INTER-AMERICAN TROPICAL TUNA COMMISSION COMISION INTERAMERICANA DEL ATUN TROPICAL

INTERNAL REPORT -- INFORME INTERNO

No. 21

A REVIEW OF THE QUESTION OF SUBPOPULATIONS OF SKIPJACK TUNA, KATSUWONUS PELAMIS, IN THE PACIFIC OCEAN, AND OF POSSIBLE MIGRATION ROUTES

by

Eric D. Forsbergh

La Jolla, California

1988

PREFACE

The Internal Report series is produced primarily for the convenience of staff members of the Inter-American Tropical Tuna Commission. It contains reports of various types. Some will eventually be modified and published in the Commission's Bulletin series or outside journals. Others are methodological reports of limited interest or reports of research which yielded negative or inconclusive results.

These reports are not to be considered as publications. Because they are in some cases preliminary, and because they are subjected to less intensive editorial scrutiny than contributions to the Commission's Bulletin series, it is requested that they not be cited without permission from the Inter-American Tropical Tuna Commission.

PREFACIO

Se ha producido una serie de Informes Internos con el fin de que sean útiles a los miembros del personal de la Comisión Inter-Americana del Atún Tropical. Esta serie incluye varias clases de informes. Algunos serán modíficados eventualmente y publicados en la serie de Boletines de la Comisión o en revistas exteriores de prensa. Otros son informes metodológicos de un interés limitado o informes de investigación que han dado resultados negativos o inconclusos.

Estos informes no deben considerarse como publicaciones, debido a que en algunos casos son datos preliminares, y porque están sometidos a un escrutinio editorial menos intenso que las contribuciones hechas en la serie Boletines de la Comisión; por lo tanto, se ruega que no sean citados sin permiso de la Comisión Inter-Americana del Atún Tropical. INTER-AMERICAN TROPICAL TUNA COMMISSION COMISION INTERAMERICANA DEL ATUN TROPICAL

۰.

Û.

24

100

INTERNAL REPORT -- INFORME INTERNO

No. 21

A REVIEW OF THE QUESTION OF SUBPOPULATIONS OF SKIPJACK TUNA, KATSUWONUS PELAMIS, IN THE PACIFIC OCEAN, AND OF POSSIBLE MIGRATION ROUTES

by

Eric D. Forsbergh

La Jolla, California

1988

A REVIEW OF THE QUESTION OF SUBPOPULATIONS OF SKIPJACK TUNA, KATSUWONUS PELAMIS, IN THE PACIFIC OCEAN, AND OF POSSIBLE MIGRATION ROUTES

TABLE OF CONTENTS

ABSTRACT														2	3
INTRODUCTION									÷						3
THE QUESTION OF SUBPOPULATIONS								i.							3
POSSIBLE MIGRATION ROUTES	4					ί.	41								5
ACKNOWLEDGEMENTS															11
LITERATURE CITED		Υ.	÷		÷	÷.		÷	÷.				4	÷.	12

ABSTRACT

A review of the work on possible subpopulations of skipjack in the Pacific indicates that the problem of whether there is more than one subpopulation remains unresolved. The eastward migration routes remain unknown, but migration in the eastward-flowing North Equatorial Countercurrent and the Equatorial Undercurrent would enable skipjack to make greater progress using less energy than swimming against the North and South Equatorial Currents.

INTRODUCTION

The problem of whether there is more than one subpopulation of skipjack in the Pacific was considered during workshops sponsored by the South Pacific Commission (Anonymous, 1980 and 1981a). The data primarily investigated were the gene frequencies of the serum napthyl esterase, serum transferrin, and erythrocyte guanine deaminase in skipjack blood, and releases and recaptures of tagged fish. It was concluded during the workshops that skipjack in the Pacific were not panmictic. A panmictic population is one in which all fish belong to a single population and any adult fish has an equal chance of breeding with any other in the entire range of the geographical distribution. Two major hypotheses were considered most feasible for the population structure of skipjack in the Pacific: the clinal hypothesis, and the discrete-subpopulation hypothesis.

The hypothesis that skipjack caught in the eastern Pacific originated in the central Pacific was first proposed by Schaefer (1963: 50) on the basis of morphometrics, blood types, two skipjack tagged in the eastern Pacific and recaptured in the central Pacific, and the fact that there is comparatively little spawning in the fishing areas of the eastern Pacific. Rothschild (1965) discussed the evidence for the hypothesis in greater detail. Robert E. Kearney, formerly with IATTC, however, has suggested that skipjack in the eastern Pacific could have originated there if the survival of the larvae, juveniles, and young were very high, even though there is little spawning in the eastern Pacific.

THE QUESTION OF SUBPOPULATIONS

The frequency of serum napthyl esterase was constant from 80°W to 140°W, and increased from 140°W to 130°E (Anonymous, 1981a: Figure 3). According to the clinal hypothesis, skipjack in the Pacific belong to only one population, but the chance of any two fish breeding is inversely proportional to their distance apart, and the longitudinal differences in frequency represent a continuous cline or a stepped cline. Richardson (1983) proposed what appears to be a similar model of population structure for skipjack in the Pacific, based on the assumptions of random movement and no obstacles to movement other than distance.

