CONSIDERATION OF THREE PROPOSED MODELS OF THE MIGRATION OF YOUNG SKIPJACK TUNA (KATSUWONUS PELAMIS) INTO THE EASTERN PACIFIC OCEAN

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ABSTRACT

Previous evidence suggested that most exploited skipjack tuna (Katsuwonus pelamis) in the eastern Pacific Ocean have a central Pacific spawning origin. Three models are now proposed of the migration of young skipjack into eastern Pacific fishery areas; these are (i) the active migration model, (ii) the passive migration model, and (iii) the gyral migration model. Data utilized and theories advanced in the detailed development of the models are discussed. Mechanisms and timing in all three migration models are dependent on oceanographic conditions and events in the central-east Pacific, which thus have a controlling effect on migration success of incoming young fish. Current skipjack research cruises, in part designed to test the validity of the models, are outlined.

Skipjack tuna (Katsuwonus pelamis) are widely distributed in tropical and subtropical surface waters of world oceans. In the Pacific Ocean there are three principal fisheries: the Japanese home islands fishery, including the Ryukyu-Tokara-Izu-Bonin Islands (1956-1969, range 87,000-252,000 short tons); the Hawaiian Islands fishery (1956-1969, range 3,000-8,000 short tons); and the eastern Pacific fishery from California to northern Chile (1956-1970, range 52,000-132,000 short tons). In addition, there are skipjack fisheries off Taiwan and the Philippines, developing ones of various sizes in Micronesia, Melanesia, and Indonesia, and subsistence fisheries in many other island groups, such as the Society-Tuamotu Islands. With the regulation of yellowfin catches in the eastern Pacific through an annual catch quota and the general decline in Japanese longline catch rates of tunas, the fishing industry has been showing increased interest in skipjack for a greater share of total tuna catches.

Fujino (1967, 1970, and in press) has shown that genetic studies indicate a subpopulation of skipjack in the western Pacific distinct from that present in the central-east Pacific. Seasonal mixing of the two subpopulations, or replacement one by the other, is considered to take place in the area immediately to the east of an arc through the New Hebrides-Solomon-Caroline-Mariana-Bonin Islands chains to the waters off the northeast coast of Japan.

The hypothesis on North Pacific skipjack advanced by Kawasaki (1965a, b) proposed a transpacific population with a common element and radiation outwards of juveniles from a central Pacific spawning area with eventual return to that area of sexually mature fish. This aspect of Kawasaki's hypothesis does not seem tenable, in view of Fujino's work. It is possible though that Pacific-wide changes in environmental conditions may cause apparently similar fluctuations in skipjack abundance in different areas through effects on recruitment and distribution.

Schaefer (1963) and Rothschild (1965) reported on the structure of skipjack populations in the central-east Pacific and stated that skipjack in the eastern Pacific fishery have a central Pacific origin. This inference was based primarily on the indicated general lack of spawning.

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in the eastern Pacific (east of long 130°W), by few fish with fully developed gonads (Schaefer and Orange, 1956; Orange, 1961) and few larvae (Matsumoto, 1958; Klawe, 1963), and the occurrence of some long distance tag returns indicating movements from Baja California to the central Pacific, including the Hawaiian Islands (Schaefer, 1963; Inter-American Tropical Tuna Commission, 1964). (Subsequent data on skipjack larval distribution and tagging have supported the inference for a central Pacific origin.) Schaefer's and Rothschild's opinions differed, however, as to whether skipjack from south of the equator entered into this common genetic pool. Fujino (1970) indicated there was no genetic evidence to suggest South Pacific skipjack are not part of the central-east Pacific subpopulation(s) and also stated that present evidence for any differences between skipjack from varying parts of the central-east Pacific (Hawaiian Islands, Line Islands, Ecuador, Baja California) is very slight.

Rothschild (1965) generated a hypothesis on the movements of skipjack within the central-east Pacific (Figure 1). He postulated that skipjack juveniles in the central Pacific are continually dispersing from that region and that a large component of them move eastward into the eastern Pacific, where one contingent enters the Baja California fishery and the other the Central-South American fishery. Recruitment to these fisheries commences at about 35-40 cm (Rothschild, 1965; Joseph and Calkins, 1969). The fish remain in the eastern Pacific until they are maturing or mature at 40-65 cm, which probably is for 12 months or less, but only rarely longer than this. Thereafter, the fish leave the region and return to the presumed spawning grounds in the central Pacific and do not usually return to the eastern Pacific surface fishery.

The boundary between the two eastern Pacific fishery groups appears to be centered on the Gulf of Tehauntepec, with the northern fishery mainly off Baja California and the southern one mainly off Central America and Ecuador. There appears to be little mixing between these fishery groups as seen by lack of intergroup returns (Joseph and Calkins, 1969; Fink and Bayliff, 1970) and morphometric analysis (Hennemuth, 1959) even though genetic data (Barrett and Tsuyuki, 1967; Fujino, 1970) show no gross intergroup differences. The degree of geographic separation of the groups varies considerably from year to year (Williams, 1970).

According to Rothschild (1965) the mechanism causing the split into northern and southern fishery groups could be many and not fixed in time or space. The extent to which they split the skipjack into the northern and southern groups could be a function of the north-south and temporal distribution of the incoming eastward-moving recruits. One possible splitting mechanism was considered to be the warm water cell (surface temperatures > 28°C) in the vicinity of lat 15°N off the Central American coast (see monthly average temperature conditions, Wyrtki, 1964). Blackburn (1962) suggested that this same warm water cell impeded north-south movement and intermingling of the groups, the extent of which varied with surface temperature from year to year. Williams (1970) has shown that in the eastern Pacific, skipjack occur at all temperatures > 17°C with the majority from 20° to 30°C, though apparent abundance was only high up to 29°C. This increase of 1°C, from 28° to 29°C, in the limiting temperature for skipjack in quantity is important. The monthly average temperature charts of Wyrtki

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**Figure 1.**—Diagram showing the flow of skipjack between the central Pacific and the Mexican and South American fisheries of the eastern Pacific Ocean (from Rothschild, 1965, Figure 2).
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(1964) show the area of water >29°C is much less extensive than that >28°C, particularly offshore to the westward, and also in duration, e.g., in April-May 28°C water normally extends out to long 118°-119°W, but 29°C water only to long 102°-103°W. Even if the 28°C water was accepted as a splitting mechanism, it is shown in a subsequent section that not being fully developed in offshore extent (to long 120°W) until April, it is too late to initiate the separation of incoming recruits into the northern and southern fishery groups.

ENTRY OF RECRUITS INTO AREAS OF FISHERY

Fink and Bayliff (1970) discussed the migration of skipjack in the inshore areas of the eastern Pacific based on tagging experiments from 1952 to 1964 (Figure 2). The data are substantial for the immediate coastal areas of the fishery but much less so for the offshore island areas. In the northern fishery (Figure 2A) the principal entry point for small fish is the Revillagigedo Islands (lat. 19°N, long 111°W) in April, and from there they move inshore from about May to June. In the southern fishery (Figure 2B) the situation is more complicated, but the entry of small fish only appears confirmed for the northern Panama Bight in April (and also into the Gulf of Guayaquil).

