PRE-EXPLOITATION ABUNDANCE OF TUNAS IN THE EQUATORIAL CENTRAL PACIFIC

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ABSTRACT

The tuna resources and the environment in the equatorial central Pacific were investigated from 1950 to 1954. This report summarizes the data from these investigations and examines the distribution and relative abundance of tunas in relation to the environment.

The circulation of the waters of the equatorial region is described. The generally accepted view of a zonally oriented flow pattern of the South Equatorial Current between the equator and the Countercurrent is modified, and a model is proposed which regards the circulation as a series of homologous northwestward flowing cells. The evidence supporting this type of flow pattern is presented and discussed.

The variation in abundance of deep-swimming yellowfin tuna in space and in time is analyzed in relation to various environmental features. The hypothesis developed is that the change in abundance of yellowfin tuna is a function of the variation in the wind-driven ocean circulation and the attendant changes in the development of forage organisms.

A study of the distribution and abundance of surface tunas (skipjack tuna and small yellowfin tuna) revealed that more schools are sighted near land than in the open ocean. In the open ocean more tuna schools were observed in the countercurrent than in the zone from the equator to lat 5°N, where deep-swimming yellowfin tuna are most abundant. Rather than respond to the general level of standing crop of forage, the surface tunas appear to respond to secondary factors that make it possible to forage more effectively. The distribution of "fronts" is such a secondary factor influencing the distribution of surface schools.

In 1949, before the establishment of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu,[3] the tuna resources of the equatorial central Pacific were little known and even less well understood. In the eastern tropical Pacific the Americans had a highly developed fishery for surface schools of yellowfin and skipjack tunas, and in the western Pacific the Japanese had an active longline fishery for the larger subsurface tunas. In the central Pacific, however, information on the tuna resources was limited to the experiences of a few commercial operators who had prospected in the area.[4]

From 1950 to 1953 the Bureau of Commercial Fisheries surveyed this unknown area, roughly the region between long 120°W and 180°, and between lat 15°N and 10°S. Studies undertaken during this period involved the distribution of tunas, the productivity of the waters, and the circulation of the ocean. The results of the surveys of the tunas form the substance of this report. Although the other investigations are detailed elsewhere, they are brought to bear wherever they help to explain the distribution of the tunas. Studies in the equatorial central Pacific

[4] It should be noted that today (1972) the oceanwide longline fishery is fully developed (see, for example, Suda and Schaefer, 1965). The results reported herein are representative of "virgin stock" conditions, and it is highly unlikely that a similar assessment can ever be repeated.

after 1953 focused on special problems (Iversen and Yoshida, 1956) and are not considered in this report.

This paper on the equatorial tuna is in part documentary and summarizes the results of the Laboratory's experimental fishing and scouting; however, the major effort is a review of the distribution of yellowfin and skipjack tunas as it relates to the distribution of properties in the environment. To a lesser extent, we discuss two other tuna species, the albacore and the bigeye tuna. The results suggest that the abundance of yellowfin and skipjack tunas in the region varies according to the properties in the environment. The variation in abundance of deep-swimming yellowfin tuna in space and time is relatable to variations in the wind-driven ocean circulation that alter the rate of enrichment of the euphotic zone. How albacore and bigeye tuna are related to the environment is less clear. The occurrence of these species in deeper water than yellowfin tuna suggests that other factors may be of greater importance. The apparent abundance of surface tunas is not believed to be closely related to basic enrichment; rather, it appears that secondary factors, such as food-concentrating mechanisms, are more important.

Most of the data in this report have been published. The fish distributions have been described by Ikehara (1953), Murphy and Shomura (1953a, 1953b, 1955), Murphy and Ikehara (1955), and Shomura and Murphy (1955). The oceanographic data were published by Cromwell (1951, 1953), Austin (1954), Cromwell and Austin (1954), Cromwell, Montgomery, and Stroup (1954), Stroup (1954), and Stroup and Austin (1955). The plankton catches were reported by King and Demond (1953), Hida and King (1955), and King and Hida (1957).