According to the discrete-subpopulation hypothesis there are two or more genetically distinct subpopulations of skipjack in the Pacific which are largely reproductively isolated, and the longitudinal differences in frequency do not represent a cline. The western and eastern subpopulations could overlap, but interbreeding between the two would have to be prevented by some behavioral mechanism, such as spawning in different seasons or in different areas (Anonymous, 1984). It was observed, however, that sea-surface temperature (SST) and surface salinity show gradients across the Pacific, and that the longitudinal differences in the frequency of serum napthyl esterase might be related to some such environmental variable (Anonymous, 1981).

Fujino, Sasaki, and Okumura (1981), based on the frequencies of serum esterase and serum transferrin, found significant differences between skipjack from the Indian Ocean and the Atlantic, and skipjack from the Indian Ocean and the western Pacific. They proposed that skipjack originated in the Indian some dispersed to the other oceans, forming four Ocean. and that subpopulations through reproductive isolation: the Indian, the Atlantic, the western Pacific, and the central-eastern Pacific subpopulations. From 525 samples consisting of 24,191 skipjack captured across the Pacific, Fujino, Sasaki, and Okumura (1981: Figure 2) show: 1) that the frequency of serum napthyl esterase remains low from 80°W to 175°E; 2) that in the southern hemisphere there is a marked increase in frequencies from about 0.50 at 175°E to about 0.67 at 160°E; and 3) that in the northern hemisphere between 140°E and 175°E both high and low frequencies occur. From the second observation they concluded that the population structure was not clinal but was discontinuous, supporting the proposal by Fujino (1970) that there are two discrete subpopulations of skipjack in the Pacific. They regarded the third observation as supporting Fujino's (1979) proposal that fish from the central-eastern Pacific subpopulation occurred also off the east coast of Japan.

Kohno, Shimizu, and Nose (1985) reported significant variations in the morphometric characteristics among skipjack larvae from nine areas of the Pacific. Using cluster analysis they found three clusters separated by marked differences in characteristics: one in the northern hemisphere including localities south of Japan and off the Philippines to northwest of the Hawaiian Islands; one in the southern hemisphere between Papua New Guinea and 180°; and one in the eastern Pacific between 11°N and 8°S and 116°W and 148°W. These results support the hypothesis of multiple subpopulations for skipjack in the Pacific proposed by Fujino (1970) and Sharp (1978).

Graves and Dizon (1986) stated that: "Restriction enzyme analysis of mitochondrial DNA (mtDNA) provides the most powerful, practical tool currently available for determining the genetic basis of population structure." They analyzed mitochondrial DNA from skipjack from around the Hawaiian Islands and the Atlantic and found no significant genetic differentiation. They suggested that genetic contact has been maintained, at least until recently, by way of migration around South Africa. These results indicate that there may be no significant differentiation for skipjack in the eastern and western Pacific, since mixing of genetic material in the Pacific probably is greater than it is between the two oceans.

Ehrlich and Raven (1969), however, have proposed that the forces of natural selection are more important in speciation than are those of reproductive isolation, and that when selection is similar, isolated populations of the same species will remain similar, whereas when selection differs the populations will evolve eventually into different species. They mentioned several species of sexually reproducing animals whose populations have been isolated from each other for thousands or millions of generations and yet maintain similar phenotypes. Voss (1972) stated that about 50% of the species of marine animals on each side of the Isthmus of Panama are similar, and that some are even identical. About 1% of the fish species on both sides are regarded as identical species (Briggs, 1967). Thus it is possible that skipjack from the Atlantic and Pacific are similar because of similar selection, rather than because of genetic exchange between the two oceans as proposed by Graves and Dizon (1986).

Sharp (1978) shows ranges of two subpopulations in the eastern Pacific. Fujino, Sasaki, and Okumura (1981) note a difference in the frequencies of serum esterase north and south of the Equator in the Pacific east of Hawaii, lending some support to Sharp's (1978) delineation of two subpopulations in the eastern Pacific.

Skipjack are infrequently captured in an area of warmer water off southern Mexico centered at about 15°N (Joseph and Calkins, 1969: Appendix Figures 1A-15A). It has long been considered that skipjack caught off northern Mexico, northwest of this area, and those caught off Central America and northern South America, southeast of this area, might be from two different subpopulations. In late 1955 and in 1956, however, considerable amounts of skipjack were caught in this area (Broadhead and Barrett, 1964), showing that the distribution occasionally could be continuous from northern Mexico to northern South America. Williams (1970) states that data on the occurrence of skipjack show varying degrees of continuity along the Mexican coast during the first and last quarters when SSTs were lowest. In 1980 and 1981, large catches of skipjack were made between 10°N and 20°N, west of this area (Anonymous, 1981b and 1982: Figure 3) showing that the distribution of skipjack could be continuous around the area, and suggesting that skipjack caught north and south of it could belong to the same subpopulation. In Anonymous (1983) and Bayliff (1984) it was suggested that there is a single group of skipjack distributed in an arc-shaped area surrounding the area of warmer water off of southern Mexico. The evidence for this was: 1) that 23 skipjack tagged in the northeastern area north of 10°N were recaptured off the Hawaiian Islands; 2) that of three of the fish tagged in the southeastern area south of 10°N, one had been recaptured near Hawaii, one near 10°N-134°W, and one near 9°S-105°W; 3) that a fish tagged near 4°N-119°W was recaptured near Hawaii (Anonymous, 1982: Figure 6); 4) that two fish tagged in the southeastern area were recaptured in the northeastern area (Fink and Bayliff, 1970); and 5) that two fish tagged at Clipperton Island (10°18'N-109°13'W) were recaptured near Hawaii and one other was recaptured near 2°S-107°W.

