HAWAIIAN-CAUGHT SKIPJACK TUNA AND THEIR PHYSICAL ENVIRONMENT

GUNTER R. SECKEL¹

ABSTRACT

Empirical associations between the occurrence of skipjack tuna (Katsuwonus pelamis) in Hawaiian waters and environmental conditions point to the current system as an important cause for the variations in the Hawaiian fishery. Large interyear differences of sea-air interactions in the skipjack spawning areas may affect larval survival and year-class strength. A numerical drift model was used to investigate the contribution of currents to the travel of skipjack from the eastern North Pacific to Hawaii. Floating objects introduced in the model ocean at long 120°W and lat 10° to 20°N converge toward the northern edge of the North Equatorial Current near Hawaii in 21 to 23 months. The time of freedom of skipjack tagged in the eastern North Pacific and recovered in Hawaiian waters is of the same magnitude. It is concluded that for skipjack a possible mode of travel from the eastern North Pacific to Hawaii is drifting in the North Equatorial Current. The variability in abundance and size-frequency distributions observed in the Hawaiian fishery can be caused by changes in the current system. Numerical models of the type presented can be verified and so permit progress from the exploratory to the experimental phase in fisheries investigations.

Over a decade ago empirical associations were established between environmental parameters and the availability of skipjack tuna (*Katsuwonus pelamis*) to the Hawaiian fishery. Since that time oceanographic studies have provided additional information to augment these associations that can now be used to postulate causal relationships. Such hypotheses are an essential step in bringing ecological studies from the exploratory to the experimental phase, numerical analysis, and, eventually, prediction.

In this paper I will briefly review the empirical associations that were established and introduce new information that has resulted from the Trade Wind Zone Oceanography investigation. The empirical associations lead to two environmental processes that must be included in numerical models describing the distribution of skipjack. One concerns the sea-air interaction processes that may affect productivity and larval survival, and the other concerns the current field that affects the distribution of skipjack schools. The latter is illustrated by a numerical "drift model" for a portion of the Pacific North Equatorial Current.

The purely physical explanations that are given for the varying availability of skipjack in the Hawaiian fishery and the implications of the drift model results may conflict with beliefs based on biological considerations. Such conflicts can be resolved if the proposed hypotheses are tested experimentally as suggested in this paper.

It is fitting that this work should be reported in Dr. Sette's Festschrift. He provided great impetus and leadership to the integration of environmental studies with fisheries research. The work on Hawaiian-caught skipjack and on their environment was initiated at the time Dr. Sette directed the Pacific Oceanic Fishery Investigations (POFI) in Hawaii.

REVIEW OF EMPIRICAL ASSOCIATIONS

THE HAWAIIAN SKIPJACK FISHERY

The Hawaiian skipjack fishery has been described by Yamashita (1958) and Uchida

¹ National Marine Fisheries Service, Pacific Environmental Group, Monterey, CA 93940.

(1966). Landings from this fishery range from about 91 tons² (200,000 lb) per month in February to more than 907 tons (2 million lb) per month in July. Total annual landings also show wide variations ranging from 2,676 tons (5.9 million lb) as in 1969 to 7,302 tons (16.1 million lb) as in 1965.^s Hawaiian fishing vessels fish within sight of land, mainly in the vicinity of the islands of Oahu to Maui and Hawaii (Uchida, 1970). Thus, Hawaiian skipjack landings provide, in contrast to other fisheries where fishing fleets may follow the fish concentrations, a time sequence measure from a fixed area.

Uchida (1967) analyzed the catch and effort in the Hawaiian fishery and found that although there has been a decline in the number of vessels fishing on a full-time basis during the last 15 years, there is no clear evidence that this decline has affected total landings. It appears that the decline in the number of fishing vessels occurred primarily among the smaller boats (Uchida 1966: Table 6) and, also, that the decline was offset by increased efficiency of fishing. For purposes of this paper, it is important to note that the large fluctuations in total annual landings are also reflected by the average annual catch per standard effective trip (Uchida, 1967: Figure 8). The annual landings of skipjack, therefore, reflect availability near Hawaii.

THE OCEAN ENVIRONMENT NEAR HAWAII

The oceanographic climate of the Hawaiian Islands region was described by Seckel (1962). Of interest are the North Pacific Central and the North Pacific Equatorial water types and the transition water of the California Current Extension between these water types (Figure 1). Seckel (1968) defined the North Pacific Central water as that with a salinity of more than $34.8\%_o$ and the North Pacific Equatorial water as that with a salinity of less than $34.2\%_o$. These salinities are always found in the salinity gradients that actually define the water type boundaries.

The boundary of the North Pacific Central water lies near the Hawaiian fishing area and is displaced north-southward both seasonally and nonseasonally. Usually the boundary lies just south of the islands in fall and winter and within or north of the islands during spring and summer. The boundary displacement is reflected by the salinity as measured at Koko Head. Oahu (Seckel and Yong, 1971). Low salinities occur during spring and summer and high salinities during fall and winter. During some years, such as in 1957 and 1958, the islands were bathed in North Pacific Central water throughout the year and in 1968 the islands were bathed in the transition water of the California Current Extension throughout the year.

The large effect of heat exchange across the sea surface tends to obscure the effect of advection on the sea-surface temperature. Nevertheless, the change of temperature due to advection is apparent in graphs of the change of temperature per month (Seckel, 1962). Warm advection in late winter and early spring causes the temperature in Hawaiian waters to rise before it would rise due to the onset of seasonal heating across the sea surface. The temperature increases and the salinity decreases southward near Hawaii. Warm advection is therefore associated with a northward component of flow that also causes a decline in the salinity.

Extremes of temperature and salinity as observed at Koko Head, Oahu, range from about 22.5°C in February or March to 27.4°C in September or October and from 34.4% in July to 35.5% in late fall or early winter. Inorganic phosphate concentrations in the Hawaiian region as well as in the North Equatorial Current are about 0.3 µg at./liter. Seasonal variations have not been observed.

In the Hawaiian region 10 to 40 cc of zooplankton per 1,000 m^a of water are filtered by a 1-m net in 200-m oblique tows (King and Hida, 1954, 1957a, 1957b; Nakamura, 1967). King and Hida (1954: Figure 16) indicate that an average zooplankton volume of about 25 cc per 1,000 m³ of water filtered near Hawaii compares with 20 to 25 cc in the North Equatorial Current and with about 38 cc near the equator to the south of Hawaii. There is no clear indication of a sea-

² Metric tons are used throughout this paper.

^{*} Source: Hawaii State, Division of Fish and Game.



FIGURE 1.-Schematic chart of the major North Pacific water types and currents.

sonal variation in zooplankton concentrations in Hawaiian waters but longer term variations appear to take place. There has been no systematic sampling of tuna forage by midwater trawls.

SKIPJACK AND THE ENVIRONMENT

Blackburn (1965) summarized the range of environmental conditions within which skipjack are known to exist. The conditions summarized in the previous section fall well within this range. The seasonal changes in the Hawaiian environment are therefore not the probable cause for the variations in skipjack availability. Inorganic phosphates, as possibly affecting primary productivity, or the concentration of zooplankton vary insufficiently to explain a tenfold increase in catch rates during the summer months.

It is common to think of temperature and salinity changes in terms of their physiological effect on the biota. These changes, however, also reflect dynamic properties of the environment such as heat exchange across the sea surface and advection that, in turn, affect biological distributions. Thus, when temperature and salinity changes were used in the Hawaiian region as indices of heat exchange and advection (Seckel, 1962) associations between the dynamic properties of the environment and the availability of skipjack became apparent. Development of the empirical associations and their implications can be traced in Seckel and Waldron (1960), Murphy, Waldron, and Seckel (1960), Seckel (1962), U.S. Bureau of Commercial Fisheries (1963).

It was found that the seasonal intrusion of the California Current Extension water into the Hawaiian region, as reflected by the surface salinity, coincides with the seasonal increase in the availability of skipjack. To monitor this association, the salinity measured at Koko Head, Oahu, during July can be used as an index of the water type during the peak of the fishing season.

The northward component of flow during late winter and early spring that causes the displacement of North Pacific Central water by California Current Extension water near Hawaii, also causes warm advection. It was found that strong or early warm advection as reflected by

TABLE 1.—Annual landings of skipjack in Hawaii, 1952-1970, with time of initial warming and mean July salinities of sea-surface water.

