipjack tuna fishing vessels, June-August 1967. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Spec. Sci. Rep. Fish. 629, 25 p.

UCHIYAMA, J. H., and P. STRUHSAKER.

1981. Age and growth of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 79:151-162.

UDA, M.

1933. The shoals of "katuwo" and their angling. [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 2:107-111. [Engl. transl. by W. G. Van Campen, 1952. *In* U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 83:68-78.]

1940. The time and duration of angling and the catch of "katsuo", *Euthynnus vagans* (Lesson). [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 9:103-106. [Engl. transl. by W. G. Van Campen, 1951. *In* U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 51:12-17.]

1941. The body-temperature and the bodily features of "katuo" and "sanma." [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 9:231-236. [Engl. transl. by W. G. Van Campen, 1951. *In* U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 51:18-24.]

1957. A consideration on the long years trend of the fisheries fluctuation in relation to sea conditions. Bull. Jpn. Soc. Sci. Fish. 23:368-372.

1961. Fisheries oceanography in Japan, especially on the principles of fish distribution, concentration, dispersal and fluctuation. Calif. Coop. Oceanic Fish. Invest. Rep. 8:25-31.

1962a. Cyclical fluctuation of the Pacific tuna fisheries in response to cold and warm water intrusions. [Abstr.] *In* J. C. Marr (editor), Pacific Tuna Biology Conference, Honolulu, Hawaii, August 14-19, 1961, p. 39. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 415.

1962b. Localized concentration of tunas in the eddies along oceanic fronts. [Abstr.] *In* J. C. Marr (editor), Pacific Tuna Biology Conference, Honolulu, Hawaii, August 14-19, 1961, p. 39-40. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 415.

UDA, M., and J. TSUKUSHI.

1934. Local variations in the composition of various shoals of "katuwo", *Euthynnus vagans* (Lesson), in several sea-districts of Japan. [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 3:196-202. [Engl. transl. W. G. Van Campen, 1952. *In* U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 83:51-67.]

UEYANAGI, S.

1969. Observations on the distribution of tuna larvae in the Indo-Pacific Ocean with emphasis on the delineation of the spawning areas of albacore, *Thunnus alalunga*. [In Jpn., Engl. synop.] Bull. Far Seas Fish. Res. Lab. (Shimizu) 2:177-256.

1970. Distribution and relative abundance of larval skipjack tuna (*Katsuwonus pelamis*) in the western Pacific Ocean. *In* J. C. Marr (editor), The Kuroshio. A symposium on the Japan Current, p. 395-398. East-West Center Press, Honolulu.

1971. Larval distribution of tunas and billfishes in the Atlantic Ocean. *In* Symposium on Investigations and Resources of the Caribbean Sea and Adjacent Regions. FAO Fish. Rep. 71.2:297-305.

UEYANAGI, S., K. MORI, Y, NISHIKAWA, and A. SUDA.

1973. Report on experiments on the development of tuna culturing techniques (April, 1970-March, 1973). [In Jpn., Engl. summ.] Far Seas Fish. Res. Lab., S Ser. 8, 165 p.

UEYANAGI, S., Y. NISHIKAWA, and T. MATSUOKA.

1974. Artificial fertilization and larval development of skipjack tuna, *Katsuwonus pelamis*. [In Jpn., Engl. summ.] Bull. Far Seas Fish. Res. Lab. (Shimizu) 10:179-188.

VALENCIENNES, A.

1836. Les poissons. *In* G. Cuvier, Le règne animal. Fortin, Masson et Cie, Paris, 392 p.

VAN PEL, H.

1960. Report on the sea fisheries of Western Samoa. South Pac. Comm., Noumea, Misc. Pap. 14, 24 p.

VOOREN, C. M.

1976. Biological data on skipjack in New Zealand waters, 1973-76. *In* Proceedings of the Skipjack Tuna Conference, July 1976, p. 12-16. [New Zealand.] Minist. Agric. Fish., Fish. Res. Div., Occas. Publ. 11.

WADE, C. B.

1950. Observations on the spawning of Philippine tuna. U.S. Fish Wildl. Serv., Fish. Bull. 51:409-423.

1951. Larvae of tuna and tuna-like fishes from Philippine waters. U.S. Fish Wildl. Serv., Fish. Bull. 51:445-485.

WALDRON, K. D.

1963. Synopsis of biological data on skipjack *Katsuwonus pelamis* (Linnaeus) 1758 (Pacific Ocean). FAO Fish. Rep. 6(2):695-748.

1964. Fish schools and bird flocks in the central Pacific Ocean, 1950-1961. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 464, 20 p.

WALDRON, K. D., and J. E. KING.

1963. Food of skipjack in the central Pacific. FAO Fish. Rep. 6(3):1431-1457.

WALTERS, V., and H. L. FIERSTINE.

1964. Measurements of swimming speeds of yellowfin tuna and wahoo. Nature (Lond.) 202:208-209.

WANKOWSKI, J. W. J.

1980. Recent history and summarized statistics of the industrial fisheries for tuna and tuna-like species in the area of the Papua New Guinea declared fisheries zone, 1970-1979. [Papua New Guinea.] Res. Bull. 24, 82 p.

WEBB, P. W.

1975. Hydrodynamics and energetics of fish propulsion. Fish. Res. Board Can. Bull. 190, 158 p.

WELSH, J. P.

1949. A trolling survey of Hawaiian waters. Hawaii Div. Fish Game, Board Comm. Agric. For., Fish Res. Progr. Rep. 1(4), 30 p.

WETHERALL, J. A.

1977. Catch statistics and abundance of nehu, *Stolephorus purpureus*, in Kaneohe Bay. *In* R. S. Shomura (editor), Collection of tuna baitfish papers, p. 114-118. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 408.