It appears that it would be necessary to analyse considerably more genetic data before the population structure of skipjack across the Pacific could be described with any degree of confidence (Anonymous, 1984). The conclusion of Fujino, Sasaki, and Okumura (1981) that the population structure across the Pacific is discontinuous, with discrete western and central-eastern subpopulations, as first proposed by Fujino (1970), appears to be more likely than the clinal hypothesis, but there are not enough data to confirm this.

POSSIBLE MIGRATION ROUTES

Harden Jones (1968) classified "migratory movements" under three headings: drifting passively with the currents, random locomotory movements, and oriented locomotory movements. In a 1984 paper he stated, "I use the word migration in the sense of coming and going with the seasons on a regular basis." Forsbergh (1988) showed that catch rates of skipjack recruits in the eastern Pacific generally peaked in the second quarter of the year, indicating some degree of seasonality. In this report displacement from the eastern to the central Pacific, or vice versa, is referred to as migration.

From the results of skipjack tagging by the South Pacific Commission in the western and central Pacific, Kearney (1983: Figure 1) concluded that "few probable consistent migratory pathways in tropical areas" were revealed. Kearney, formerly with the IATTC, proposed that skipjack. Robert E. considered on a Pacific-wide basis, and particularly in the central and western tropical areas, do not to migrate toward specific areas for feeding or They are instead simply "vagile," meaning that they are highly spawning. mobile, but move in more or less random directions within broad limits, responding to short-term local stimuli. If this is true then many skipjack, having followed a short-term food trail or preferred environmental habitat, arriving in areas of poor forage, might starve; and many spawning skipjack might find themselves in areas unsuitable for the survival of the larvae and juveniles.

Using a numerical model, Seckel (1972) showed that skipjack could migrate from northern Mexico to the Hawaiian Islands by drifting westward in the North Equatorial Current (NEC). The minimum time required was 21 to 23 months. A total of 21 skipjack tagged off Baja California and the Revillagigedo Islands have been recaptured near Hawaii. Sixteen of these were recovered after 12-15 months, three after 20-25 months, one after 28 months, and one after 32 months. In addition, two skipjack tagged off Clipperton Island were recovered off Hawaii after 8-9 months, one tagged at 4°11'N, 119°02'W after 21 months, and one tagged at 4°56'N, 86°38'W after 16 months (data supplied by William H. Bayliff, IATTC). Since the majority of the fish made the journey in less time than the minimum required for drifting, it appears that the difference could be explained by a net swimming with the flow in the NEC.

Bayliff (1984: 29) found that the movement of skipjack tagged in the Gulf of Panama on two cruises was primarily toward Ecuador, and for those tagged on another cruise in the same area the movement was primarily parallel to the coast of southern Central America toward the west-northwest, and secondarily toward Ecuador. For skipjack tagged on three cruises off southern Central America the movement was primarily toward the Panama Bight and northern South America. That skipjack show some consistency of direction in the central portion of the eastern Pacific may indicate oriented movement there, rather than "vagile" or random movement. Keeping in mind the other hypotheses mentioned above, the discussions in the remainder of this section are based on the assumption that most of the skipjack caught in the eastern Pacific have migrated from the western and/or central Pacific as pre-recruits.

Gillett and Kearney (1983) reported that none of the 35,524 skipjack tagged in French Polynesia by the South Pacific Commission has been recovered in the eastern Pacific. Based on average speeds of about 0.32 knot (kt) for migrating skipjack tagged in French Polynesia, they estimated that it would take 300 to 350 days to reach the eastern Pacific fishing area, and by this time all of them would be larger than the size of the recruits in that area. Skipjack are recruited at about 35-40 cm in the eastern Pacific (Anonymous, 1985: Figure 51). Assuming a growth rate of 12 cm/year for skipjack from the SPC area (Gillett and Kearney, 1983), and 11 months to make the voyage, the fish would have to have been about 23-29 cm long when departing from the Marquesas Islands. Assuming an average growth rate of 24 cm/year, estimated for fish from the eastern Pacific (Forsbergh, 1988), the fish would have to have been about 11-18 cm long when departing from the Marquesas Islands. Gillett and Kearney (1983: Appendix C) show that all but a few of the fish tagged near the Marquesas were over 39 cm long. Assuming a growth rate of 12 cm/year, they estimated that fish tagged during the largest tagging experiment in the Marquesas Islands would be about 59 cm long on arrival in the eastern Pacific. Since fish larger than this comprised less than 10% of the eastern Pacific catch, they concluded that only a small part of the skipjack catch in that area could have come from fish of post-recruit lengths from the Marquesas Islands. These results do not detract from the possibility that large numbers of pre-recruits move eastward and reach recruit size in the eastern Pacific, since none of the data on skipjack movements include pre-recruits.