Year	Time of initial warming ¹	July mean salinity (‰) ¹	Total landings 10 ³ metric tons
1952	March	>34.8	3.31
1953	February	<34.8	5.47
1954	February	<34.8	6.36
1955	March	<34.8	4.40
1956	February	34.72	5.05
1957	March	34.98	2.78
1958	March	34.87	3.10
1959	February	34.73	5.63
1960	March	34.69	3.34
1961	February	34.77	4.94
1962	March	34.86	4.27
1963	February	34.84	3.67
1964	March	34.82	4.09
1965	February	34.67	7.33
1966	March	35.01	4.26
1967	January	34.83	3.65
1968	January	34.50	4.23
1969	February	34.72	2.71
1970	March	34.98	3.33

¹ Time of warming and July salinities are based on observations at Koko Head, Oahu, except 1952 to 1955 when they are based on observations irregularly made in the vicinity of Oahu.

initial warming occurring before the end of February precedes favorable fishing conditions. Weak or late warm advection is reflected by initial warming in March and precedes unfavorable fishing conditions.

The empirical associations are summarized in Table 1, giving the time of initial warming (temperature index), the mean July salinity, and the annual landings of skipjack in Hawaii. The indices are based on measurement, regularly made at Koko Head, Oahu, since November 1955. Indices between 1952 and 1955 are estimates based on sea-surface temperature and salinity observations irregularly made in the vicinity of Oahu. Prior to 1952 there were insufficient data to make estimates.

When the associations between availability of skipjack and time of initial warming were first established, monthly mean temperatures were used. Now Koko Head temperatures are expressed by harmonic functions of time (Seckel and Yong, 1971). These functions have been used to determine objectively the time of initial warming given in Table 1. Formerly, a salinity of 35% was used to indicate the boundary between North Pacific Central and California Current Extension waters. Here, in keeping with the definitions given by Seckel (1968), a salinity of 34.8% has been used to indicate this boundary.

The temperature and salinity indices can each be assigned a rating of favorable (F) or unfavorable (U) for fishing. There are therefore three categories according to which the landings are classified and shown in Figure 2a: Both indices favorable (FF), one unfavorable (FU or UF), and both unfavorable (UU).

The 1968 and 1969 landings did not fall within the FF range of previous years. Examination of environmental conditions revealed that during these years minimum salinities were the lowest recorded since the sampling series began at Koko Head, Oahu (Seckel and Yong, 1971). A sharp drop in values took place in late winter 1968 and the salinity remained low until late summer of 1969 when values rose to a normal level. Minimum salinities occurred in June 1968 and May 1969 and averaged 34.49% and 34.59% , respectively. This information, as well as that to be introduced in the next section, indicates that favorable "skipjack water" is confined to the high-salinity portion of the California Current Extension. For favorable fishing conditions, therefore, the additional constraint is introduced that mean monthly salinities during spring must be above 34.6%. With this new constraint, landings for 1968 and 1969 fall into the FU category (Figure 2b).

Of the 19 years for which skipjack landings in Hawaii can be associated with environmental conditions, 6 years fall in the FF category, 7 in the UU category, and 6 in the FU category when the revised salinity index is used. Figure 2b illustrates that there is a clear separation between the landings in the FF category on the one hand and the FU and UU categories on the other. The average annual landings are 5,800 tons, and 3,700 tons and 3,600 tons in the FF, FU, and UU categories, respectively. The lowest value in the FF category (4,900 tons) is higher than the highest value in the FU category (4,400 tons) or in the UU category (4,300 tons). The 19year average of annual landings was 4,300 tons.

Annual landings, therefore, can be classified into two groups. One group comprises the landings in the FU and UU categories that average 3,600 tons and range from 2,710 to 4,400



FIGURE 2.—Annual skipjack landings in Hawaii grouped according to the temperature and salinity indices being both favorable, FF, one favorable and the other unfavorable, FU, and both unfavorable, UU. Panel A: Salinity index is favorable with July salinity less than 34.8‰. Panel B: Salinity index is favorable with July salinity less than 34.8‰ but spring salinity higher than 34.6‰.

tons. The other group comprises the landings in the FF category that average 5,800 tons and range from 4,940 to 7,330 tons. Landings in the first group occur two-thirds of the time and are normal for Hawaii. Landings in the latter group are clearly exceptional.

Into which of the two groups landings will fall is in part predictable. The temperature index is determined in April, well before the beginning of the summer fishing season. The salinity, however, is monitored during spring and has little predictive value. During the 19 years under consideration there have been 4 years when the temperature index was favorable but the salinity was unfavorable. Two of these years were 1968 and 1969, when the spring salinity was the lowest recorded at Koko Head. Thus, the temperature index can be used to predict the exceptional fishing years in four out of five cases. This predictability can be improved by subjective interpretation of the salinity trends prior to the fishing season.

SKIPJACK AND THE TRADE WIND ZONE OCEANOGRAPHY RESULTS

In the Trade Wind Zone Oceanography (TW-ZO) investigation, oceanographic stations were occupied at fixed locations between lat 10° and 26.5°N along long 148°, 151°, 154°, and 157°W at approximately monthly intervals from February 1964 to June 1965 (Figure 3). Although



FIGURE 3.—Track of the Trade Wind Zone Oceanography cruises. Numbered circles indicate oceanographic stations.



FIGURE 4.—Salinity (%) distribution at 10 m, lat 10° to 26°N, long 148°, 151°, 154°, and 157°W, February 1964 to June 1965. Small circles indicate location of plankton tows. The number of skipjack (SJ), yellowfin (YF), and other tunalike larvae (OTH) captured are shown.

no fishery studies were undertaken to complement the oceanographic studies, results of the TWZO investigation augment the associations between skipjack and the environment that were described above. During each of the cruises, which lasted about 20 days, 1/2-hr plankton tows were made every evening between 8 and 9 o'clock with a 1-m net just below the sea surface. From each of the 19 or 20 plankton samples per cruise the tuna larvae were separated and identified.⁴

The descriptive results of the TWZO investigation have been summarized by Seckel (1968). Figure 4 shows the time variation in the meridional, 10-m salinity distribution for long 148°, 151°, 154°, and 157°W. The positions of the plankton tows and the number of skipjack, yellowfin or other tunalike larvae are superimposed on these graphs. The salinity isopleths 34.8%and 34.2% are drawn heavier to demark the southern boundary of the North Pacific Central water and the northern boundary of the North Pacific Equatorial water, respectively.

Along the meridian 157°W that passes through the Hawaiian Islands, the seasonal northward displacement in the spring of 1964 of the North Pacific Central water is evident. Subsequent southward retreat was stopped when a sharp northward displacement took place in October and November. Another sharp northward displacement of the 34.8% salinity isopleth took place in May. A pronounced feature along all meridians presented is the intrusion of the North Pacific Equatorial water during the spring and summer of 1964.

The TWZO observations spanned the entire 1964 and the beginning of the 1965 fishing seasons in Hawaii. With landings of 4,093 tons, 1964 fell into the normal category of fishing years (Figure 2b). Landings of 7,329 tons, in 1965, however, were the best on record and fall into the exceptional year category. The salinity distribution along long 157°W shows an important year-to-year difference in the meridional salinity gradient. During the winter and spring of 1964 the gradient was small or diffuse. During the winter and spring of 1965 the gradient was pronounced or high. Qualitatively, the differences in meridional gradients means that the currents were only weakly convergent in 1964 in contrast to the strong convergence or shear that existed in 1965.

This interpretation provides an additional lead towards an understanding of the association between the availability of skipjack and the environment. The concentration of organisms, whether drifting with the water, such as plankton, or swimming relative to the water, such as skipjack, is affected by water motion. Thus, the strongly convergent flow pattern evident from the high-salinity gradient would concentrate the skipjack schools and so increase their availability, unless, of course, the effect of the convergent flow is deliberately opposed. The concentrating effect is evident in Figure 5 showing the weekly. skipjack landings in Hawaii and the Koko Head salinities. The sharp drop in Koko Head salinity at the beginning of May 1965 is coincident with the movement of the salinity gradient through the fishing area (Figure 4) and with the pronounced increase in weekly landings. A similarly pronounced change in landings with change in salinity was reported by Murphy et al. (1960).

Consider now the distribution of skipjack



FIGURE 5.—Weekly skipjack landings at Oahu, March to September 1965 (upper panel), and Koko Head salinities (lower panel).