In view of the indications of size-specific movements through certain areas of the eastern Pacific fishery (Rothschild, 1965), the skipjack length-frequency data of the Inter-American Tuna Commission (IATTC) for 1954-1967 were reexamined, albeit subjectively, to obtain possible information on time of entry of young fish. Size range in the eastern Pacific fishery is about 36-74 cm, but more usually 42-62 cm. [Eastern Pacific length data from the U.S. fleet are selective because of the California minimum

![Figure 2](image-url)
landing size of 4½ lb (≈45-50 cm), but in South American landings by local boats (Manta) the smallest fish are about 36 cm.

The length-frequency data in general show that the smallest skipjack in the northern fishery are found offshore at the Revillagigedo Islands from March to June. The modal size of these fish is <50 cm, and often between 40 and 45 cm. From March to May some similar sized fish are also seen in catches from adjacent inshore areas between the southern Gulf of California and Cape Corrientes (lat 25° to 20°N). Most of these small fish subsequently migrate into the skipjack fishery off western Baja California. In October (± 1 month) of most years there appears to be a small entry of fish, modal length ≤45 cm, at the Revillagigedo Islands, which is often reflected in the length-frequency distributions for November in the Baja California area.

In the offshore areas of the southern fishery a main influx of small fish, modal lengths <50 cm, appears to be at the Galapagos Islands from November to April with the peak in January and February. Data from the adjacent inshore area off Ecuador subsequently seems to reflect this entry of small fish. In addition, small numbers of skipjack of modal lengths ≤45 cm often occur in August (± 1 month) off Ecuador, as well as in Peru-northern Chile catches in abnormally warm oceanographic years. In the Cocos Island area fish of modal lengths ≤45 cm are found in January and February (there is some evidence this entry of small fish starts in November or December and lasts into March). Fish in this same size range subsequently occur in some years in the Gulf of Panama from April to June.

The apparent times and places of entry of small skipjack into the eastern Pacific fisheries are summarized below:

<table>
<thead>
<tr>
<th>Fishery</th>
<th>Area of entry</th>
<th>Time of entry</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern</td>
<td>Revillagigedo Is.</td>
<td>March-June, October (± 1 month)</td>
</tr>
<tr>
<td>Southern</td>
<td>Ecuador</td>
<td>August (± 1 month)</td>
</tr>
<tr>
<td></td>
<td>? Galapagos Is.</td>
<td>November-April (peak January-February)</td>
</tr>
<tr>
<td></td>
<td>Galapagos Is.</td>
<td></td>
</tr>
</tbody>
</table>

These findings are generally consistent with those of Fink and Bayliff (1970) for the northern fishery and expand those for the southern fishery.

Work on the growth of central-east Pacific skipjack using length-frequencies has been complicated by the problem of size-specific movements through the fisheries. Additionally, there is as yet no secondary age estimation method for the species. Recent work by Yoshida (1971), on young skipjack from the stomachs of longline-caught billfish in the central Pacific, has indicated that a 1-year-old skipjack may be about 31 cm. This is a similar length to that deduced from tagging data (averaged) for eastern Pacific fish by Joseph and Calkins (1969), who discuss the various deduced growth rates for the species, whereas Rothschild (1967), on the basis of short-term tag returns, indicated about 44 cm for a 1-year-old fish. Depending on the accepted growth rates, recruits to the eastern Pacific fisheries might thus be between 8 and 15 or 12 and 24 months old on entry and between 15 and 24 or 24 and 36 months old when departing the region for first spawning in the central Pacific.

CIRCULATION IN THE EASTERN TROPICAL PACIFIC

The oceanography of the eastern equatorial Pacific was reviewed by Wyrtki (1966, 1967). The circulation of intertropical surface waters shows the west-flowing North and South Equatorial Currents (NEC, SEC) with between them the relatively narrow (180-360 miles) east-flowing North Equatorial Countercurrent (NECC) at about lat 5°-10°N (Figure 3). At or just south of the equator below a depth of 20-50 m is the Equatorial Undercurrent (EUC) (Cromwell Current) with eastward flow.

However, Wyrtki (1965, 1966) indicated marked seasonal fluctuations in surface currents in the eastern Pacific. From June to December the NECC is fully developed through to the central American coast, while during January and May it is intermittent, and from February to
April absent, east of long 120°W. Although Tsuchiya (1968) showed that below a depth of 50-100 m the NECC eastward transport is continuous throughout the year, more recent calculations of geostrophic flow from EASROPAC data (M. Tsuchiya, unpublished data and personal communication) show that the subsurface transport is separate (deeper and slightly farther south) and that the surface NECC does cease or become minute and variable from January to May.

A striking relationship between development of the surface NECC and the latitudinal position of the Intertropical Convergence Zone (ITCZ) (meteorological equator) at the meridian of 120°W was presented in Wyrtki (1965). The NECC ceases east of long 120°W with the annual movement of the ITCZ south of lat 8°N about January, and when it returns north of lat 8°N about May, the NECC is reestablished. Hence, variations in the ITCZ position at long 120°W may be reflected in the time of cessation and resumption of the surface NECC, i.e., duration of the interruption. Abrupt interruption of the current is apparently not the case, and at least in January and May, it is weak and intermittent, and eddies and meanders may occur.

Superimposed on the overall monthly trend is also variability due to short-term (daily) fluctuations in ITCZ position. Monthly ITCZ positions at long 120°W and NECC position based on Wyrtki (1965, Figure 18) are reproduced here as Figure 4, together with ITCZ monthly positions based on a 77-year mean of observations from the National Weather Records Center and prepared by the Goddard Space Flight Center, NASA (Allison et al., 1969). The position of the ITCZ is controlled by the variations in the location and strength of the wind fields in the central-east Pacific, the northeast and southeast trades, and the pressure fields associated with them.

Wyrtki (1966) stated the California Current is strong and penetrates farthest south and contributes most of the water to the NEC in the period February to April. The California Current is weak and located north of lat 20°N from August to December while in January and May-July it shows intermediate positions and strengths.

Tsuchiya (1968, 1970) has reviewed the present scanty information on the zonally narrow

![Figure 3: Schematic chart of surface circulation in the tropical central-east Pacific Ocean. NEC = North Equatorial Current; NECC = North Equatorial Countercurrent; SEC = South Equatorial Current; SECC = South Equatorial Countercurrent.](image-url)

![Figure 4: Seasonal variations in the position of the Intertropical Convergence Zone (ITCZ) and of the boundaries of the North Equatorial Countercurrent (NECC) at long 120°W.](image-url)
(2°-3° of latitude) South Equatorial Counter-current (SECC), and shows that there appears to be a subsurface component at about lat 5°S. The surface SECC is ill-defined in the eastern Pacific (east of long 140°W) and M. Tsuchiya (personal communication) states that so far there is no physical oceanographic evidence from EASTROPAC data to confirm its existence.