Williams (1972) hypothesized three models for the migration of skipjack from the central Pacific to the eastern Pacific: an active migration model where the fish swim eastward against the westward-flowing North and South Equatorial Currents (NEC and SEC); a passive migration model where the fish are carried eastward by the North and South Equatorial Countercurrents (NECC and SECC); and a gyral migration model where the fish of the northern fishery are carried in the counterclockwise gyre of the northern equatorial water mass of the eastern Pacific, and most of the fish of the southern fishery are carried in a clockwise gyre formed by the NECC and the SEC.

The NECC could be a major migration route eastward if sufficient numbers of skipjack were spawned in the current and remained in it, or if sufficient numbers spawned outside the current were able to move into it, and sufficient forage of the size required for the various stages of skipjack development were available along the current. Of 15 buoys equipped with parachute drogues at 30 m and placed in the NECC between 160° W and 150° W, 7 drifted in the current as far east as 116° W to 107° W, before being carried to the northwest in the NEC. They moved eastward over 4500 km (2428 miles) in 4 months (Wyrkti *et al.*, 1981). At these velocities of about 0.83 kt, skipjack could be transported from 180° to 85° W (5700 miles) in about 9 months, and from 135° W to 85° W (3000 miles) in about 5 months. The NECC extends eastward to about 85° W from May to December, but reaches only to about 120° W in February and March (Wyrtki, 1967).

It was suggested by Gunter R. Seckel, formerly with U.S. National Marine Fsheres Service (NMFS), Honolulu, Hawaii, that variations in the speed of the NECC should be investigated in relation to catch rates of skipjack in the eastern Pacific. Considering Williams' (1972) passive migration model, it was hypothesized that more young skipjack could be carried from the spawning areas to the fishing areas when the NECC is strong, and fewer young skipjack could be carried eastward when it is weak. Forsbergh (1988), however, found no correlation between the catch rate of skipjack recruits in the eastern Pacific and the speed of the NECC.

For his passive migration model Williams (1972) mentioned the SECC as another possible migration route when it occurred at the surface in the eastern Pacific, but stated that recruitment to the southern part of the fishery would be prevented by low temperatures in the southern winter. In four sections from 20°N to 17°S along 150°W during the NORPAX Shuttle Experiment from January 1977 to February 1978, the SECC between $9^{\circ}S$ and $13^{\circ}S$ (Wyrtki *et al.*, 1981) had geostrophic velocities in the core of about 10 cm/sec (about 0.2 kt), while core velocities in the NECC were about 40 to 60 cm/sec (about 0.8 to 1.2 kt; Taft and Kovala, 1979). In four similar sections along 150°W from March to June 1979, there was no eastern flow south of 5°S that would indicate the presence of the SECC (Taft and Kovala, 1981). From these results it is here concluded that the potential for transport of skipjack eastward in the SECC is small relative to that in the NECC.

It has been suggested by Richard A. Barkley and Richard S. Shomura (Williams, 1972) that the eastward-flowing Equatorial Undercurrent (EUC, *i.e.*, Cromwell Current) might also carry young skipjack to the eastern Pacific. Williams (1972) believed that temperatures were marginal $(18^{\circ}-20^{\circ}C)$ for skipjack of fishable size (length >35 cm) and too low for the larvae in the upper part of the EUC east of 120°W. Skipjack larvae and juveniles <15 cm are seldom found in waters with SST <24°C (Ueyanagi,1969; Mori, 1972). In the eastern Pacific, Broadhead and Barrett (1964) and Blackburn (1969) showed that fishable concentrations of skipjack occasionally were found when SSTs were as low as 17°C and as high as 30°C, but usually were found between 20° and 28°C; Williams (1970) gave the usual range as $20^{\circ}-29^{\circ}C$.

The EUC flows beneath the surface at the equator from depths of about 25 to 300 m, as indicated by the velocity of 25 cm/sec (0.5 kt) or greater. The core, at depths of 50 to 100 m, attains maximum speeds of 2 to 3 kt (Knauss, 1960 and 1966). In a section through the EUC at 140°W in 1958, Knauss (1960: Figure 9) shows that the temperature at the core was 18°C, and temperature at the top was >26°C. Knauss (1966: Figure 3) shows the 25 cm/sec flow near the top of the EUC at 140°W in 1961 to be at 75 m, where the temperature was 22.8°C (Anonymous, 1966: 4-5). Colin *et al.* (1971: Figure 4) show three sections through the EUC at 156°W, 148°W, and 140°W in 1970: temperatures were around 19°-20°C in the core, and around 25°-26°C at zero flow at the top of the current.