⁴ The identifications of tuna larvae were made by Walter M. Matsumoto of the National Marine Fisheries Service, Southwest Fisheries Center, Honolulu Laboratory.

larvae shown in Figure 4. The size of skipjack larvae caught in plankton nets such as were used in the TWZO investigation range from 2.3 to 20.1 mm (Matsumoto, 1958). During the first month, growth is rapid and larvae may reach a length of 9 cm (Yoshida, 1971). Thus, presence of larvae indicates recent presence of adults. Only the presence or absence of larvae in a tow is considered, and tows with different larvae counts are not distinguished. General absence of larvae as between October 1964 and April 1965 may mean absence of adults or cessation of spawning. During the spring and summer of 1964 and spring of 1965, skipjack larvae, and therefore adults, occurred in all latitudes sampled during the TWZO cruises. The distribution, however, was not uniform. There were only few tows that captured larvae in water with a salinity above 35% and none in water with a salinity of less than 34%.

Remembering that the salinity is used as an index of water type, the total number of plankton tows and the number of tows with skipjack larvae are listed in Table 2 as a function of salinity. The highest number of tows with skipjack larvae occurred in a salinity range from 34.61 to 34.8%c. Although there were 23 tows in water with a salinity below 34%c, no skipjack larvae were captured. The percentage of tows with larvae as a function of salinity is shown in Figure 6. The highest capture rate, 60%, occurred in water with a salinity of 34.61 to 34.8%c.

Quantitative sampling for tuna larvae is difficult and results must be interpreted with caution. However, during February to June of 1964 and 1965, 97 and 95 plankton tows were made, respectively. For all tows the same sampling procedures were followed. Interyear compar-



FIGURE 6.—Percent of plankton tows with skipjack larvae as a function of salinity from Trade Wind Zone Oceanography cruises, February 1964 to June 1965.

isons of the larvae capture rates, therefore, provide additional leads in gaining an understanding of the environment-skipjack relationship.

It is evident from Figure 4 that there were fewer tows with skipjack larvae in 1965 than there were in 1964. The number of tows with larvae and the total number of tows are listed in Table 3 for the cruises from February to June of each year as a function of salinity. With almost the same number of tows in each case, those with larvae in 1964 numbered 45 and those in

 TABLE 2.—Summary of plankton tows with and without skipjack larvae as a function of salinity for all the Trade

 Wind Zone Oceanography cruises, February 1964 to June 1965.

Salinity Rang o ‰	33.01 33.2	33.21 —33.4	33.41 —33.6	33.61 —33.8	33.81 34.0	34.01 34.2	34.21 34.4	34.41 —34.6	34.61 —34.8	34.81 35.0	35.01 35.2	35.21 —35.4	35.41 35.6	Total
Number of tows with skipjack larvae	0	0	0	0	0	6	7	18	34	21	9	5	0	100
Tot al number of tows	1	2	0	7	13	23	39	54	57	44	40	22	3	305

Salinity Range ‰		33.81 34.0	34.01 —34.2	34.21 —34.4	34.41 —34.6	34.61 —34.8	34.81 35.0	35.01 35.2	35.21 35.4	35.41 35.6	Total
February to June 1964	Number of tows with skipjack larvae		2	2	3	16	12	5	5		45
	Total num- ber of tows		2	11	16	26	17	13	12		97
February to June 1 965	Number of tows with skipjack larvae		1	4	13	11	3				32
	Total num- ber of tows	1	7	22	29	18	9	8	1		95

TABLE 3.—Summary of plankton tows with and without skipjack larvae as a function of salinity for the Trade Wind Zone Oceanography cruises, February to June 1964 and February to June 1965.

1965 numbered 32. This comparison is consistent with that made by Yoshida (1971) of the relative number of skipjack larvae found in billfish stomachs. The number of juveniles per 100 billfishes taken in 1964 was 21.3 and in 1965 the juveniles numbered 19.1.

The relative number of tows with larvae as a



FIGURE 7.—Percent of plankton tows with skipjack larvae as a function of salinity from Trade Wind Zone Oceanography cruises, February to June 1964, solid bars, and February to June 1965, open bars.

function of salinity for each year is shown in Figure 7. In 1964, although the total number of tows with larvae was highest in the 34.61 to 34.8% water, the highest capture rate was in 34.81 to 35.0% water. In 1965 highest capture rates were shifted to lower salinities. The highest percentage of tows with larvae, 60%, occurred in water with salinities of 34.61 to 34.8%. The restrictions placed on the salinity index in the previous section is consistent with the capture rates of larvae during the TWZO cruises.

It seems paradoxical that during 1965, the year with the highest skipjack landings in Hawaii, the number of tows with larvae (reflecting presence of adult skipiack) was lower than in 1964. Figure 7 shows that larvae were spread over a wider range of salinities in 1964 than in 1965, the difference occurring between 35 and 35.4%. Although there were fewer tows in the high-salinity water during 1965 than during 1964, assuming the same capture rate as in 1964, there should have been three or four tows with larvae in the 35 to 35.4% salinity range during 1965. Thus, there were possibly as many or more skipjack in 1964 than in 1965 but their concentration was lower in 1964 resulting in lower Hawaiian landings. This picture is consistent with the salinity distribution, which had a high meridional gradient in 1965 as compared to 1964, reflecting stronger convergence.

Another possible cause for the difference in capture rates of larvae between 1964 and 1965 was recognized early in this century. Hjort (1914) suggested the possibility that the availability of food at the time of yolk absorption is critical for the survival of larvae. In a large portion of the tropical and subtropical oceans food supply (plant production) may be governed by sea-air interaction processes. During the TWZO investigation there were large differences in sea-air interactions between the early parts of 1964 and 1965 (Seckel, 1970a,b). As an example, the heat of evaporation, Q(E), the net heat exchange across the sea surface, Q(N), and the zonal component of the wind stress, $\tau(x)$, for lat 17°N, long 152°W are listed in Table 4. The

TABLE 4.—Intervear differences of the heat of evaporation, Q(E), the net heat exchange across the sea surface, Q(N), and the zonal component of wind stress, τ_x , lat 17°N, long 152°W. Q(E) and Q(N) are positive if the sea gains heat, τ_x is positive to the east. (Seckel, 1970a,b.)

	Q(E)	Q(N)	τ _x
	cal cm-2 day-1	cal cm - 2 day - 1	dynes cm-2
Jan-Apr 1964 average			-1.71
Jan-Apr 1965 average	134	100	
Interyear difference	307	144	.95

evaporation rate in January to April of 1964 was almost three times as large as during the same months of the following year. The sea-surface layer gained an average of 144 cal cm⁻² day⁻¹ more heat during the early part of 1965 than it did during the same time of 1964. The wind stress was more than twice as strong in 1964 than in 1965. Such interyear differences take place throughout the spawning areas of skipjack. For example, the large year-to-year temperature variations at Christmas Island (Seckel and Yong, 1971) reflect large changes in sea-air interaction processes.

IMPLICATIONS OF ENVIRONMENTAL ASSOCIATIONS

THE DRIFT HYPOTHESIS

The pronounced salinity gradient at the boundary of the North Pacific Central water in 1965 (Figure 4) implies strong convergence. Organisms drifting or skipjack schools swimming in the converging currents also converge into the boundary region. The availability of fish is therefore expected to be larger within than outside of the zone of convergence. Interyear differences in the intensity of convergence as reflected by the meridional salinity gradient in the springs of 1964 and 1965 contribute to the interyear differences in availability. The boundary or convergence zone need not remain at the same location and may shift northward as indicated by the low Koko Head salinities during 1968 and 1969. Consequently, fish concentrations were also shifted out of the Hawaiian fishing grounds resulting in the low landings for these years.

The convergence of skipjack schools concept can be applied on a broader scale. Rothschild (1965) postulates that a component of Hawaiiancaught skipjack originates in the eastern Pacific. This hypothesis is supported by the recapture of fish in Hawaiian waters that were tagged in the eastern Pacific (Table 5).^{*} Consider now skipjack schools that entered the North Equatorial Current in the eastern Pacific. Throughout the time while the skipjack schools are carried westward by the current, they are also displaced northward by a meridional component of the trade wind-driven surface current. The magnitude of the mean annual westward component of wind stress long 120° to 160°W between lat 10° and 25°N (University of California, 1948) is shown schematically with the associated northward component of the winddriven surface current in Figure 8. Under these wind conditions an object would take on average about 22 months to drift from lat 10° to 20°N.

Figure 8 also shows that the northward winddriven current decreases with increasing latitude. The number of skipjack schools drifting from the 10° - 15° into the 15° - 20° latitude band is larger than the number drifting from the 15° - 20° to the 20° - 25° latitude band. In other words, schools in the North Equatorial Current would converge north of lat $15^{\circ}N$.