SAMPLING METHODS AND MATERIAL

Longlining, trolling, and surface sighting, the latter supplemented by occasional live-bait fishing, were used to assess the abundance of tunas. None of these was completely satisfactory, chiefly because no single type of gear sampled all species and sizes of fish within each species with equal effectiveness. Further studies will undoubtedly reveal additional weaknesses in our general assumption that catches represent relative density of tunas.

Longlining

More effort was devoted to longlining (Figure 1) than to the other sampling methods, mainly because it proved to be the best way to capture significant numbers of tuna systematically.

Figure 2 shows the type of longline gear used during the survey. Niska (1953) gave details of its construction and operation. Basically the gear consists of (1) a mainline suspended at intervals from buoys and (2) branch lines that hang from the mainline, each with a baited hook. The amount of tackle between two buoys is called a "basket."

The mainline hangs slack in the water, presumably in the shape of a catenary (Figure 2). Since the mainline was 384 m long and the buoys were generally spaced about 274 m apart, the deepest hooks should have fished at about 152 m and the shallowest at about 76 m. The gear, however, fished at shallower depths than the expected depth because of differences in the forces exerted on the buoys by wind and surface currents and on the mainline by the deeper, sometimes opposing currents. Consequently the deep hooks may frequently have fished as shallow as 76 m (Murphy and Shomura, 1955).

At a typical longline station, 40 to 60 baskets of gear were set in the early morning and retrieved in the afternoon.

The longline catches are presented as numbers of fish per 100 hooks. Valid comparisons of availability can be based on this statistic, provided the construction of the gear and the operational details remain constant. Fortunately all of the catches were obtained in a nearly standardized manner that satisfied most of the assumptions, e.g., construction did not vary, roughly the same amount of gear was fished each day, and the fishing schedule was the same each day.
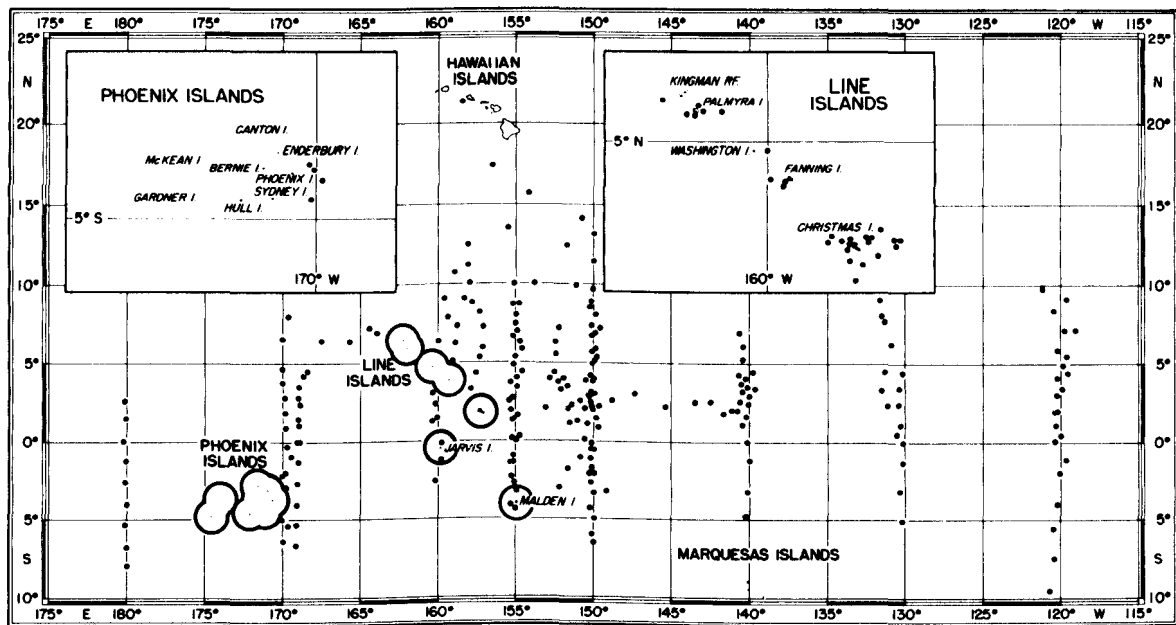
FIGURE 1.—Locations of longline stations. The circles show the location of an island or group of islands.
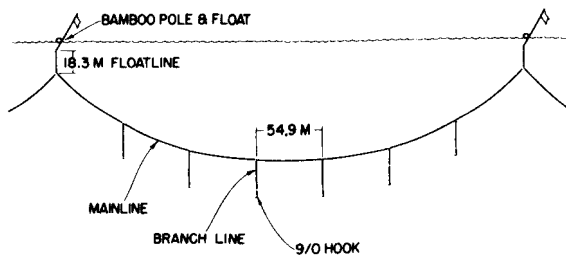