While temperatures may be suitable for skipjack at some depth in an area, or in a current, oxygen concentrations may be too low. Barkley, Neill, and Gooding (1978) mention experiments with skipjack in tanks where the fish appeared to be under stress at oxygen concentrations of 2.8 ml/l, and only one out of six survived over 4 hours at 2.5 ml/l, at temperatures of 23°-24°C. They selected a conservative lower limit of 3.5 ml/l for their model of the habitat available to skipjack. Little is known, however, about the metabolic requirements of juvenile skipjack since they are rarely found in places other than the stomachs of predators. Christofer H. Boggs, U.S. NMFS, Hawaii, has suggested that juveniles may prefer colder deeper water than adults and larvae, finding a refuge there from cannibalism. Gooding, Neill, and Dizon (1981) found that weight-specific metabolic rates of skipjack ranging from 0.6 to 5.2 kg increased with weight. This indicates that juveniles may have lower weight-specific rates and lower oxygen requirements than adults. Colin et al. (1971: Figure 4) show that oxygen concentrations were about 3 ml/l at the core of the EUC, and about 4 ml/l at the top. It appears that temperatures may be suitable for skipjack of fishable size in the upper part of the EUC at 156°-140°W, but that oxygen concentrations may be close to the lower limit for them, but may be suitable for juveniles. Temperatures appear to be too low in the EUC for skipjack larvae and juveniles <15 cm.

Farther east, from sections across the EUC in 1967 and 1968 (Love and Allen, 1970-1977), temperatures at 25 m at the equator averaged 22.8°, 21.5°, 21.8°, and 20.6°C at 119°W, 112°W, 105°W, and 98°-95°W, respectively. At these longitudes Knauss (1966, Figure 3) shows that the 25 cm/sec (0.5 kt) flow near the top of the EUC was at 35-40 m, and temperatures at these depths from Love and Allen (1970-1977) could be considered too cold for skipjack of fishable size. In 1961 temperatures at the 25 cm/sec flow near the top of the EUC were 19.6°, 15.2°, and 15.5°C at 118°W, 96°W, and 93°W, respectively (Knauss, 1966: Figure 3: Anonymous, 1966: 14, 24, and 43), indicating that temperatures in the EUC were probably too low for skipjack of fishable size at these longitudes. Robinson (1976) shows temperatures in the Pacific north of 5°S at the surface and at increments of 100 ft (30 m) to a depth of 400 ft Examination of temperatures along the equator at depths of 300 (91 (122 m). m) and 400 ft (122 m), in conjunction with Figure 3 in Knauss (1966) and Figure 1 in Colin et al. (1971), suggest that temperatures may be suitable (>20°C) for skipjack of fishable size in the upper part of the EUC west of around 140°W, but are too cold east of this longitude. Possibly young skipjack are carried eastward in the EUC to around 140°W, and may then avoid colder water by moving out of the EUC into the surrounding SEC.

Assuming that significant spawning by skipjack in the central Pacific extends from about 25° of latitude in the summer hemisphere to about 15° of latitude in the winter hemisphere (Nishikawa *et al.*, 1985), the range of spawning would be about 40° of latitude at any given time. Mori (1972: Figure 3) shows the geographic distribution of skipjack found in the stomachs of predators. In the Pacific between 180° and 120°W the latitudinal range of occurrence of juveniles <15 cm was 24°N-28°S from May to October and 15°N-23°S from November to April. Ranges for 15- to 35-cm skipjack were similar. It appears that significant numbers of juveniles are found within a latitudinal range of abut 40°, similar to that for the larvae.

Nishikawa et al. (1978 and 1985) show the concentration of skipjack larvae from Japanese larval net tows in the Pacific, but the data are judged insufficient to determine whether the concentration of skipjack larvae in the central Pacific is related to zonal currents. Similarly Mori's (1972) geographic distribution of catches of predators from which stomach samples were taken is judged inadequate east of 180° to determine whether the concentration of juvenile skipjack is related to zonal currents. Argue, Conand, and Whyman (1983) found juvenile skipjack, mostly <15 cm, in the stomachs of skipjack and other predators caught west of 180° in the South Pacific Commission area to be scarce in the NECC and in the region of equatorial upwelling west of 180°.

In an attempt to estimate the proportions of juvenile skipjack carried eastward in the NECC, the following assumptions are proposed on the basis of the preceding discussion: 1) the range of significant spawning and distribution of larvae and juveniles in the central Pacific is about 40° of latitude; 2) the latitudinal concentrations of juveniles east of 180°, at adequate temperatures, are similar in the NEC, the NECC, and the SEC; 3) the width of the NECC below the surface at adequate temperatures is the same as at the surface, as shown by velocity sections in Taft and Kovala (1979 and 1981); 4) the eastward transport of juveniles in the SECC is negligible because the current, when it exists, is much weaker than the NECC; and 5) few juveniles exist in the EUC because temperatures are too low. The average monthly width of the NECC at 130°W varies from 3° to 6° of latitude (Wyrtki, 1965: Figures 1-12) comprising 7.5 to 15% of the 40° latitudinal range of the juveniles. Sections along 150°W during 1977 and 1978 show the NECC to vary from 4° to 6° of latitude (Taft and Kovala, 1979). If the preceding assumptions are true, only 7.5 to 15% of the juvenile skipjack will be carried eastward in the NECC, the major portion being carried westward in the NEC and the SEC. Those spawned in the NEC or the SEC would either have to swim against these currents when large enough to do so, or swim north or south into the NECC, and possibly the EUC, to reach the eastern Pacific. Mean monthly speeds of the westward currents east of 140°W from Wyrtki (1965: Figures 14 and 16) are given below:

Curre	nt Re	gion	Months	Speed (kt)				
				Mean	Range			
NEC	15°-21°N.	140°-130°W	January-December	0.31	0.28-0.36			
SEC	0° - 3°N,	130°-110°W	December-May	1.06	0.72-1.41			
SEC	0° - 3°N,	130°-110°W	June-November	1.64	1.44-1.87			
SEC	0° - 5°S,	130°-110°W	January-December	0.86	0.80-0.91			
SEC	0°-10°S,	140°-130°W	January-December	0.68	0.59-0.80			

Skipjack larvae and small juveniles are presumably dependent upon currents for any extensive horizontal movements. The degree of dependence on currents decreases with size as swimming speed increases with size. Skipjack between 38 and 50 cm in length must swim at a minimum speed of 1.5 body lengths per second (1/sec) to maintain hydrostatic equilibrium (Magnuson, 1978: Figure 1). The maximum sustainable speed is estimated to be 6 1/sec (Dizon, Brill, and Yuen, 1978). Taking 3-4 1/sec as intermediate speeds between these limits, the estimated lengths of skipjack required for various sustained speeds can be calculated: a fish must be 13-17, 26-34, and 38-51 cm long to maintain speeds of 1, 2, and 3 kt, respectively. It appears that fish of all three sizes would have no problem migrating eastward against the NEC, which has an average speed of 0.3 kt. Current speeds in the SEC, however, are about 2 to 6 times as great as those in the NEC and fish would have to swim at greater speeds to make any significant eastward movement in this current. Thus it is questionable whether the smaller skipjack could migrate eastward in the faster portions of the SEC, particularly between 0° and 3°N. If much of the swimming is random wandering then net eastward movement in the westward currents may be too slow and the fish may be able to move only eastward at an adequate speed in the eastward currents. Wandering in the eastward currents would eventually bring them into the western currents unless they were able to detect the current boundaries and turn back. The mean speed of all skipjack tagged in the eastern Pacific and recaptured in the central or western Pacific was 6.7 miles per day or about 0.3 kt; the fastest fish had a speed of 0.5 kt. At a speed of 0.3 kt skipjack would be unable to move eastward against the NEC or the SEC, and the only possible migration routes would be the NECC or the EUC.

Skipjack probably have a navigational ability which could guide them in various directions at various stages of development according to their genetic programming. Skipjack may have more than one way of sensing direction, as has

been determined for pigeons and other birds (Keeton, 1974; Gould, 1980). Possibly they can also navigate by the sun when close to the surface, using time compensation, or by the plane of polarized light on partly overcast days when some blue sky is still visible. The young skipjack in the central Pacific might receive a physiological signal to swim eastward or swim toward the NECC or the EUC at a certain developmental stage (Williams, 1972) and the survivors would eventually arrive at the rich feeding areas of the eastern The adult skipjack in the eastern Pacific might receive a signal to Pacific. swim westward at a certain stage and the survivors would eventually arrive at the spawning areas, completing the cycle. Magnetite crystals, which would enable them to orient themselves to the earth's magnetic field, have been found in the heads of yellowfin (Walker et al., 1984); it is likely that they also occur in skipjack. It is not known whether skipjack can differentiate among currents, but they would need to do so in order to cease swimming northward or southward when reaching the eastward currents. David Au, U.S. NMFS, La Jolla, California, has suggested that they may identify currents by the kind of forage available, or by the smell or taste of the water.

From the preceding discussion it is unclear whether Williams' (1972) active or passive migration model is the more realistic. Those fish spawned in the NECC and the EUC, or entering them by chance or intent would be swimming eastward in the currents while being carried eastward and make greater progress with less expenditure of energy than those swimming against the NEC and the SEC.

ACKNOWLEDGEMENTS

The manuscript was read critically by David Au, William H. Bayliff, Christofer H. Boggs, Patrice Cayré, and Robert E. Kearney.

LITERATURE CITED

- Anonymous. 1966. Physical, chemical, current measurements, and biological data. Swan Song Expedition, 21 August-1 December 1961. Scripps Inst. Oceanogr., Tech. Rep., Ref. 66-1: 125 pp.
- Anonymous. 1980. Review of preliminary results from genetic analysis of skipjack blood samples collected by the Skipjack Survey and Assessment Programme. South Pac. Comm., Skipjack Survey and Assessment Programme, Tech. Rep., 1: 22 pp.
- Anonymous. 1981a. Report of the second Skipjack Survey and Assessment Programme workshop to review results from genetic analysis of skipjack blood samples. South Pac. Comm., Skipjack Survey and Assessment Programme, Tech. Rep., 6: 39 pp.

Anonymous. 1981. Inter-Am. Trop. Tuna Comm., Annu. Rep., 1980: 234 pp.

Anonymous. 1982. Inter-Am. Trop. Tuna Comm., Annu. Rep., 1981: 303 pp.