These qualitative considerations can be expressed numerically. The displacement of a fish school, S, during a time interval, Δt , is

⁶ Tagging data were kindly supplied by Dr. William H. Bayliff, Inter-American Tropical Tuna Commission.

$$\Delta S = V \Delta t.$$

The velocity of the fish school, V, consists of two parts: the velocity of the water relative to fixed coordinates, V_W , and the velocity of the school relative to the water, V_F . The displacement equation is

$$\Delta S = (V_W + V_F) \Delta t.$$

The velocities are functions of location and of time and the net displacement of a school after a time T is

or

$$S = S_W + S_F = \sum_{i=1}^n (V_W \Delta t)_i + \sum_{i=1}^n (V_F \Delta t)_i$$

 $S = \sum_{i=1}^{n} [(V_W + V_F)\Delta t]_i$

with $T = n\Delta t$ if the time increments are all equal.

Although this displacement equation is true for any time and space scale, current or swimming velocities averaged over time intervals, Δt , of a week or a month are of interest here. Random motions of fish schools and eddying currents therefore make no contribution to the net displacement in the scales under consideration. It is evident that in migrations of thousands of kilometers taking a time of 1 to 2 years, ocean currents cannot be ignored unless

$$V_W << V_F$$

and the displacement of the school due to the current, S_w , is therefore small compared to that relative to the water.

If the environmental conditions are known, then a numerical integration can be performed to determine the displacement of a fish school



FIGURE 8.—Schematic presentation of average zonal wind stress, long 120° to 160° W, in latitude bands 10° - 15° N, 15° - 20° N, 20° - 25° N, and associated meridional component of wind-driven current in miles per month (thick arrows).

caused by currents alone. An example of a drift model that is applicable to skipjack originating in the eastern North Pacific will be given in a subsequent section.

 TABLE 5.—Skipjack tagged in the eastern Pacific and recaptured in the central Pacific.

Tag	release	Tag rec		
Date Area		Date Area		
17 Apr. 1960	Revillagigedo Is.	22 Aug. 1962	Hawaii	858
5 Sept. 1960	Baja California	12 June 1962	Hawaii	646
22 Sept. 1961	Baja California	5 Apr. 1963	Christmas Is,	561
5 June 1965	Revillagigedo Is.	27 June 1967	Hawaii	753
6 Nov. 1969	Clipperton Is.	21 July 1970	Hawaii	258
6 Nov. 1969	Clipperton Is.	8 Aug. 1970	Hawaii	276
26 Oct. 1969	lat 4°11/N, long 119°02/W	14 July 1971	Hawail	627

Data source: Dr. William H. Bayliff, Inter-American Tropical Tuna Commission.

LARVAL SURVIVAL AND YEAR-CLASS STRENGTH

Rothschild (1965) conceded that environmental conditions a few months prior to the Hawaiian fishing season affect the availability of skipjack but felt that the large variability in catch rates is due to variability in the year-class strength. The variability in catch rates is also apparent within the two broad categories of years defined earlier in this paper. In the next section it will be shown, however, that the variability can be caused by variations in the current field. Nevertheless, year-class strength is not excluded as an additional cause for the variations in catch rates. It was previously noted that the large interyear differences in sea-air interaction processes observed during the TWZO investigation would affect productivity (plant production) and, hence, also larval survival. In mid- and high latitudes, winter overturn regularly replenishes the nutrients of the surface layer. In a large portion of the tropical and subtropical ocean this cyclical replenishment does not take place and a permanent pycnocline inhibits vertical exchange of the surface nutrient-deficient with the deeper nutrient-rich water. Other than in areas of upwelling such as along the equator and possibly near islands, nutrients enter the surface layer by eddy diffusion. A net heat gain in the tropical and subtropical oceans tends to increase the stability of the pycnocline and thus inhibits the eddy diffusion process. Wind stirring, vertical current shear, and internal waves tend to enhance eddy diffusion. The wind speed also affects the evaporation which. in turn, affects the net heat exchange across the sea surface. The evaporation rate may be so large that there is a net heat loss from the sea surface and convective overturn takes place, increasing the nutrient supply of the surface layer.

Increased vertical diffusion across the pycnocline due to favorable sea-air interactions may have subtle effects in that it need not be reflected as an increase in nutrient concentration. In areas where nutrients limit productivity, an increase in the nutrient supply into the surface layer can be entirely exhausted by an increase in productivity. Thus, a low phosphate concentration and absence of a seasonal variation in the trade wind region of the North Pacific Ocean does not preclude variations in productivity.

The sea-air interactions in the trade wind zone from January to April 1964 (Table 4) favor a larger nutrient supply by diffusion and, therefore, higher productivity than do those for the same months of 1965. Consequently, a better supply of primary producers in 1964 should have enhanced larval survival. The TWZO larval captures in 1964 and 1965 are consistent with this proposition. There is presently no information to verify the hypothetical sequence of events.

In this discussion the results of the TWZO investigation are used to illustrate what probably takes place throughout the tropical and subtropical oceans and, therefore, in all the skipjack spawning areas. The illustration does not imply that the North Equatorial Current or the Hawaiian waters are major skipjack spawning grounds.

The sequence of events described is amenable to quantitative study. Productivity models exist, such as the one used by Parsons and Anderson (1970), that can be adapted to reflect the environmental changes of the skipjack spawning areas. An integral part of the productivity studies must be adequate sampling of the animal community, including skipjack larvae, that directly depend on the initial stages of the food chain. Those studies would lead to a recruitment or year-class strength model that complements the drift model. Development of a year-class strength model is not within the scope of this paper.

A DRIFT MODEL

The displacement of a fish school was expressed above by

$$S = S_w + S_F.$$

Here I wish to consider only the contribution to the total displacement of fish schools caused by the currents, S_W , in a portion of ocean between lat 10° and 25°N, and long 120° and 160°W, the model ocean. In this idealized, rectangular ocean the distances between degrees of latitude and longitude are equal, and there is a geostrophic current and a wind-driven current. The increments of displacement of a fish school or a drifting object by currents are expressed by

$$\Delta S_W = V_W \Delta t = (V_G + V_E) \Delta t$$

where V_w , the velocity of the water, is the sum of the geostrophic current, V_G , and the winddriven current, V_E . V_G and V_E are functions of position and of time. Because the velocities are vectors, numerical integration (summation of increments) is facilitated by using zonal and meridional components of the displacement

$$\Delta X = (V_{GX} + V_{EX}) \Delta t,$$

 $\Delta Y = (V_{GY} + V_{EY}) \Delta t,$ respectively.

The position of the fish school after n equal increments of time, Δt , is

$$X_{n} = X_{0} + (V_{GX} + V_{EX})_{1}\Delta t + (V_{GX} + V_{EX})_{2}\Delta t$$

+ ... + $(V_{GX} + V_{EX})_{n}\Delta t$,
$$Y_{n} = Y_{0} + (V_{GY} + V_{EY})_{1}\Delta t + (V_{GY} + V_{EY})_{2}\Delta t$$

+ ... + $(V_{GY} + V_{EY})_{n}\Delta t$

with an initial position X_0 , Y_0 .

In the model rectangle of ocean the meridional distribution of dynamic height varies sinusoidally according to

$$A_0 + C(t) \cos \frac{2\pi}{L(x)}(y-\alpha).$$

The minimum dynamic height is at lat 10° N and the maximum slopes northward from lat $20^{\circ}30'$ N at long 160° W to lat $26^{\circ}30'$ N at long 120° W (Figure 9). Thus, the geostrophic flow is zonal near lat 10° N but acquires a meridional component at higher latitudes. The amplitude of dynamic height, C(t), in the sinusoidal distribution varies seasonally. The zonal component of the geostrophic current is expressed analytically by

$$V_{\rm GX} = -K_i \left(\frac{2\pi}{L(x)} C(t) \sin \frac{2\pi}{L(x)} (y-\alpha) \right).$$

The seasonal variation of the amplitude,

$$C(t) = -[0.142 + 0.05 \cos 30(t + 1.13)],$$



FIGURE 9.—Dynamic topography of model ocean (dynamic meters) at the time of maximum velocity.



FIGURE 10.—Seasonal variation in amplitude, C(t), for the harmonic expression of dynamic height as a function of latitude.

is shown in Figure 10.

The wave length, a function of longitude, x, is twice the width of the current: L(x) = 69 - 0.3x.