FIGURE 2.—Schematic diagram of tuna longline gear.

Trolling

Systematic trolling (Figure 3) provided another useful measure of tuna abundance. Generally when the vessels were underway (7-9 knots) two 45.7-m lines were trolled astern. A variety of tuna lures was used (Murphy and Ikehara, 1955). Occasionally near the islands, the "standard trolling" was modified by reducing vessel speed and trailing more than two lures. The catches from this type of fishing are considered separately from those of standard trolling.

Surface Sighting

As a further measure of tuna abundances, the abundance of surface schools of fish, bird flocks, and other signs of life was estimated by consistently maintaining a bridge log of sightings (Figure 3). A log of these observations was kept by the wheel watch under the supervision of the scientists on board (Murphy and Ikehara, 1955). These records provided a unique body of quantitative information on the bird and fish life in the central Pacific.

SPECIES OF FISH

Though the tunas are the most abundant and commercially most valuable of the large pelagic fishes in the central Pacific, a number of other species occupy prominent positions in the biota. The following list of species is largely based on longline catches, but it includes those likely to be captured by trolling or to be seen at the surface. The vernacular names listed below are used throughout the rest of this report.
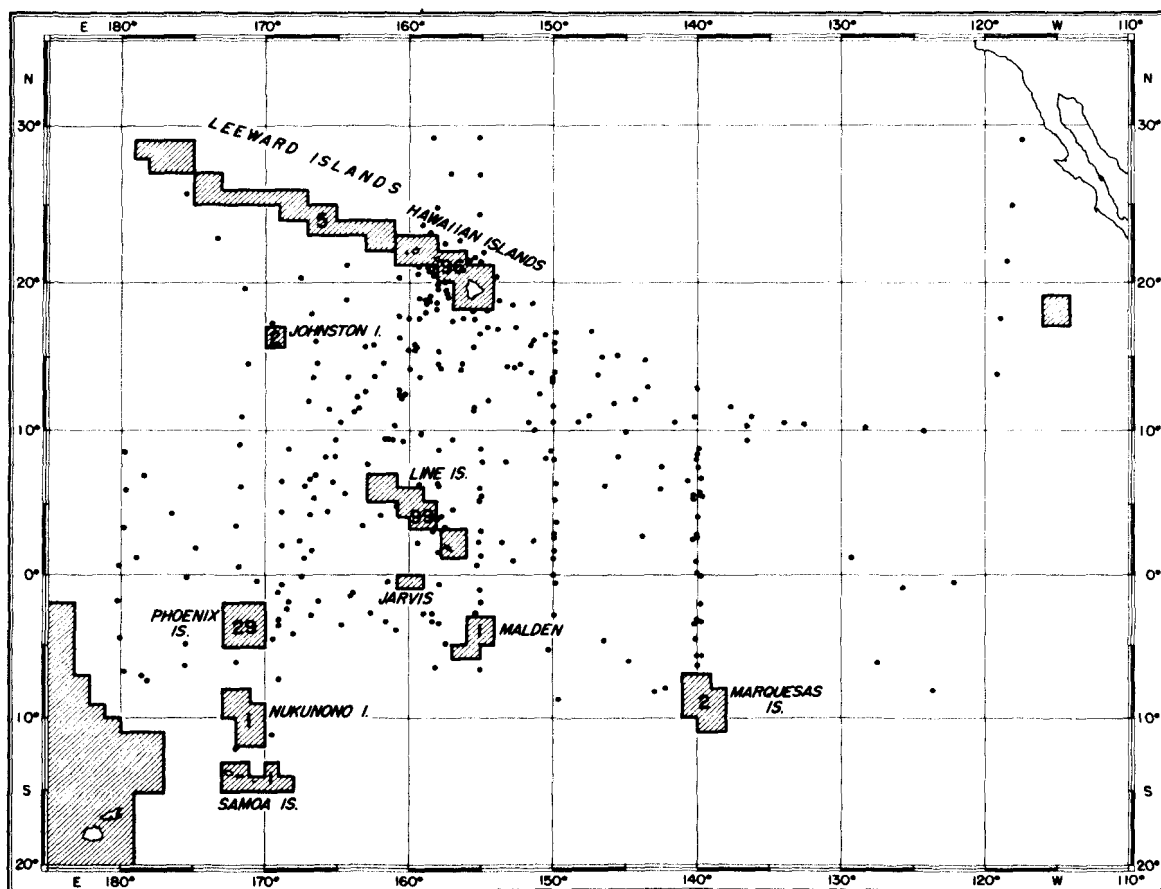
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FIGURE 3.—Noon positions of vessels while trolling and surface sighting. Each dot represents the noon position for a day's observation. The number of days' observation in each of the shaded island areas (within 96.5 km of land) is shown by the figures. (Adapted from Murphy and Ikehara, 1955.)