**FACTORS INFLUENCING SKIPJACK DISTRIBUTION**

Blackburn (1965) considered that simple oceanic properties, such as temperature, directly determine overall limits of distribution of tunas, but that oceanic features and processes, among them surface currents, determine temporal and spatial differences in abundance within these limits. Though tuna distributions sometimes follow currents, he thought such relationships were often indirect, i.e., through property distributions associated with the currents. Blackburn was also of the opinion that the case for causal relationship between distribution of water masses and that of tuna species was inconclusive. However, Nakamura (1969) hypothesized that (i) tunas, according to species and life history stage, have their centers of distribution in distinct current systems or water masses, which provide specific habitats for them, and (ii) migrations of tunas are of two types, within a habitat and between habitats.

The consideration is now of the oceanographic factors influencing possible routes taken by skipjack when migrating from the central to the eastern Pacific. Throughout the tropical central-east Pacific near-surface temperatures are optimal for skipjack, except along the equator west of the Galapagos Islands out to long 100°W in certain months, and, of course, in the cold waters of the Peru Current. Given optimal temperatures, then the next factor governing distribution is probably the supply and distribution of food (Blackburn, 1965, 1969a, b). Adult skipjack are carnivorous on macrozooplankton and micronekton, and there is no reason to believe this does not hold for juvenile and adolescent skipjack, although the size range of the diet is probably smaller, that is more zooplankton. Even in adult fish Yuen (1959) for the Hawaiian Islands, Alverson (1963) for the eastern tropical Pacific, and Nakamura (1965) for the Marquesas and Tuamotu Islands presented evidence of smaller proportions of crustaceans and/or molluscs in large skipjack (over 60 cm) than in small ones. Contradictory evidence is found in the results of Waldron and King (1963), which showed no significant differences in the principal components of stomach contents of central Pacific skipjack.

Previous work in the equatorial central Pacific (Sette, 1955, 1956, and references therein; King and Hida, 1957; King, 1958; King and Iversen, 1962; Murphy and Shomura, 1972) indicates that there occur zonal “productivity” bands, representing various stages from nutrient enrichment to trophic levels, such as those represented by zooplankton and micronekton, which may be correlated with fish distribution. The principal such band normally exists between the southern edge of the NECC and a few degrees either side of the equator. Within this range there are latitudinal displacements of the “productivity” band (and its components) with time, probably as a function of the occurrence of the prevailing wind systems, the southeast and northeast trades (see Murphy and Shomura, 1972, for detailed discussion). A second, less intense and more transient (or poorly documented) “productivity” band appears to exist close to the pycnocline at the NECC/NEC boundary. Its intermittent nature may be due to the nature of the mixing processes, such as ridging (Cromwell, 1958). Reid (1962) presented charts of average zooplankton volume (for upper 150 m) that indicated the existence of these two zonal bands in the central-east Pacific. In addition, he indicated a narrow zonal “productivity” band from lat 15°S in the east to about lat 10°S in the central Pacific. Close to the shore the zonal bands merged with features related to coastal distribution.

EASTROPAC zooplankton and micronekton data published in Atlas form (Love, 1970, and in preparation) in general confirm the existence of the northern and equatorial zonal “productiv-

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* May be due to biased sampling procedures (Blackburn and Laurs, 1972; Maurice Blackburn, personal communication).
ality" bands in the eastern tropical Pacific. More detailed statistical treatment (for significance of interactions) of EASTROPAC primary productivity, phytoplankton, zooplankton, and micronekton data (Owen and Zeitzschel, 1970; Blackburn et al., 1970) from the western EASTROPAC area (lat 16°N-3°20'S, long 100°30'-121°30'W) show clearly the equatorial zonal band(s). However, the band at the NECC/NEC boundary is not clear at trophic levels other than zooplankton, and possible reasons for such anomalies are discussed in some detail. In addition, Owen and Zeitzschel (1970) pointed out that latitudinal effects may have been eliminated due to selection of geographic zones which do not coincide with natural (zonal) current systems.

Blackburn and Laurs (1972) have discussed the distribution of that part of the EASTROPAC micronekton catches which can be classified as skipjack forage. They not only confirm the existence of equatorial bands of high forage concentrations just north of the equator, and occasionally south of it, but also of a band at the NECC/NEC boundary, particularly in daytime catches.

There is some biological evidence from EASTROPAC data of increased "productivity"-zooplankton, micronekton, occurrence of birds (Love, 1970, and in preparation; R. M. Laurs, personal communication)—at certain times between lat 5° and 15°S, particularly lat 12°-14°S, the general region where the surface SECC might be expected. Such increased "productivity" could occur if a divergence existed in these latitudes, say at the southern SECC/SEC boundary.

Generally in the EASTROPAC area standing stocks decreased from east to west (Blackburn et al., 1970), that is from inshore to offshore, as did zooplankton in the charts of Reid (1962).

**PROPOSED MIGRATION MODELS**

**ACTIVE MIGRATION MODEL (Figure 5)**

Skipjack larvae are rare east of long 130°W (Matsumoto, 1966; Ueyanagi, 1969), and this generally appears to be borne out by the results of the EASTROPAC expedition (Love, 1970, 1971, and in preparation). It would seem, therefore, that adult skipjack spawn in the surface waters to the west of long 130°W, which in some way must be ecologically suitable for optimum survival and development of the larvae. In this model it is assumed that these larvae, and early juveniles, are maintained within the central Pacific by some passive migration system, perhaps related to the equatorial zonal current systems, eddies associated with island wakes, as well as diel vertical migrations.

![Figure 5](image_url)

**Figure 5.**—Active migration model: (A) routes of young skipjack into the southern fishery and (B) routes of young skipjack into the northern fishery. NEC = North Equatorial Current; NECC = North Equatorial Countercurrent; SEC = South Equatorial Current; SECC = South Equatorial Countercurrent.
At a certain size a large component of these juveniles start an active migration eastwards which ends with them on the feeding grounds of the northern and southern fisheries off the American continent. The size at which this active migration commences is not known, but with recruitment to the fisheries at 35-40 cm it is probably at <30 cm.

When in the eastern Pacific skipjack are feeding heavily, and this appears related to both the food requirements of the adolescent fish for normal growth and for the early development of the gonads. The departure of the fish with maturing gonads from the feeding grounds is attributed to a reproductive drive to return to the central Pacific where final maturation of the gonads and spawning must take place.

Richard S. Shomura and Richard A. Barkley (personal communications), with arguments based on central Pacific data, have suggested two spawning groups (northern and southern) are present in the central-east Pacific skipjack subpopulation(s) with considerable geographic overlap in equatorial areas. One group spawns during the northern summer, peak in July, and the other in the southern summer, peak in January. There is some slight evidence (Orange, 1961) that skipjack in the eastern Pacific fisheries are from two such spawning groups. Fujino (in press) has indicated that in the western Pacific subpopulation of skipjack there are two spawning groups (northern and southern) with a large overlap in geographic distribution.