The meridional component of geostrophic current is given as a function of latitude, y, longitude, x, and the zonal component of geostrophic current, V_{GX} :

$$V_{GY} = -\frac{(y-10)}{230-x} V_{GX},$$

where x and y are the degrees of longitude and latitude in the model ocean, with the coordinates positive westward and northward. L(x) is given in degrees latitude, and t is the time of the year in months. The phase angle, α , equals 10°, and in the dynamic height expression A_0 equals 1.875 dyn m. The zonal component of geostrophic flow in cm sec⁻¹ is given by

$$K_1 = \frac{61.69}{\sin y}$$

In the drift model it is most convenient to express the flow in nautical miles per month with

$$K_1 = \frac{862.9}{\sin y}$$

The wind-driven current is based on the wind stress values of the Scripps Institution of Oceanography (University of California, 1948). The zonal and meridional components of stress were averaged between long 120° and 160°W for each month of the year and each latitude band 10°-14°N, 15°-19°N, and 20°-24°N. The variation with time, t, of the zonal components, τ_x , and the meridional components, τ_y , of the wind stress are adequately defined by the harmonic functions in Table 6, and shown in Figure 11.

The meridional and zonal components of Ekman transport are calculated from the equations $E_y = -\tau_x/f$, and $E_x = \tau_y/f$, where f is the Coriolis parameter. Most of the transport takes place in the upper 100 m of ocean. Here, it is assumed that all the transport takes place in the upper 100 m. $V_{EX} = -K_2 \tau_y$ and $V_{EY} =$

TABLE 6.—Harmonic functions of the zonal component, τ_x , and meridional component, τ_y , of wind stress in dynes cm⁻². The time of year, t, is in months.

lat 10)°-14°N, T	= 0.91 + 0.	544 cos 30 (t-	2.1)
lat 15	5°-19°Ν, τ ື =	= 0.8 + 0.	188 cos 30 (t-	1.2)
lat 20)°-24°N, $ au_x^r$	= 0.56 + 0.	022 cos 30 (t+	1.2)
lat 10)°-14°Ν, τ. =	= 0.56 - 0.3	330 cos 30 (t-	2.5)
lat 15	°-19°Ν, τ	= 0.47 - 0.4	04 cos 30 (t-	0.2)
lat 20	1°-24°N, τ	= 0.34 + 0.4	045 cos 30 (t-	1.4)

 $K_2\tau_x$ then give the mean wind-driven current for this depth in cm sec⁻¹ if K_2 for latitude bands 10°-14°N, 15°-19°N, and 20°-24°N is 3.17, 2.29, and 1.79, respectively. Again, for application in the drift model it is most convenient to express the drift current in nautical miles per month, and K_2 for latitude bands 10°-14°N, 15°-19°N, and 20°-24°N becomes 37.5, 27.0, and 21.3.

Using the geostrophic and wind-driven current speeds, the drift displacements can be calculated. Once per month 11 objects are introduced along the eastern boundary of the model ocean, equally spaced from lat 10° to 20°N. Displacements are calculated and the new position at the end of the month is determined. Again, displacements are calculated for the new time and position, and the positions at the end of the second month determined. These calculations are repeated for 36 months or stopped before that time if the western boundary (long 160°W) is crossed or when the object drifts into easterly (negative) flow at the northern boundary of the westerly setting geostrophic current. It is assumed that the drifting objects move up and down in the upper 100 m much as a skipjack school may be doing.

The result of the numerical integration is shown in Figure 12. The location of drifting objects that were introduced at the beginning of April, May, and June at lat 10° to 20° N along long 120° W are traced across the model ocean in steps of 3 months. After 12 months all drifting objects are north of lat 15° N. The objects that began north of lat 15° N are the first to drift into the northern, slow portion of the Equatorial Current and are overtaken by the objects that began at and to the south of lat 15° N. Thus a meridional distribution of objects at the beginning becomes oriented along the northern edge of the model equatorial current after 24 months of drifting.

Another presentation of the results (Figure 13) shows the location, after 30 months, of all objects that were introduced at the beginning of each of the 30 months along long 120°W. The most westerly position reached by objects during each quarter is indicated by a dotted line. Again, it is evident that objects initially located south



FIGURE 11.—Zonal and meridional components of wind stress in latitude bands 10°-14°N, 15°-19°N, 20°-24°N averaged between long 120° and 160°W (University of California, 1948). Stress is positive if directed to the east and north, respectively.

of lat 15°N rapidly drift northward. Objects appear to concentrate on the southern and northern edge of their distribution and then merge west of long 150°W in a relatively narrow band between lat 18° and 22°N. Lost in the presentation are a few objects that drifted across the northern edge of the equatorial current in the western portion of the model ocean and those that drifted west beyond long 160°W. In the western part of the model area considerable mingling of objects introduced in different seasons takes place. In some 1-degree units of area are found objects that were introduced during 3 seasons.

The concentration of drifting objects at the southern edge of their distribution is caused by the seasonal difference in the convergence of the meridional wind-driven current. The zonal component of the trades is stronger from November to June at lat 10° to $14^{\circ}N$ then at lat 15° to

19°N but weaker from June to November (Figure 11). Consequently, the meridional component of wind-driven current is strongly convergent from November to June but weakly convergent or divergent during the remainder of the year. The effect of this seasonal difference is illustrated in Figure 14. Note that in the first case with a high meridional wind-driven current only 4 objects are left south of lat 15° N but 11 objects are left in the second case. Again, in the first case with strong meridional convergence there were 14 objects between lat 15° and 17° but 8 objects for the second case.

The seasonal variation of meridional winddriven current inferred from the lat 15° to 19° and 20° to $24^{\circ}N$ curves in Figure 11 is smaller than it is south of lat $15^{\circ}N$. Consequently the northward drift near lat $20^{\circ}N$ is not as large as in the example given above. Near this latitude, however, the southward component of the



WEST LONGITUDE

FIGURE 12.—Location of drifting objects every 3 months after being introduced during April, May, and June of the first model year at long 120°W. Triangles denote objects introduced north of lat 15°N. The number of drifting objects, if there are more than one per 1-degree square, is indicated by concentric triangles or circles.



FIGURE 13.—Locations of drifting objects in June of the third model year that were introduced in each of the previous 30 months at long 120°W. Dashed lines indicate most westerly location reached by objects introduced every quarter.

geostrophic current (Figure 9) becomes important. The effect of convergence of this component of flow with the northward wind-driven current is evident at the northern edge of the distribution of drifting objects in Figure 13.

As the objects drift westward north of lat 18°N and west of long 140°N, they enter the region of decreasing speed in the North Equatorial Current (Figure 9) and therefore tend to accumulate further (Figure 13).

THE MODEL OCEAN AND SKIPJACK

The minimum duration of drift of objects from long 120°W to the quadrant north of lat 19°N and west of long 155°W ranges from 21 to 23 months (Table 7). These times are of the same order of magnitude as the times skipjack tagged in the eastern Pacific were free except for the two skipjack tagged near Clipperton Island (Table 5). If the model ocean is realistic, these results indicate that the mean velocity of the fish relative to the water (V_F) is small compared to the mean velocity of the water (V_W) . The paths of the fish, of course, are not known and many routes and modes of travel behavior can be postulated. However, there is one, the simplest mode



FIGURE 14.—Left Panel: Position of objects in March that were introduced at long 120°W during the previous October, November, and December. Right panel: Positions of objects in September that were introduced at long 120°W during the previous April, May, and June.

TABLE 7.—Minimum duration of drift from long $120^{\circ}W$ to the quadrant north of lat $19^{\circ}N$ and west of long $155^{\circ}W$.

Month of start	Year month o	and farrival	Duration of drift in month	
Jan.	2d	Oct	22	
Feb.	2d	Nov	22	
Mar.	2d	Dec	22	
Apr.	3d	Jan	22	
May	3đ	Jan	21	
June	3d	Feb	21	
July	3d	Mar	21	
Aug.	3d	Apr	21	
Sept.	3d	Jun	22	
Oct.	3d	Aug	23	
Nov.	3 di	Sep	23	
Dec.	3d	Oct	23	

of travel, that must be considered—namely, randomly swimming skipjack drift westward in the North Equatorial Current. This mode of travel means that skipjack entering the North Equatorial Current in the eastern Pacific do not migrate in the sense that they are actively swimming towards a destination. These skipjack are concentrated, or converge with the trade winddriven water near lat 15°N, and near lat 20°N they are concentrated by the southward component of the geostrophic current and the northward component of wind-driven current. As the fish schools approach Hawaii, they further accumulate because of decreasing geostrophic flow.