Anonymous. 1983. Inter-Am. Trop. Tuna Comm., Annu. Rep., 1982: 294 pp.

Anonymous. 1984. Inter-Am. Trop. Tuna Comm., Annu. Rep., 1983: 272 pp.

Anonymous. 1985. Inter-Am. Trop. Tuna Comm., Annu. Rep., 1984: 270 pp.

- Argue, A.W., F. Conand, and D. Whyman. 1983. Spatial and temporal distributions of juvenile tunas from stomachs of tunas caught by pole-and-line gear in the central and western Pacific Ocean. South Pac. Comm., Tuna and Billfish Assessment Programme, Tech. Rep., 9: 47 pp.
- Barkley, R.A., W.H. Neill, and R.M. Gooding. 1978. Skipjack tuna, Katsuwonus pelamis, habitat based on temperature and oxygen requirements. U.S. Nat. Mar. Fish. Serv., Fish. Bull., 76(3): 653-662.
- Bayliff, W.H. 1984. Migrations of yellowfin and skipjack tuna released in the central portion of the eastern Pacific Ocean, as determined by tagging investigations. Inter-Am. Trop. Tuna Comm., Internal Rep., 18: 107 pp.
- Blackburn, M. 1969. Conditions related to upwelling which determine distribution of tropical tunas off western Baja California. U.S. Fish Wild. Serv., Fish. Bull., 68(1): 147-176.
- Briggs, J.C. 1967. Relationship of the tropical shelf regions. Univ. Miami Inst. Mar. Sci., Stud. Trop. Oceanogr., 5: 569-578.
- 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. Inter-Am. Trop. Tuna Comm., Bull., 8(8): 417-473.
- Colin, C., C. Henin, Ph. Hisard, and C. Oudot. 1971. Le Courant de Cromwell dans le Pacifique Central en février 1970. Cah. ORSTOM, sér. Océanogr., 9(2): 167-186.

- Dizon, A.E., R.E. Brill, and H.S.H. Yuen. 1978. Correlations between environment, physiology, and activity and the effects of thermo-regulation in skipjack tuna. In Sharp, G.D., and A.E. Dizon (editors), The Physiological Ecology of Tunas, Academic Press, New York: 233-259.
- Ehrlich, P.R., and P.H. Raven. 1969. Differentiation of populations. Science, 165(3899): 1228-1232.
- 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. Inter-Am. Trop. Tuna Comm., Bull., 15(1): 1-227.
- Forsbergh, E.D. 1988. The influence of some environmental variables on the apparent abundance of skipjack tuna, *Katsuwonus pelamis*, in the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm., Bull., in preparation.
- Fujino, K. 1970. Immunological and biochemical genetics of tunas. Trans. Am. Fish. Soc., 99(1): 152-178.
- Fujino, K. 1979. Genetic isolation of skipjack tuna in the western Pacific Ocean. In A.Y. Takenouti (editor), The Kuroshio IV, Saikon Publ. Co., Tokyo: 732-742.
- Fujino, K., K. Sasaki, and S. Okumura. 1981. Genetic diversity of skipjack tuna in the Atlantic, Indian, and Pacific Oceans. Bull. Jpn. Soc. Sci. Fish., 47(2): 215-222.
- Gillett, R.D., and R.E. Kearney. 1983. An assessment of the skipjack and baitfish resources of French Polynesia. South Pac. Comm., Skipjack Survey and Assessment Program, Final Country Report, 7: 81 pp.
- Gooding, R.M., W.H. Neill, and A.E.Dizon. 1981. Respiration rates and low-oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis*. U.S. Nat. Mar. Fish. Serv., Fish. Bull., 79(1): 31-48.
- Gould, J.L. 1980. The case for magnetic sensitivity in birds and bees (such as it is). Am. Sci., 68(3): 256-267.
- Graves, J.E., and A.E. Dizon. 1986. Mitochondrial DNA genetic similarity of Atlantic and Pacific skipjack tuna and its management implications. In Symons, P.E.K., P.M. Miyake, and G.T. Sakagawa (editors). Proceedings of the ICCAT Conference on the International Skipjack Year Program. Int. Comm. Conserv. Atl. Tunas, Madrid: 237-241.

Harden Jones, F.R. 1968. Fish Migration. Edward Arnold Ltd., London: 325 pp.

- Harden Jones, F.R. 1984. A view from the ocean. In J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill (editors), Mechanisms of Migration in Fishes, Plenum Press, New York and London: 1-26.
- Joseph, J., and T.P.Calkins. 1969. Population dynamics of the skipjack tuna (Katsuwonus pelamis) of the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm., Bull., 13(1): 1-273.