Even though larval and early juvenile skipjack obviously make diel vertical migrations (Wade, 1951; Matsumoto, 1958; Strasburg, 1960; Ueyanagi, 1969, 1970; Higgins, 1970), the lower end of the temperature range is thought to be restricted to about 24°C, at least for larvae (Ueyanagi, 1969; Richards, 1969; Eric Forsbergh, personal communication). However, the adolescents arriving on the feeding grounds of the eastern Pacific fishery seem to have attained a physiological condition which permits them to exist at ambient temperatures down to 20°C, and occasionally 17°C, which are found in the near-surface waters of these zones (in other areas of the world, such as Tasmania, they may be as low as 15°C, Robins, 1952). Ability of skipjack to tolerate low ambient temperature (conserve internal heat) is probably a function of size (sequential physiological events), and this is also important in relation to the depth capability of the fish in its search for food at various life history stages. It is worth noting that skipjack have been shown (see below) to maintain body muscle temperatures considerably above ambient water temperatures:

<table>
<thead>
<tr>
<th>Skipjack length (cm)</th>
<th>Ambient water temperature (°C)</th>
<th>Body muscle temperature (°C) above ambient</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>43-47</td>
<td>25.6</td>
<td>8.5-9.1</td>
<td>Stevens and Fry (1971)</td>
</tr>
<tr>
<td>47-56</td>
<td>19.4-30.6</td>
<td>5-6</td>
<td>Barrett and Hester (1964)</td>
</tr>
<tr>
<td>71-76</td>
<td>26.6</td>
<td>4-8</td>
<td>Stevens and Fry (1971)</td>
</tr>
<tr>
<td>--</td>
<td>18.5, 29, 30</td>
<td>11.7, 7.8, 8.3</td>
<td>Carey et al. (1971)</td>
</tr>
</tbody>
</table>

Obviously the principal factors to be explained eventually in the the active migration model are those which induce the juvenile skipjack to migrate out of the central Pacific. Such a genetically fixed behavioral pattern undoubtedly would be a response to a summation of effects caused by exogenous and endogenous stimuli. Baggerman (1960) considered that migration, basically a function of locomotion and orientation, only occurs when fish are in the proper physiological condition and subject to external "releasing" factors (stimuli). This physiological condition, in turn, is brought about by endocrinal activity initiated by endogenous rhythms and external "priming" factors. This concept of causation of migration possibly may well apply in the case of tuna.

Hoar (1959) noted that for fishes with mass cyclical migrations at certain life history stages (such as reproduction, movement from nursery to feeding grounds) changes in endocrine secretions (gonadal, thyroidal) appear to play a major part in the generalized appetitive behavior associated with migration. Woodhead (1959a, b) discussed the role of the thyroid in the migrations of mature and immature Barents Sea cod described by Trout (1957). It appeared that the "dummy run" contranatant migration of the im-
mature cod was under thyroid control, a distinct cycle in thyroid follicular cell height being observed although less than in mature fish. Woodhead (1959a) and Woodhead and Woodhead (1965) suggested production of such an active migration could be due to a general increase in swimming activity and in reaction to water currents (particularly a tendency to swim against them) caused by the increase in thyroid hormones. The thyroid in tuna, unlike most teleosts (including the cod), is a discrete bilobed structure (Honma, 1956—bluefin tuna; Williams, unpublished—skipjack and yellowfin tuna). If, as the juvenile skipjack approaches the size associated with first migration, the thyroid becomes more active and one effect of this is to initiate a similar behavioral response as in the cod (increased locomotor activity), then there would be a subsequent demand for more food if the growth of the animal is to be continued. At such time it is suggested that the increased food requirements—amount, type, size—cannot be supplied in the central Pacific near-surface waters, or that the young skipjack come increasingly into competition for the available food with other species and also their own adults. (See also discussion of evolution of migration patterns in Rothschild and Yong, 1970.) Additionally, the endocrine induced internal stimuli may also act to lower thresholds for recognition of changes in environmental conditions to the magnitude of those found in the equatorial central Pacific.

Sequences of events, such as mentioned above, could possibly trigger the active migration of juvenile skipjack out of the central Pacific—the main component being to the feeding grounds in the neritic eastern Pacific. It is proposed that the migrating skipjack juveniles are principally located in the equatorial areas of the west-flowing NEC and SEC. With near-surface temperatures optimal, except at the equator west of the Galapagos Islands at times of intense upwelling, the fish are located within or close to the equatorial and northern “productivity” bands described previously. In view of the apparent intermittent nature of the northern band, it is possible that the incidence of small, but frequent fronts may also act as concentrating mechanisms for food organisms normally observed at a low density in this area, lat 5°-10°N (Murphy and Shomura, 1972). Skipjack may also be associated with the possible “productivity” band around lat 10°-15°S.

The mechanisms which maintain the overall eastward orientation of the skipjack in an offshore oceanic area (in the absence of reference points) are unknown, although as Hoar (1953) commented “fish possess an elaborate and delicate array of highly specialized peripheral sense organs and appendages” and these could all be involved in some type of navigating ability in tuna. In this respect the probable role of the pineal apparatus of tunas as a photoreceptor (Rivas, 1953) should not be overlooked. Royce, Smith, and Hartt (1968) in a discussion of possible guidance mechanisms in oceanic migration models of Pacific salmon concluded that they may depend on electromagnetic cues from ocean currents and that responses to all migratory cues are inherited. Recent work by Yuen (1970) on tracking of small skipjack (with ultrasonic tags and continuous-transmission frequency-modulated sonar) moving on and off banks in the Hawaiian Islands lead him to imply that skipjack can navigate and have a sense of time.

It is hypothesized that incoming juvenile skipjack move continuously eastwards past the meridian of long 130°W, orientating largely to the zonal “productivity” bands (northern and equatorial) until entering the offshore areas of the southern fishery from August to April. However, the interruption or cessation of the surface NECC east of long 120°W in the period January-February to April-May might be expected to disrupt the orientation and movement of incoming skipjack juveniles, mainly through significant changes in the position or continuity of the “productivity” bands and food-concentrating mechanisms. It is at this period of the year that recruitment to the northern fishery is postulated.

Certainly the cessation of the NECC would cause the deepening of the mixed layer in the vicinity of the previous northern boundary of the NECC, and hence the elimination of possible ridging and subsequent increased biological productivity, though it is very difficult to estimate the lag period. In the case of the equatorial band (east of long 120°W) the annual southward
passage of the ITCZ causes a rapid change from predominantly southeast trades to either northeast trades or light easterly winds/doldrumlike conditions. In the former case, there would be divergence at the equator and formation of a weak convergence some distance south of the equator, while in the latter case there would be equatorial divergence but no convergences. Either way it would seem that there might be significant disruption of the “productivity” bands. However, EASTROPAC data do not show this very clearly, perhaps due to the lag period in the establishment of the higher trophic levels.

If a surface SECC is present in the eastern Pacific (even seasonally) then eastward movement of juvenile skipjack could possibly take place in the SEC near a southern “productivity” band (at the SECC/SEC southern boundary). Subsequently there would be an active migration of juveniles from near the SECC terminus into the southern fishery. However, water temperatures alone could prevent any direct recruitment from this area to the southern fishery during part of the southern winter. [In this and subsequent migration models speculations are not made on skipjack distribution south of the possible SECC/SEC southern boundary.]