COMPARISON OF THE MODEL WITH THE REAL OCEAN

In the model the effects of characteristic features in the geostrophic and wind-driven currents on the distribution of drifting objects were demonstrated. The simplest analytic expressions for the North Equatorial Current and the wind distribution were used in order to facilitate numerical integration. How well do these simple expressions reflect the average conditions as we know them to exist in the ocean?

First, consider the field of geostrophic flow. In the model area, data from historic oceanographic cruises are sparse, but a chart of the Pacific Ocean dynamic topography prepared by Reid (1962) shows that maximum and minimum dynamic heights differ by about 0.4 dyn m as they do in Figure 9. Average geostrophic speeds in the model and the ocean are therefore of the same magnitude.

There is some uncertainty in the width of the North Equatorial Current at long 120° W. At this meridian Reid's chart shows the northern edge to be at about lat 15°N. A qualitative geostrophic interpretation of Barkley's (1968) depth of the sigma-t 25.4 surface, in the main pycnocline, places the northern edge near lat 25°N at long 120°W and near lat 21°N at long 160°W.

Many more bathythermograph data than oceanographic station data are available. A geostrophic interpretation of Wyrtki's (1964) depths of the center of the permanent thermocline places the northern edge of the Equatorial Current to the north of lat 20°N in the eastern part of the model area. More recently, charts of the temperature distribution at 400 ft prepared from bathythermograph data by Robinson and Bauer[°] places the northern edge of the Equatorial Current near lat 18° or 19°N at long 160°W and from about lat 20° to 25°N at long 120°W. In the vicinity of the Hawaiian Islands, the northern edge of the Equatorial Current inferred from Robinson's charts compares well with the results of the TWZO investigation (Charnell, Au, and Seckel, 1967a,b,c,d,e,f).

The seasonal variation of the geostrophic flow in the North Equatorial Current observed during the TWZO investigation was reported by Seckel (1970c). The meridional slope of dynamic height between lat 10° and 20°N computed for each cruise of this investigation, reflecting the mean, zonal component of geostrophic current

[•] Robinson, M. K., and R. A. Bauer, Atlas of monthly mean sea surface and subsurface temperature and depth of the top of the thermocline, North Pacific Ocean. Unpublished manuscript reproduced by Fleet Numerical Weather Central, 1971.



FIGURE 15.—Meridional slopes of dynamic height, lat 10° to 20°N for every month from February 1964 to June 1965 of the Trade Wind Zone Oceanography cruises, connected by straight lines. Numerals indicate the meridional slopes of dynamic height for the cruises of the *Carnegie*, 1929, and *Hugh M. Smith* (HMS), 1950-1957.



FIGURE 16.—Schematic presentation of geostrophic flow in the North Equatorial Current with meridional components of geostrophic flow and wind-driven current (insert).

is shown in Figure 15. Also shown are the meridional slopes computed from historic cruises. These values fall into the seasonal pattern. Qualitative interpretations of Wyrtki's and Robinson's charts referred to above confirm the TW-ZO results and show that the seasonal variation extends to long 120°W.

The model east-west component of geostrophic flow, therefore, compares well with available oceanographic station and bathythermograph data. Although a small north-south component of geostrophic flow is computed from the analytical expression of dynamic height used in the model, this component is not adequately represented. A schematic presentation of geostrophic flow in Figure 16 illustrates that south of lat 15°N the Equatorial Current is essentially zonal but north of this latitude, the meridional component increases to north of lat 20°N where the geostrophic current is mostly meridional.

The underestimate of the meridional component of geostrophic flow in the northern portion of the model has the effect of shifting the main concentration of drifting objects north. The underestimate, however, does not affect the duration of east to west drift.

In the model only drift within the North Equatorial Current is considered and objects that pass across its northern boundary are not plotted in Figures 12 and 13. In the ocean, drifting objects that pass across the northern boundary are carried back into the convergence by easterly and southerly components of geostrophic flow. Thus, the concentration of drifting objects in the convergence near Hawaii is expected to be larger than shown in the model.

The wind stress values of the Scripps Institution of Oceanography (University of California, 1948) that were used represent average conditions in the trade wind region. Important in the drift model is a northward component of wind drift that is proportional to the zonal component of wind stress. This characteristic feature is not lost by averaging wind stress values in 5-degree latitude bands between long 120° and $160^{\circ}W$.

The simple procedure of dividing the Ekman transport by 100 m to obtain the wind-driven current may be questioned. This procedure, however, affects the magnitude of wind drift and not the characteristic feature essential in the drift model; a meridional component of winddriven current.

The results of the drift model are therefore the same as those to be expected in the portion of ocean under consideration if average conditions prevail. Drifting objects or skipjack schools uniformly distributed along long 120°W between lat 10° and 20°N drift westward and southward with the geostrophic North Equatorial Current. A component of surface wind-driven current in the direction to the right of the wind stress vector displaces the skipjack schools northward. In consequence of the converging flow fields, the concentration of drifting schools increases westward much as in the model.

The drift model is based on a smooth North Equatorial Current representing average conditions. From Figure 17, showing the time variation of the east-west component of geostrophic flow at long 148°W during the TWZO investigation, it is evident that the North Equatorial Current is not a smooth flowing stream. Cells of high westerly speeds alternate with low speeds or even easterly flow directions. A fish school caught in high westerly flow of more than 25 cm sec⁻¹, such as occurred near lat 15°N during August to October 1964, would in 2 months be carried about 1,300 km (700 nautical miles) westward. Thus, much shorter drift durations can occur than those given in the model. An



FIGURE 17.—Zonal component of geostrophic flow (cm sec⁻¹) at long 148°W from Trade Wind Oceanography cruises, March 1964 to June 1965. Hatching indicates flow to the west.

example are the skipjack that were tagged near Clipperton Island (Table 5).

Large interyear differences in mean geostrophic flow take place. Between March of 1964 and 1965, the average geostrophic speeds, as interpreted from the meridional slopes of dynamic height, Figure 15, differed by more than a factor of two. In August, historic cruise data indicate a factor of 1.8 in the interyear difference. Large interyear differences in wind stresses as listed in Table 4 also occur (Seckel, 1970b). The path of a drifting skipjack school therefore is expected to vary from year to year. Also to be expected are year-to-year changes in location and intensity of the converging southward component of geostrophic flow with the northward component of wind drift, as evidenced in Figure 4.

SUMMARY AND DISCUSSION

Oceanographic studies have led to the discovery of environmental changes that are associated with the seasonal and intervear differences in availability of skipjack to the Hawaiian fishery. Important is the seasonal northward movement in spring and summer of low salinity, California Current Extension water that replaces high salinity, North Pacific Central water in the Hawaiian region. Intrusion of the California Current Extension water coincides with the seasonal increase of skipjack landings. Koko Head salinities as well as the larval distributions observed during the TWZO investigation indicate that the high salinity range (34.6 to 34.8%) of the California Current Extension is most favorable. Failure of this water to move into the fishing region results in low catches.

Northward movement of surface water during late winter and early spring causes warm advection or a warming of the water earlier than can be expected from heat exchange across the sea surface. If initial warming occurs before the end of February catches tend to be good. Initial warming in March indicates unfavorable conditions.

Using as indices the time of initial warming and the spring and summer salinity in the Hawaiian Islands, one finds that catches are normal when either or both indices are unfavorable, and exceptional when both indices are favorable. Normal annual catches average 3,600 tons and range from 2,700 to 4,400 tons. Exceptional annual catches average 5,800 tons and range from 4,940 to 7,330 tons.

Both indices reflect dynamic conditions in the environment. This view is supported by results of the TWZO investigation. A diffuse salinity gradient separating the North Pacific Central water from the California Current Extension water in 1964 (Figure 4) coincided with a normal fishing year, a sharp gradient in 1965 coincided with an exceptional year. The character of the gradient is determined by the currents.

The importance of currents in marine biology is recognized. Examples of how currents affect marine life have been given by Laevastu and Hela (1970). However, the active part that ocean currents play in the migration of adult fish has not been stressed. The role of currents in fish migrations including the movements of fish without reference to landmarks has been described by Harden Jones (1968). The role has been covered only qualitatively, however, and tuna migrations were not amongst his examples.