WHITLEY, G. P.

1964. Scombroid fishes of Australia and New Zealand. *In* Proceedings of the Symposium on Scombroid Fishes, p. 221-253. Mar. Biol. Assoc. India, Symp. Ser. 1.

WILD, A., and T. J. FOREMAN.

1980. The relationship between otolith increments and time for yellowfin and skipjack tuna marked with tetracycline. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 17:509-560.

WILLIAMS, F.

1956. Preliminary survey of the pelagic fishes of East Africa. G. B. Colon. Off. Fish. Publ., Lond. 8, 68 p.

1964. The scombroid fishes of East Africa. *In* Proceedings of the Symposium on Scombroid Fishes, p. 107-164. Mar. Biol. Assoc. India, Symp. Ser. 1.

1970. Sea surface temperature and the distribution and apparent abundance of skipjack (*Katsuwonus pelamis*) in the eastern Pacific Ocean, 1951-1968. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 15:231-281.

1972. Consideration of three proposed models of the migration of young skipjack tuna (*Katsuwonus pelamis*) into the eastern Pacific Ocean. Fish. Bull., U.S. 70:741-762.

YABE, H.

1954. A study on spawning of skipjack in the Satsunan Sea area. *In* General view of fishery science, Tokyo. [In Jpn.] Jpn. Assoc. Adv. Sci. 182-199. [Engl. transl. by G. Y. Beard, 1959, 9 p.; in files of Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

1955. Studies on the fish larvae in the western Pacific Ocean. 1. The postlarvae of *Katsuwonus pelamis*. [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 20:1054-1059. [Engl. transl. by G. Y. Beard, 1958, 2 p.; in files of Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

YABE, H., and T. MORI.

1950. An observation on the habit of bonito, *Katsuwonus vagans*, and yellowfin, *Neothunnus macropterus*, school under the drifting timber on the surface of ocean. [In Jpn., Engl. abstr.] Bull. Jpn. Soc. Sci. Fish. 16:35-39. [Engl. transl. by W. G. Van Campen, 1954, 12 p.; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

YABE, H., Y. YABUTA, and S. UEYANAGI.

1963. Comparative distribution of eggs, larvae and adults in relation to biotic and abiotic environmental factors. FAO Fish. Rep. 6(3):979-1009.

YAMANAKA, H., Y. KUROHIJI, and J. MORITA.

1966. General results of the investigation in the south western Pacific Ocean by the fish-finder. [In Jpn., Engl. summ.] Rep. Nankai Reg. Fish. Res. Lab. 24:115-127.

YAMASHITA, D. T.

1958. Analysis of catch statistics of the Hawaiian skipjack fishery. U.S. Fish Wildl. Serv., Fish. Bull. 58:253-278.

YAO, M.

1955. On the ovaries of the skipjack, *Katsuwonus pelamis* (Linnaeus), captured in the fishing grounds along the Japanese coast. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 5:43-52. [Engl. transl. by T. Otsu, 1959, 9 p.; Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

1962. Skipjack biting by the mathematical estimate. [In Jpn., Engl. summ.] Bull. Tohoku Reg. Fish. Res. Lab. 20:28-32.

YASUI, M., and M. INOUE.

1977. Oceanographic factors related to skipjack fishing conditions in the Kinan and Izu regions. Bull. Jpn. Soc. Sci. Fish. 43:1059-1067.

YOKOTA, T., M. TORIYAMA, F. KANAI, and S. NOMURA.

1961. Studies on the feeding habit of fishes. [In Jpn., Engl. summ.] Rep. Nankai Reg. Fish. Res. Lab. 14, 234 p.

YORK, A. G.

1974. Acoustic detection and attraction of tuna in New Zealand waters. Proc. Indo-Pac. Fish. Counc. 15(Sect. 3):470-480.

YOSHIDA, H. O.

1960. Marquesas area fishery and environmental data, January - March 1959. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 348, 37 p.

1966. Skipjack tuna spawning in the Marquesas Islands and Tuamotu Archipelago. U.S. Fish Wildl. Serv., Fish. Bull. 65:479-488.

1971. The early life history of skipjack tuna, *Katsuwonus pelamis*, in the Pacific Ocean. Fish. Bull., U.S. 69:545-554.

YOSHIHARA, T.

1960. On the mechanism of fishing II. [In Jpn., Engl. abstr.] Jpn. J. Ecol. 10:109-112.

YUEN, H. S. H.

1959. Variability of skipjack response to live bait. U.S. Fish Wildl. Serv., Fish. Bull. 60:147-160.

1966. Swimming speeds of yellowfin and skipjack tuna. Trans. Am. Fish. Soc. 95:203-209.

1970. Behavior of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic devices. J. Fish. Res. Board Can. 27:2071-2079.

ZAVALA CAMIN, L. A.

1978. Anotaciones sobre la presencia del listado en el sudeste y sur del Brazil. [In Span., Engl. and Fr. summ.] Collect. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas (SCRS-1977) 7:82-83.

ZHAROV, V. L.

1967. Classification of the scombroid fishes (Suborder Scombrodei, Order Perciformes). [In Russ.] AtlantNIRO, Kalingrad obl.—Atl. Res. Inst. Fish. Oceanogr., Voprosy Ikhtiologii 43:209-223. [Engl. transl. by A. R. Gosline, 1968, 22 p.; in files of Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.]

ZHUDOVA, A. M.

1969. Larvae of scombroid fishes (Scombroidei, Perciformes) of the central portion of the Atlantic Ocean. [In Russ.] Tr. AtlantNIRO 25:100-108. [Engl. transl. by W. L. Klawe, 1970, 17 p.; Inter-Am. Trop. Tuna Comm., La Jolla, Calif.]