Tuna have to swim continually to ensure ventilation across the gills and to maintain hydrostatic equilibrium, and maximum speeds in excess of 10 body lengths per second (bl/sec) have been reported (Blaxter, 1969, and references therein). For the closely related little tuna (*Euthynnus affinis*), Magnuson (1970) reported the minimum speed for hydrostatic equilibrium in a 42-cm fish was about 1.4 bl/sec and calculated for a 10-cm fish it would be about 3 bl/sec. After feeding, the average speed of the same captive fish increased to about 2 bl/sec, while Walters (1966) recorded for a 40-cm fish a speed of 5.9 bl/sec on a feeding run on dead fish and a maximum speed of 12.5 bl/sec. Magnuson (1970) also pointed out that the little tuna appears to spend most of its time swimming at speeds near the minimum hydrostatic speed and relatively little near the maximum. For captive skipjack of 38, 39, and 48 cm, John J. Magnuson (personal communication to Maurice Black-burn) indicated that the observed mean speed was about 2 bl/sec; for calculations for model fish the minimum speed for a 15-cm juvenile skipjack would be about 3 bl/sec. Actively migrating juvenile skipjack may be expected to have a narrow range of theoretical minimum speed, from 2 to 3 bl/sec.

The tracking of 40-42 cm skipjack in the Hawaiian Islands by Yuen (1970) showed that movement off a bank at night, principally from 1800 to 0200 hr, was mainly near the surface and without frequent directional changes, at speeds equivalent to about 1.5-6.0 bl/sec. However, during daylight, apparent speeds fell well below Magnuson’s calculated minima which, Yuen concluded, must indicate considerable turning from a straight line track, presumably due to food searching and feeding—[skipjack are primarily daylight feeders (Nakamura, 1962)]. In addition, there was a greater variability in depth during the day than the night. On a recent cruise (Williams, 1971) small groups of skipjack were observed from the deck and underwater bow chamber swimming just ahead of the RV David Starr Jordan for considerable lengths of time. For the size of fish involved, a sample of four ranged from 60 to 64 cm FL, and the ship’s trolling speed of 6½ knots, the skipjack were maintaining speeds of about 5.5 bl/sec.

In view of the above data it is considered reasonable to assume a mean swimming speed for incoming young skipjack equivalent to about 3 bl/sec “made good” in the direction of the oriented movement (migration) over the 24-hr period, i.e., about 50 miles per day. Hence, the first recruits entering the offshore areas of the southern fishery at the beginning of August may well have passed the meridian of 120°W about 6 weeks earlier, i.e., in mid-June shortly after the surface NECC is reestablished east of that meridian. Similarly, the last recruits to this fishery, in entering the offshore areas about the beginning of April, would have passed long 120°W about mid-February close to the time of, or shortly after, the interruption of the surface NECC east of that point. Thus, at the time of entry of the principal component of recruits from November to April, peak January and February, the surface NECC is established.
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east of long 120°W. It is considered that from February to April-May, when the surface NECC is absent east of long 120°W, the juvenile skipjack are being recruited to the northern fishery where they occur in the offshore area (the Revillagigedo Islands) from about March to May-June (arrival April-June onwards in Baja California). From long 120°W (lat 0°-10°N) about 2-4 weeks would be required for the skipjack to reach the Revillagigedo Islands, which agrees closely with the actual occurrence of juvenile skipjack at that location.

It will be recalled that one of the possible splitting mechanisms proposed by Rothschild (1965) was the >28°C surface water cell off Central America, but which it has been shown is not well developed out to long 120°W until April. Thus, even if >28°C water was limiting for skipjack (in quantity), and not >29°C water as shown recently (Williams, 1970), then that cell could not initiate the split as early as February.

The occurrence of small size fish at the Revillagigedo Islands in October (± 1 month) in some years is not accounted for in this model. This could occur if in midsummer some recruits destined for the southern fishery and located close to the northern boundary of the NECC (about lat 10°N) were deflected northward from their migration route by the >29°C water cell normally stretching southward from Central America at that time.

It is proposed that a gating or shunting mechanism operates at about long 120°W across the equatorial and northern migration routes of juvenile skipjack. When the NECC is continuous east of long 120°W, the gate is open and recruitment is to the southern fishery (Figure 5A). Then, with the annual southward movement of the ITCZ, the surface NECC ceases east of long 120°W, and the gate is closed from about February to April-May. Recruitment to the southern fishery ceases and instead the flow of recruits is to the northeast and into the northern fishery (Figure 5B). When the gate is closed there is a loss of west-east orientation due to changes consequent on the breakdown of the surface NECC, such as the loss of the current boundary conditions (with NEC and SEC), possible interruption (total and partial) of the zonal “productivity” bands, loss of food concentrating mechanisms (minor fronts), etc. The principal question then is how the recruit skipjack become oriented to the northeast, i.e., towards the Revillagigedo Islands. There could well be random dispersal of incoming recruits when the gate closes at long 120°W, with only a small proportion moving northeastwards into the California Current Extension and the majority eventually recycling to the central Pacific. Possibly those fish moving northeast pick up a “food bridge” linking the area around long 120°W in the vicinity of the NECC with the Revillagigedo Islands and Baja California. Such a “food bridge” could be provided offshore by the pelagic stages of the red crab (Pleuroncodes planipes) which are found in the California Current Extension (Longhurst, 1967, 1968; Longhurst and Seibert, 1971), the gradient of abundance of which increases towards the northeast (shorwards). It will be remembered that the California Current Extension is strongest and farthest to the southwest at this period. Red crab are known to form a large part of the diet of skipjack in Baja California waters during the fishing season (Alverson, 1963). A “food bridge” facilitating the northeast movement of recruit skipjack, because of survival value, may have become an inherited behavioral response when west-east orientation is lost around long 120°W in the period February to April-May.

One possible objection to the gating mechanism could concern efforts by the juvenile skipjack to dive below its effects. This is considered unlikely in view of adverse temperatures (<20°C) at depths where subsurface eastward flow is continuous and low oxygen concentrations at relatively shallow depths, at least as far south as lat 10°N. Oxygen content as low as 3 ml/liter has been suggested as possibly limiting for skipjack (Commercial Fisheries Review, 1965).

PASSIVE MIGRATION MODEL (Figure 6)

In this model it is hypothesized that larval and juvenile skipjack are passively carried eastward in the equatorial countercurrent(s) from the central Pacific spawning grounds to the offshore areas of the eastern Pacific fisheries.
FIGURE 6.—Passive migration model: (A) routes of young skipjack into the southern fishery and (B) routes of young skipjack into the northern fishery. NEC = North Equatorial Current; NECC = North Equatorial Countercurrent; SEC = South Equatorial Current; SECC = South Equatorial Countercurrent.

Many of the larval and early juvenile skipjack in the central Pacific would originate in, or be involuntarily transported into, the NECC and while developing in this current (few larvae are found east of long 130°W) would be transported eastward with it. Although generally increasing in a west-east direction the productivity, in terms of zooplankton, of the NECC appears relatively low (Reid, 1962), though the incidence of small fronts in the NECC area (Murphy and Shomura, 1972) would be likely locations for aggregations of food organisms. The rapidly growing and increasingly active skipjack juveniles would need therefore to forage extensively for food and, in view of the large numbers involved, this may also necessitate foraging near the edges of the “productivity” bands at or close to the NECC boundaries (the net transport of the fish would necessarily be eastwards).