The destination and migration path of a fish is the vector sum of the water velocity and the swimming velocity relative to the water. The contribution of the currents to the migration of skipjack that enter the North Equatorial Current in the eastern Pacific has been examined by means of a simple drift model. Essential in this model are the geostrophic flow of the North Equatorial Current and a northward component of surface wind-driven current resulting from the trades. In this current system floating objects or fish schools uniformly distributed between lat 10° and 20°N at long 120°W would be concentrated by the meridional component of wind-driven flow as they drift westward.

This concentrating mechanism is evident in Figure 13 where the southern boundary of the drifting objects (fish schools) shifts northward with increasing west longitude. Additionally, objects (fish schools) are concentrated where a southerly component of geostrophic flow and a northerly component of wind drift converge north of lat 20°N (Figure 13). The minimum time required to reach the Hawaiian Islands ranges from 21 to 23 months (Table 7). The computed drift time is of the same magnitude as the time of freedom of tagged fish (Table 5).

Before examining the consequences of this result, it is useful to place some limits on the navigational abilities of skipjack. (See also Harden Jones, 1968.) In terms of physics, it is hard to understand how, in the open ocean without a fixed reference, a fish knows that he is in a current. Only in accelerating flow would he be able to feel a force. The fish, therefore, does not know whether he is swimming with or against the current.

Easier to understand is the ability of a fish to swim in the direction of his choice. He may also know from the water properties, the type of forage, or from celestial navigation, that he is not in the area of his choice and therefore may set a course for a more desirable environment. Even in this eventuality, his destination is affected by the current.

Thus, the distribution of skipjack, whether they swim randomly and drift with the current or swim in a predetermined direction, is affected by the northward component of the wind-driven current and the convergence near the northern edge of the Equatorial Current.

As a result of the numerical model it can be postulated that a possible, and the simplest, mode by which skipjack travel from the eastern Pacific to Hawaii, is by swimming randomly and drifting with the current. This mode of travel is consistent with the empirical associations that were described and does not contradict the applicable portion of Rothschild's (1965) migration model. Rothschild statistically related the time of warming in Hawaiian waters with annual landings and stated "... that 44 percent of the variation in catch is accounted for by time of warming, the other 56 percent being unexplained." This statement can be misinterpreted in that it implies a causal relation between time of warming and catch rates. Rothschild apparently wishes to demonstrate that there is a variation in catch rates that is not associated with the variation of time of warming. This conclusion is also evident from Figure 2 which shows a relatively large range of catch rates within the exceptional and normal types of years. Rothschild examined the differences and their causes in the size frequency distributions of the eastern North Pacific and Hawaiian skipjack fisheries. He concluded "... that year-class associated phenomena play an important role in controlling the abundance of skipjack in Hawaiian waters." Rothschild, however, neglected to consider the effects of currents on the distribution of skipjack.

Currents, as is evident from the drift model results, also cause variability in annual landings and in the size-frequency distributions. It was noted that in the western portion of the model, drifting objects were found in a single degreesquare area that had been introduced along long 120°W during 3 seasons. If the drifting objects are fish schools an age difference of 9 months would be reflected in the sizes of fish caught.

TWZO results have shown that the mean geostrophic flow in the North Equatorial Current can vary by up to a factor of 2 from year to year and that there are large interyear differences in the wind stress. The time of drift from the eastern to the central North Pacific can therefore vary more than the range indicated by the drift model, and it is possible for skipjack schools that entered the North Equatorial Current during 1 year to catch up with those that entered during the previous year.

Rothschild (1965) also states that lack of growth, or slow growth, as reflected by size frequency distributions, can be due to a movement of fish through the fishery. This movement can be fish schools drifting with the currents.

The size of fish caught in the Hawaiian fishery is also affected by the time, place, and size of fish entering the North Equatorial Current. Fish recovered in Hawaii were tagged in April. June, September, October, and November near Baja California, the Revillagigedo Islands, Clipperton Island, and near the boundary of the Equatorial Counter Current and South Equatorial Current at lat 4°N, long 119°W (Table 5). The size-frequency distributions of skipjack caught in the Baja California and Revillagigedo Islands regions presented by Rothschild showed large variation from season to season and year to year. Williams (1972), in another article of this issue, proposes three alternate migration models that explain the recruitment of skipiack into the eastern North Pacific. He concludes that oceanographic conditions in the central and eastern Pacific have a vital controlling effect on the abundance of skipjack in the eastern Pacific fishery.

Finally, year-class strength determined by survival of larvae and juveniles, as suggested by

Rothschild, is not ruled out as contributing to the catch rate variations in the Hawaiian fish-Large intervear differences in oceanoerv. graphic conditions as reflected by the sea-surface temperatures at Christmas Island (Seckel and Yong, 1971) and the large intervear differences in sea-air interactions observed during the TWZO investigation undoubtedly affect the survival of larvae, as suggested previously, and, therefore, the population size. However, variations of year-class strength of medium and large fish in the Hawaiian fishery may be masked by the effects of varying currents in the eastern and central North Pacific on the distribution of skipjack.

An attractive aspect of the drift hypothesis is its simplicity. Skipjack while in the North Equatorial Current need not do, know, or remember anything other than to search for food. They need not be able to recognize the concentration of salt in the water or distinguish between water types and then know what corrections to make in order to reach the preferred location. They need not be able to recognize time of warming early in the year and then know whether they should or should not enter the Hawaiian fishery. The salinity and temperature indices correlate with availability of skipjack in Hawaiian waters, because the same water motions that affect the distribution of temperature and salinity in the North Equatorial Current (Seckel, 1962) also affect the distribution of skipjack.

In general, it is important to recognize that what is loosely called migration consists of the two components of travel: one resulting from the mean velocity of the water (V_w) and the other from the mean velocity of the fish or fish school relative to the water (V_F) . Extreme situations are those where one component is very much smaller than the other so that it can be neglected. There are probably many cases where V_F and V_W are of the same magnitude. An example of these are the migrations of Pacific salmon (Royce, Smith, and Hartt, 1968). During certain times of the oceanic life of salmon, average travel speeds $(V_F + V_W)$ of about 6 to 12 miles per day (13 to 26 cm sec⁻¹) are indicated. Ocean currents (V_w) with speeds of only 5 to 10 cm sec⁻¹ are therefore of the same magnitude as the mean velocity of the salmon relative to the currents and cannot be neglected. In fact, it is important to consider V_F rather than $(V_W + V_F)$ when studying the navigational abilities or behavior of fish. Even if V_W is one order of magnitude smaller than V_F , when travel times of 1 or 2 years are involved, V_W may not be neglected and the destination will reflect the effect of the current system.

An example of V_w being negligible in comparison with V_F is the travel of albacore across major portions of the North Pacific Ocean. The example where V_F is very much smaller than V_w may be the travel of skipjack from the eastern to the central North Pacific Ocean.

When skipjack reach the vicinity of islands a fixed reference becomes available and the swimming behavior is likely to become different from that in the open ocean. The fish that were tagged by a sonic device near the Hawaiian Islands (Yuen, 1970) are an example of such behavior. The current field is also affected by the proximity of islands. Although the relative magnitudes of the current velocities and swimming velocities may differ from the open ocean case, both velocities must still be considered. The travel behavior of skipjack near islands is, however, a different problem from that considered in this paper because the time scale is in the order of hours rather than weeks.

Finally, the relative magnitude of V_F as compared with V_W may vary throughout the travel history of a particular species of fish. This variation was documented by Royce et al. (1968) for the case of Pacific salmon and may also apply to albacore. Williams (1972) tends to favor "active" migration of skipjack into the eastern North Pacific fishery. Therefore, V_F may not be small when compared with V_W throughout the travel history of skipjack.

CONCLUSION

A plea is made in this paper by way of proposing a model, much as was done by Rothschild (1965), to progress from the exploratory phase of skipjack distribution studies to the experimental phase. Results from exploration (assemblage of data collected without experimental design) were used to demonstrate empirical associations between the availability of skipjack to the Hawaiian fishery and environmental indices. Important to an understanding of the life history is the linkage between environment and the distribution of skipjack that the empirical associations do not provide.

Insight into the linkage mechanisms is gained if the associations are used as leads to hypotheses or models that can be tested experimentally.

Modern technology together with the powerful analytical tools now available make it possible to construct a complete migration-distribution model of skipjack from the eastern and central North Pacific Ocean. In such a model the North Equatorial Current portion would be linked with one of the eastern Pacific models of Williams (1972) and with a larval survival-year class strength model. Swimming velocities of skipjack can be simulated and included in the model. Numerical evaluation of such a model depends upon adequate environmental information, e.g., large-scale sea-air interaction processes, geostrophic and wind-driven velocities of ocean currents.