- Kearney, R.E. 1983. Assessment of the skipjack and baitfish resources in the central and western tropical Pacific Ocean: a summary of the Skipjack Survey and Assessment Programme. South Pac. Comm.: 37 pp.
- Keeton, W.T. 1974. The mystery of pigeon homing. Sci. Amer., 231(6): 96-107.
- Knauss, J.A. 1960. Measurements of the Cromwell Current. Deep-Sea Res., 6(4): 265-286.
- Knauss, J.A. 1966. Further measurements and observations on the Cromwell Current. J. Mar. Res., 24(1): 205-240.
- Kohno, H., M. Shimizu, and Y. Nose. 1985. Geographic variation of the larval skipjack tuna, Katsuwonus pelamis (LINNAEUS), from the Pacific Ocean. Bull. Far. Seas Fish. Res. Lab., 22: 131-146.
- Love, C.M., and R.M. Allen (editors). 1972-1977. EASTROPAC Atlas. U.S. Nat. Mar. Fish. Serv., Circ. 330, Vols. 1-11.
- Magnuson, J.J. 1978. Locomotion by scombrid fishes: hydrodynamics, morphology, and behavior. In Hoar, W.S., and D.J. Randall (editors), Fish Physiology, Vol. 7, Academic Press, New York: 239-313.
- Mori, K. 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). Bull. Far Seas Fish. Res. Lab., 6: 111-168.
- Nishikawa, Y., M. Honma, S. Ueyanagi, and S. Kikawa. 1985. Average distribution of larvae of oceanic species of scombroid fishes, 1956-1981. Far Seas Fish. Res. Lab., S Ser., 12: 99 pp.
- Nishikawa, Y., S. Kikawa, M. Honma, and S. Ueyenagi. 1978. Distribution atlas of larval tunas, billfishes and related species--results of larval surveys by R/V Shunyo Maru and Shoyo Maru, 1956-1975. Far Seas Fish. Res. Lab., S Ser., 9: 99 pp.
- Richardson, B.J. 1983. Distribution of protein variation in skipjack tuna (Katsuwonus pelamis) from the central and south-western Pacific. Aust. J. Mar. Freshwater Res., 34(2): 231-251.
- Robinson, M.K. 1976. Atlas of North Pacific Ocean monthly mean temperatures and mean salinities of the surface layer. U.S. Naval Oceanogr. Office, RP-2: xix, 173 figs.
- Rothschild, B.J., 1965. Hypotheses on the origin of exploited skipjack tuna (Katsuwonus pelamis) in the eastern and central Pacific Ocean. U.S. Fish. Wild. Serv., Spec. Sci. Rep. Fish., 512: 20 pp.
- Schaefer, M.B. 1963. Report on the investigations of the Inter-American Tropical Tuna Commission for the year 1962. Inter-Am. Trop. Tuna Comm., Annu. Rep., 1962: 35-149.

- Seckel, G.R. 1972. Hawaiian-caught skipjack tuna and their physical environment. U.S. Nat. Mar. Fish. Serv., Fish. Bull., 70(3): 763-787.
- Sharp, G.D. 1978. Behavioral and physiological properties of tuna and their effects on vulnerability to fishing gear. In Sharp, G.D., and A.D. Dizon (editors), The Physiological Ecology of Tunas, Academic Press, New York: 397-449.
- Taft, B., and P. Kovala. 1979. Temperature, salinity, thermosteric anomaly and zonal geostrophic velocity sections along 150°W from NORPAX Shuttle Experiment (1977-78). Univ. Wash., Dept. Oceanogr., Spec. Rep., 87. Ref. M79-17: 28 pp.
- Taft, B., and P. Kovala. 1981. Vertical sections of temperature, salinity, thermosteric anomaly and zonal geostrophic velocity from NORPAX Shuttle Experiment. NOAA Data Rep. ERL PMEL-3, Pac. Mar. Envir. Lab., Seattle: 98 pp.
- 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*. Bull. Far Seas Fish. Res. Lab., 2: 177-256.
- Voss, G.L. 1972. Biological results of the University of Miami Deep-Sea Expeditions. 93. Comments concerning the University of Miami's Marine Biological Survey related to the Panamanian Sea-level Canal. In M.L. Jones (editor), The Panamic Biota. Some Observations Prior to a Sea-level Canal, Bull. Biol. Soc. Wash., 2: 49-58.
- Walker, M.M., J.L. Kirschvink, S.R. Chang, and A.E. Dizon. 1984. A candidate magnetic sense organ in the yellowfin tuna, *Thunnus albacares*. Science, 224(4650): 751-753.
- Williams, F. 1970. Sea surface temperature and the distribution and apparent abundance of skipjack (Katsuwonus pelamis) in the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm., Bull., 15(2): 229-281.
- Williams, F. 1972. Consideration of three proposed models of the migration of young skipjack tuna (*Katsuwonus pelamis*) into the eastern Pacific Ocean. U.S. Nat. Mar. Fish. Serv., Fish. Bull., 70(3): 741-762.
- Wyrtki, K. 1965. Surface currents of the eastern tropical Pacific Ocean. Inter-Am. Trop. Tuna Comm., Bull., 9(5): 269-304.
- Wyrtki, K. 1967. Circulation and water masses in the eastern equatorial Pacific Ocean. Int. J. Oceanol. Limnol., 1(2): 117-147.
- Wyrtki, K., E. Firing, D. Halpern, R. Knox, G.J. McNally, W.C. Patzert, E.D. Stroup, B.A. Taft, and R. Williams. 1981. The Hawaii to Tahiti Shuttle Experiment. Science, 211(4477): 22-28.