The concept of a passive migration eastwards with the NECC eliminates the otherwise difficult question of orientation in the young fish. The dispersion of juveniles from the NECC, at its nearshore terminus, to the southern fishery would be relatively simple and similar to that in the active migration model (Figure 6A). For recruitment to the northern fishery the problem is more complex, depending on whether the fish destined for that area are transported when the NECC flows through to the coast or when it is intermittent or stopped east of long 120°W.

The surface current system along the central American coast (Wyrtki, 1965), at least from May-June to December, is such that juveniles could be passively transported from the nearshore terminus of the NECC to the Revillagigedo Islands area (Figure 6B). However, from about April to September warmwater cells (>29°C) of varying sizes off Central America would prevent transport of the juveniles close to the coast and with increasing offshore distance the risk would increase of passive transport westwards into the NEC and not to the Revillagigedo Islands. With the principal influx of fish into the offshore areas of the northern fishery being from March to June, approach to these areas would need to be taking place in the first months of the year, and this is in fact the time when the coastal current system appears least likely to support such a passive migration. Thus, there are some real problems of timing with the passive migration of young skipjack into the northern fishery in the NECC and Central American coastal currents.

If recruitment to the northern fishery takes place after the cessation of the NECC east of long 120°W, then it would require an active migration from the terminus of the NECC to the
Revíllagigedo Islands (as proposed in the active migration model at this time of year). In the period prior to cessation, when the NECC is intermittent, juvenile fish would increasingly lose their eastward orientation, some being deflected into the weak NEC and with a sufficient northward component in the current might passively reach the Révíllagigedo Islands, though such conditions would be short-lived.

Should recruitment to the northern fishery not take place at the time of cessation of the NECC, juvenile skipjack at that time being recycled to the central Pacific in the NEC and SEC, then all recruits to the eastern Pacific fisheries would have to be carried to the coast in the NECC in the period May–June to December–January. From long 130°W (eastern limit of spawning area) to 85°W (approximate NECC nearshore terminus) is 2,700 nautical miles and with an average NECC speed of 3/4 knot, continuous passive movement over this distance would take about 5 months. This would make the arrival time at long 85°W October–November to May–June. Obviously transport time could be much longer than this, if, for instance, (i) daylight hours were entirely spent foraging and with near-zero movement eastward, and/or (ii) real transport rates were lower due to the effects of diel vertical migrations. From the NECC terminus at about long 85°W recruitment, even passive, to the initial southern fishery areas would probably take no more than 4–6 weeks, i.e., arrival November–January to June–August. But a passive drift from the NECC terminus northwest to the Révíllagigedo Islands with surface currents about 1/2 knot would take in the order of 4–5 months, i.e., arrival February–May to September–December. However, the recruitment size of the skipjack to both northern and southern fisheries appears similar. Several factors might be proposed to account for this fact: (i) the spawning grounds of the fish found in the southern fishery are farther west in the central Pacific than those of the northern fishery, (ii) the early life history stages enter the NECC at different sizes, (iii) behavioral patterns of the juveniles (from the two groups) in the NECC are different, or (iv) the juveniles stay longer in the offshore areas of the southern fishery than the northern one. Of these proposals the first seems most likely, and would be understandable if the two fishery groups did represent parts of two spawning groups (northern and southern) as suggested earlier (see page 748). One feature which could influence the eastern boundary of the groups spawning in the central Pacific, particularly the southern one, would be the westward extent of the influence of low near-surface temperatures at and south of the equator due to equatorial upwelling and effects of Peru Current water.

A wide degree of geographic overlap of the spawning groups in the central Pacific would alleviate problems of recruitment of young stages of southern spawners into the NECC, as trans-equatorial migration might not then be involved to any extent. In addition, the occurrence of a surface SECC would provide a possible mechanism by which young stages of southern spawners from south of the equator could be carried passively into the eastern Pacific. However, as previously stated, the existence of a surface SECC has not yet been confirmed in the eastern Pacific.

Thus, as our knowledge stands at the moment the NECC could be passively carrying juveniles of both spawning groups into the eastern Pacific fisheries but at different sizes.

**GYRAL MIGRATION MODEL** (Figure 7)

The two models described so far are based on the assumption that larval or juvenile fish migrate, passively or actively, out of the central Pacific to feed in coastal surface waters of the eastern Pacific and then subsequently return to the central Pacific for first spawning. Between spawnings the adult fish diffuse outwards from the central Pacific to feed but rarely reenter the adolescent feeding grounds.

Incidental longline catches of skipjack through 1967 (Miyake, 1968; Walter M. Matsumoto, personal communication) indicate the widespread distribution of the adults. According to Matsumoto there is some evidence that areas of high longline catch-per-unit-effort of skipjack in the central-east Pacific show seasonal shifts which tend to coincide with the direction of flow of the
major ocean currents. Such movements appear to be counterclockwise in the southern hemisphere and clockwise in the northern hemisphere. The exception is in the eastern North Pacific where movement seems to be counterclockwise and corresponds to the narrow gyre of the northern equatorial water mass.

The above findings have suggested consideration of another type of model for skipjack, the gyral migration model, which involves all life history stages and both passive and active migrations. [Generalized gyral migration patterns are briefly discussed in Harden Jones (1968).]

For the northern fishery group it is proposed that the fish are moving counterclockwise around a zonally narrow equatorial gyre consisting of the NECC and the NEC, with the western limit some considerable distance west of long 130°W (possibly as far as long 170°W). In this model it is considered that mature skipjack spawn primarily in the northern spring-summer (May to October) in equatorial waters west of long 130°W, a large proportion of the subsequent larvae and early juveniles entering the NECC and with development then taking place in that current as proposed in the passive migration model (Figure 7A). The majority of the juveniles on reaching the terminus of the NECC are carried northwestwards with the coastal current off Central America, outside the warm-water cells >29°C. Movements of the adults would generally parallel the young stages, but they are in no way restricted to the NECC and may be found in a wide band covering the NECC.

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**Figure 7.** Schematic representation of gyral migration model: (A) routes of young skipjack into the northern fishery, (B) routes of adult skipjack of northern fishery, and (C) routes of young skipjack into the southern fishery. NECC = North Equatorial Countercurrent; SECC = South Equatorial Countercurrent.
and adjacent areas of the NEC and the section of the SEC north of the equator (Figure 7B). This implies a navigational system in the adults. Thus, spent and spent-recovering fish would be expected in the areas immediately to the east of the spawning grounds. When the juveniles are off Central America and Mexico, the adults have also turned north and are located farther offshore and/or in deeper water. [It should be recalled that tag returns show little interchange of fish of the size caught in the eastern Pacific between the northern and southern fisheries (Fink and Bayliff, 1970).]