Important elements that were not discussed in this paper must be evaluated. For example, there are the effects of dispersion on the distribution due to the random motions of skipjack schools and due to large eddies within the current system. Currents, either geostrophic or wind driven, are not necessarily constant within the range of vertical movement of skipjack. The current drift must therefore be tuned to the depth range within which skipjack swim.

The sources for the required environmental information are meteorological observations from ships, that in the future may be supplemented by buoys. Geostrophic current speeds can be monitored by the use of vertical temperature sections obtained from merchant ships regularly traveling specific routes. The dispersive effect of random fish school motions can be determined by using a sonic tag to track skipjack as was described by Yuen (1970). The dispersive effect of eddying currents can be determined from drifting buoys whose positions are monitored by satellite. Predicted drift or progress of fish schools based on numerical integration can be verified by drifting buoys and by following fish tagged with a sonic device.

The experimental approach will also aid to answer such questions as the following: Why is there little evidence of spawning between the eastern North Pacific and long 140°W? Why are skipjack schools not evident at the sea surface? Is the productivity of the water adequate to support the skipjack schools with a slow net movement? What is the effect of varying forage abundance on the search pattern and therefore the dispersion of skipjack schools?

The implications of an experimental, numerical approach to the skipjack distribution problem are far-reaching. The principal results of the simple drift model used in this paper will hold in a more sophisticated model where observed rather than climatic boundary conditions are used. The results indicate that the probable drift path and concentration of skipjack schools is predictable. Such predictions will increase the harvest efficiency of the skipjack resource. The insight gained into the life history of skipjack, particularly if the survival mechanisms of early life stages are included in the model, will permit elegant management of the skipjack resource.

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LITERATURE CITED

BARKLEY, R. A.

1968. Oceanographic atlas of the Pacific Ocean. Univ. Hawaii Press, Honolulu, 20 p., 156 fig.

BLACKBURN, M.

1965. Oceanography and the ecology of tunas. Oceanogr. Mar. Biol. Annu. Rev. 3:299-322. CHARNELL, R. L., D. W. K. AU, AND G. R. SECKEL.

- 1967a. The Trade Wind Zone Oceanography Pilot Study, Part I: *Townsend Cromwell* cruises 1, 2, and 3, February to April 1964. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 552, 75 p.
- 1967b. The Trade Wind Zone Oceanography Pilot Study, Part II: Townsend Cromwell cruises 4, 5, and 6, May to July 1964. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 553, 78 p.
- 1967c. The Trade Wind Zone Oceanography Pilot Study, Part III: Townsend Cromwell cruises 8, 9, and 10, September to November 1964. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 554, 78 p.
- 1967d. The Trade Wind Zone Oceanography Pilot Study, Part IV: Townsend Cromwell cruises 11, 12, and 13, December 1964 to February 1965. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 555, 78 p.
- 1967e. The Trade Wind Zone Oceanography Pilot Study, Part V: Townsend Cromwell cruises 14 and 15, March and April 1965. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 556, 54 p.
- 1967f. The Trade Wind Zone Oceanography Pilot Study, Part VI: Townsend Cromwell cruises 16, 17, and 21, May and June 1965 and January 1966. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 557, 59 p.
- HARDEN JONES, F. R.

1968. Fish migration. St. Martin's Press, N.Y., 325 p.

HJORT, J.

- 1914. Fluctuations in the great fisheries of northern Europe, viewed in the light of biological research. Cons. Perm. Int. Explor. Mer, Rapp. P.-V. Réun. 20, 228 p.
- KING, J. E., AND T. S. HIDA.
 - 1954. Variations in zooplankton abundance in Hawaiian waters, 1950-52. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 118, 66 p.
 - 1957a. Zooplankton abundance in the central Pacific, Part II. U.S. Fish Wildl. Serv., Fish. Bull. 57:365-395.
 - 1957b. Zooplankton abundance in Hawaiian waters, 1953-54. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 221, 23 p.

LAEVASTU, T., AND I. HELA.

- 1970. Fisheries oceanography, new ocean environmental services. Fishing News (Books) Ltd., Lond., 238 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.

MURPHY, G. I., K. D. WALDRON, AND G. R. SECKEL.

1960. The oceanographic situation in the vicinity of the Hawaiian Islands during 1957 with comparisons with other years. Calif. Coop. Oceanic Fish. Invest. Rep. 7:56-59.

NAKAMURA, E. L.

^{1967.} Abundance and distribution of zooplankton in

Hawaiian waters, 1955-56. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 544, 37 p.

- PARSONS, T. R., AND G. C. ANDERSON.
 - 1970. Large scale studies of primary production in the North Pacific Ocean. Deep-Sea Res. 17: 765-776.
- REID, J. L., JR.
 - 1962. On circulation, phosphate-phosphorus content, and zooplankton volumes in the upper part of the Pacific Ocean. Limnol. Oceanogr. 7:287-306.
- ROTHSCHILD, B. J.
 - 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.
- ROYCE, W. F., L. S. SMITH, AND A. C. HARTT.
 - 1968. Models of oceanic migrations of Pacific salmon and comments on guidance mechanism. U.S. Fish Wildl. Serv., Fish. Bull. 66:441-462.
- SECKEL, G. R.
 - 1962. Atlas of the oceanographic climate of the Hawaiian Islands region. U.S. Fish Wildl. Serv., Fish. Bull. 61:371-427.
 - 1963. Climatic parameters and the Hawaiian skipjack fishery. In H. Rosa, Jr. (editor), Proceedings of the World Scientific Meeting on the Biology of Tunas and Related Species, La Jolla, Calif., U.S.A., 2 - 14 July 1962. FAO Fish. Rep. 6:1201-1208.
 - 1968. A time-sequence oceanographic investigation in the North Pacific trade-wind zone. Trans. Am. Geophys. Union 49:377-387.
 - 1970a. The Trade Wind Zone Oceanography Pilot Study, Part VIII: Sea-level meterological properties and heat exchange processes, July 1963 to June 1965. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 612, 129 p.
 - 1970b. The Trade Wind Zone Oceanography Pilot Study, Part IX: The sea-level wind field and wind stress values, July 1963 to July 1965. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 620, 66 p.
 - 1970c. Geostrophic speeds of the Pacific North Equatorial Current. (Abstr. 024.) EOS Trans. Am. Geophys. Union 51:765-766.

SECKEL, G. R., AND K. D. WALDRON.

1960. Oceanography and the Hawaiian skipjack fishery. Pac. Fisherman 58(3):11-13.

SECKEL, G. R., AND M. Y. Y. YONG.

- 1971. Harmonic functions for sea-surface temperatures and salinities, Koko Head, Oahu, 1956-69, and sea-surface temperatures, Christmas Island, 1954-69. Fish. Bull., U.S. 69:181-214.
- UCHIDA, R. N.
 - 1966. The skipjack tuna fishery in Hawaii. In T. A. Manar (editor), Proceedings, Governor's Conference on Central Pacific Fishery Resources, State of Hawaii, p. 147-159.
 - 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.

U.S. BUREAU OF COMMERCIAL FISHERIES.

- 1963. Skipjack—a world resource. U.S. Fish Wildl. Serv., Circ. 165, 28 p.
- UNIVERSITY OF CALIFORNIA, SCRIPPS INSTITUTION OF OCEANOGRAPHY.

WILLIAMS, F.

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.

WYRTKI, K.

- 1964. The thermal structure of the eastern Pacific Ocean. Ergänzungsh. Dtsch. Hydrogr. Z. Reihe A (8°), Nr. 6, 84 p.
- YAMASHITA, D. T.
 - 1958. Analysis of catch statistics of the Hawaiian skipjack fishery. U.S. Fish Wildl. Serv., Fish. Bull. 58:253-278.
- Yoshida, H. O.
 - 1971. The early life history of skipjack tuna, Katsuwonus pelamis, in the Pacific Ocean. Fish. Bull., U.S. 69:545-554.
- YUEN, H. S. H.
 - 1970. Behavior of skipjack tuna, Katsuwonus pelamis, as determined by tracking with ultrasonic devices. J. Fish. Res. Board Can. 27:2071-2079.

^{1948.} The field of mean wind stress over the North Pacific Ocean. Univ. Calif. Scripps Inst. Oceanogr. Oceanogr. Rep. 14, 11 p.