As the gyral group approaches the southern part of the northern fishery area, south and southeast of the Revillagigedo Islands, the juvenile skipjack actively migrate out of the gyre into the waters around the Revillagigedo Islands and subsequently into the feeding grounds off Baja California. The cue for the start of the active migration of the juveniles out of the gyre could involve a summation of external stimuli, such as those received on encountering California Current Extension (CCE) water, coupled with internal endocrinal stimuli, such as increased thyroidal and gonadal activity. Some adults migrate with the juveniles but the majority probably remain offshore. With the southerly advance of cold water (18°-21°C isotherms) along the west coast of Baja California in late fall, the adolescent skipjack leave the area of the northern fishery (Blackburn, 1969a; Fink and Bayliff, 1970; Williams, 1970). They do via the CCE and rejoin the gyre, although no longer dependent on it for movement, the general transport of which is in a west-southwesterly direction (NEC). The adolescent skipjack, now maturing for the first time, and the adults thus return to the spawning grounds in the central Pacific in time for the next spawning season.

With regard to timing of movements in the gyre, the only real fact is that the principal recruitment to the offshore areas of the northern fishery, the Revillagigedo Islands, lasts from about March to June, with movement to Baja California waters normally from May onwards. A continuous passive migration of young stages from long 130°W to 85°W in the NECC and then to the Revillagigedo Islands in coastal currents might take about 9-10 months (see page 753). Backtracking from the entry time at the Revillagigedo Islands would suggest movement past the meridian of 130°W from about May-June to August-September. This is close to the suggested principal spawning season, May to October, west of that meridian for the northern spawning group. The adolescent skipjack leave offshore Baja California waters principally from November to January and, even if only moving at the speed of the current (CCE, then NEC), there is adequate time to reach the central Pacific west of long 130°W by spawning time.

The time between the proposed spawning period and first entry into the offshore areas of the northern fishery is about 10-12 months and might suggest that the higher of the growth rates mentioned earlier (see page 754) is the more likely in the first year, i.e., >40 cm. With a spawning period of May to October the proposed passive transport of juveniles east of long 130°W coincides with the period when the NECC flows through to the Central American coast. When the gyre is interrupted by the breakdown of the NECC east of long 120°W from February to April, there are probably no northern group young stages to be transported eastwards.

It is proposed that the skipjack forming the southern fishery group (from which the catch is usually much greater than that in the northern fishery) spawn principally in the southern spring and summer, November to April, in the central equatorial Pacific. A large proportion of the larvae and juveniles eventually enter the NECC where development ensues during the passive migration eastwards towards the American coast (Figure 7C). As with the northern group, movements of the southern group adults would parallel the juveniles in the NECC but would be primarily in the SEC. On reaching the terminus of the NECC, the juveniles migrate actively into the offshore areas, and subsequently the feeding areas, of the southern fishery off Central and South America (mainly off Ecuador). It is difficult to suggest a specific environmental cue which may act as the external stimulus involved in triggering this change from passive to active migration. Perhaps in the southern part of the area of the NECC terminus the cue could be
related to the waters of the Equatorial Front, especially those of Peru Current origin.

The adult skipjack at this period would normally remain offshore in the eastern Pacific. When the adolescents leave the feeding grounds they, and the adults, are maturing and would move westwards in the SEC (north and south of the equator), and possibly even in the NEC, to the central Pacific spawning grounds. There is some indication from the data of Miyake (1968) that maximum occurrence of longline caught skipjack was at about lat 10°-15°S east of long 105°W, at lat 5°-10°S from long 105° to 130°-140°W, and at lat 0°-5°S west of long 130°-140°W, that is tending towards the equator away from the coast. This could be related to equatorial low temperature areas west of the Galapagos Islands.

A principal problem with a gyral model for the southern fishery group concerns the entry of larvae and early juveniles into eastbound currents. For those originating in the equatorial areas of the NEC, or the SEC north of the equator, access to the NECC through known circulatory mechanisms is relatively simple (similar to that in the passive or northern gyral migration models). For larvae and early juveniles of this group south of the equator the problem is more complex. Here the SEC has a southerly component in the westward transport tending for passively drifting animals to be carried away from the equator. For those between lat 0° and 5°S a passive movement northwards and across the equator, and hence into the NEC, could occur under the stress of unusually strong southeast or south winds, the equatorial divergence then being farther south than usual.

This problem related to skipjack young stages south of the equator raises the question of the role of the SECC in the southern gyral migration model. Migration in the subsurface SECC is improbable as mean temperatures are about 14°C (M. Tsuchiya, personal communication). However, the existence of a surface SECC, even if as narrow as 120 miles, could be of importance in completing the gyre south of the equator (see Figure 7C). Larvae south of the equator in the central Pacific would tend to be carried towards the SEC/SECC boundary, and then eastwards with it. As mentioned earlier EASTROPAC and other data showed increased “productivity” in the general region where a surface SECC might be expected (lat 10°-15°S), and this would obviously be of importance in development of the juveniles. Subsequent movement of juveniles from the surface SECC terminus would presumably be in the form of an active migration. There could also be some type of link with the Peru Countercurrent. In the southern summer adolescent skipjack often occur off northern Chile and the north-south migration route of these fish must be offshore in view of the low coastal temperatures off Peru. Fish that migrated onshore in the SECC would move, after feeding off South America, westwards in the SEC and return to the central Pacific.

Obviously timing in the two gyral migration models would be different, even though they share a common eastbound current, the NECC. When this current is flowing through to the coast, it would carry recruit skipjack of two different sizes representing the two groups. Southern fishery group recruits would be considerably larger (4-5 months older) than those of the northern group. Separation of the juveniles of the two groups at the NECC terminus would be little problem as only those of southern group origin would be in the developmental physiological state requisite to active migration. Those juveniles belonging to the northern group would continue their passive migration. Intermingling of groups could occur if some northern group juveniles were passively carried into southern fishery areas especially off Central America.

As in the passive migration model (see page 753), to account for the size differences in incoming recruits, one would have to propose that: the southern group spawning grounds are farther west than those of the northern group, and/or the transfer mechanisms involved in the movement of young stages into eastbound currents are complex and take longer (certainly true if no SECC). Either or both of these proposals could account for southern group juveniles, spawned November to April, not reaching the area of long 130°W at the time when the NECC has stopped east of that meridian. Alternatively, if juveniles from the southern spawning group
(southern fishery group) were somehow retained west of long 130°W from February to April, when the NECC is stopped, then this would reduce the apparent distance westward from the coast that the entry times to the southern fishery would otherwise imply.

The existence of a surface SECC would certainly facilitate the recruitment of juvenile skipjack (of southern origin) into the southern fishery. However, one would expect such a current to be highly variable in space and time, and hence such recruitment would be similarly affected.

**GENERAL COMMENTS AND RECENT RESEARCH**

An active migration of juvenile skipjack from the central to the eastern Pacific would be categorized as a "between habitat migration," using the definition of Nakamura (1969). Similarly with the gyral migration models, the active migration of juveniles from the gyres to the feeding grounds would fit this definition. This type of migration, Nakamura suggested, takes place following a change in ecological state, for which one might perhaps synonomize developmental physiological state. Nakamura also hypothesized that "between habitat migrations," which entail changes in environment (current systems, water masses), occur principally at the equinoxes, about March in the northern hemisphere and September in the southern hemisphere, and that the movements are rapid and on a large scale. In the eastern Pacific the principal recruitment into the offshore areas of the northern fishery starts about March and lasts to about June; there is also some recruitment about October (± 1 month). However, recruitment to the offshore areas of the southern fishery appears to be over a considerably longer period, November to April, and perhaps from as early as August (± 1 month).

The Bureau of Commercial Fisheries (now the National Marine Fisheries Service), Honolulu, undertook five quarterly cruises, from May 1969 to May 1970, between lat 12°N and 3°30'S along the meridian of long 145°W, to consider the distribution and abundance of skipjack in the equatorial current systems. Preliminary data from these cruises (Walter M. Matsumoto, personal communication) show longline skipjack catches were generally low except in the area of the NECC (lat 7°30'N), where they were relatively high in the first and fourth quarters (February and October-November). Trolled catches of skipjack on the last three cruises were variable but consistently high in the NECC. Catches by both methods were lowest at the equator in the vicinity of the EUC. Catches of juvenile skipjack made with a midwater trawl were relatively high in the SEC at lat 3°30'S through most of the year, while catches in the NECC peaked in the second and third quarters (May and June). Plankton hauls (1-m net) showed largest catches of larvae were made in the SEC just south of the NECC.

These results suggest that skipjack north of the equator spawn in the second and third quarters, or even slightly earlier, and that the juveniles are concentrated in the NECC at this time. The high year-round abundance of juveniles at lat 3°30'S apparently indicates either sequential seasonal spawning of the northern and southern groups or continual equatorial spawning of a single group. Richard A. Barkley and Richard S. Shomura (personal communications) have previously suggested that the shallow EUC could be involved in the eastward transport of skipjack young stages. At least east of long 120°W this seems unlikely as even in the upper regions of the EUC temperatures (18°-20°C) are marginal for adult skipjack let alone larvae. Even in the vicinity of the EUC at long 145°W, where temperatures may be about 20°C, the lack of juveniles and adults would appear to confirm this finding.

Hida (1970) reported on an exploratory fishing cruise for tuna made by the Bureau of Commercial Fisheries, Honolulu, in October-November 1969 concentrated in the area, lat 6°N-8°S, long 115°-125°W. Surface schools of tuna fishable by pole-and-line were found from lat 2°-5°N (just south of the NECC); skipjack predominated in the catches, though some large schools consisted of yellowfin, bigeye, or all three mixed. The skipjack, caught by this method and trolling, ranged from 45 to 79 cm FL (means 47-68 cm) and gonads were maturing or mature (only one
spent). Only one school of small skipjack was fished by pole-and-line, at lat 4°S, and the fish were from 36 to 51 cm (mean 40 cm). However, enroute to and from Hawaii (lat 10°N-5°S, long 125°-145°W) troll catches of skipjack were mainly of small fish, <45 cm. The data from this cruise add little to the proposed migration models except to indicate the wide geographic range of recruit size skipjack west of long 125°W in October-November 1969. In addition, east of long 125°W fish were in the medium to large category and in schools large enough to be fished successfully by a commercial method—live bait pole-and-line. None of these fish had recently spawned.

Williams (1971) described plans for a series of eight cruises, initiated by the NMFS, La Jolla, and the Scripps Tuna Oceanography Research (STOR) Program, to investigate the distribution of skipjack in relation to environmental conditions in two offshore areas of the eastern Pacific. The two areas, (A) lat 15°N-5°S, long 115°-125°W, and (B) lat 5°N-15°S, long 95°-115°W, were considered the most important for testing migration models for skipjack, including the three new proposed for recruits.

The first cruise (two vessels) was to Area A in October-December 1970, with trolling as the principal fishing method. Recruit size fish (<40 cm) were found in the NEC some distance to the north of the NECC, as well as immediately to the north and south of the NECC. Large fish were widely distributed, but with fewest found in the NECC and most in the section of the SEC north of the equator. About 27% of the fish ≥45 cm, the gonads of which were examined, were found to be in a spent or spent-recovering condition; most were found in or close to the NECC, and none south of the equator. A first sorting of midwater trawl samples showed no skipjack juveniles; data on occurrence of larvae are not yet available.

The second cruise to the same area, in March-April 1971, caught few small fish and none <40 cm. More large fish were caught north of the equator than on the previous cruise. The presence of a surface NECC, even though weak and narrow (180-120 miles wide), at this time of year and at this meridian was anomalous. About 60% of the fish examined had gonads in a recovering state and were from all current systems north of the equator.

The results of these two cruises confirm that some skipjack spawn in the equatorial zone not too distant from long 120°W. Those fish taken in March-April 1971 appeared to have gonads in a more advanced state of recovery than most taken in October-December 1970 (subjective analysis). Presence of these spent and spent-recovering fish could indicate support for the gyral migration models, where it is proposed that after spawning west of long 130°W adults move eastwards paralleling the movement of the young stages. However, even with the active and passive migration models there could be small-scale diffusion movements of adults out of the central Pacific (including east of long 130°W) subsequent to spawning. The appearance of spent and spent-recovering gonads in October-December skipjack suggests they were of northern summer spawning origin, while the recovering gonads in March-April fish rather indicate southern summer spawners; or alternatively that spawning in skipjack is truly a year-round function in the equatorial zone. The apparent absence of juveniles in the trawl hauls may be due to ineffective sampling gear. The presence of very small fish (<40 cm) in areas of high forage concentrations at the NECC boundaries, as well as in the NEC somewhat further north, would tend to support the active migration models. They could be either some of the last recruits destined for the southern fishery or early ones for the northern fishery; their presence in the NEC as far north as lat 13°N, and size (30-40 cm) suggests the latter. The significance of the shift in the center of apparent abundance of large fish from lat 1°-5°N to 9°-11°N between October-December and March-April is not yet apparent.

A further six cruises, starting with one to the southern area (B) in August-October 1971, are planned. Data from this series of cruises will undoubtedly increase our ability to describe, particularly for offshore areas, the distribution, apparent abundance, life history, and environment of the skipjack. Although input of these data will be valuable in preparing models, such as
those of migrations, there is also a need for a greater input related to the physiology, behavior, and genetics of the species than is presently available.

The hypothetical nature of certain aspects of the proposed models of skipjack migrations advanced here cannot be denied. However, at this stage in the development of research on the skipjack resources of the central-east Pacific, a presentation of existing data and ideas on skipjack migrations, in the form of models, appears fully justified. Indeed present research plans were formulated on the basis of the active migration model (the first proposed), although they are equally applicable to testing the other models as well.

With any of the proposed migration models it is obvious that oceanographic conditions in the central-east Pacific will have a vital controlling effect on the subsequent abundance of skipjack in the eastern Pacific fishery. First, through year-class strength of recruits (spawning success/larval survival) and second, through the number of recruits actually entering the fishery (migration success). Not only is it necessary to test the mechanisms of these, and other, migration models, but monitoring and more detailed analyses of inter- and intraseasonal fluctuations in the central-east Pacific environment will assist in understanding, and perhaps in predicting, the fishery-independent changes in skipjack apparent abundance.

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1968. The biology of mass occurrences of galatheid crustaceans and their utilization as a fisheries re-


Sette, O. E. 1955. Consideration of midocean fish production as

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