Albacore, *Thunnus alalunga* (Bonnaterre)
Barracuda, *Sphyraena* sp.
Bigeye tuna, *Thunnus obesus* Lowe
Black marlin, *Makaira indica* (Cuvier)
Blue marlin, *Makaira nigricans* Lacépède
Blue shark, *Prionace glauca* (Linnaeus)
Dolphin, *Coryphaena hippurus* Linnaeus
Longnose lancetfish, *Alepisaurus ferox* Lowe
Mako shark, *Isurus* sp.
Oceanic whitetip shark, *Carcharhinus longimanus* (Poey)

Sailfish, *Istiophorus platypterus* (Shaw and Nodder)
Shortbill spearfish, *Tetrapturus angustirostris* Tanaka
Silky shark, *Carcharhinus falciformis* (Bibron)
Skipjack tuna, *Katsuwonus pelamis* (Linnaeus)
Striped marlin, *Tetrapturus audax* (Philippi)
Swordfish, *Xiphias gladius* Linnaeus
Wahoo, *Acanthocybium solanderi* (Cuvier)
Yellowfin tuna, *Thunnus albacares* (Bonnaterre)

ECOLOGICAL SUBDIVISION OF TUNAS

On the basis of size and behavior, populations of yellowfin tuna, bigeye tuna, and albacore can be conveniently separated into two groups: (1) the smaller surface fish and (2) the larger deep-swimmers. The two groups (Figure 4) cannot be readily sampled by any one fishing method; most surface fish are caught by trolling and live-bait fishing and most deep-swimmers by long-line. This situation evokes a query as to whether the separation represents a real difference in vertical distribution or whether the two apparent groups result simply because one type of fishing is more effective for small fish and one for large. The differences in catch rates on longline hooks fished at different relative depths (Table 1) strongly suggests that large tunas do, in fact, tend to spend their lives well below the surface. For instance, the catches of large yellowfin tuna on the deep and intermediate hooks were half again as numerous as on the shallow hooks. The differences were even more striking for bigeye tuna and albacore.

The separation of the population into two components, surface and deep-swimming, is accompanied by a horizontal dichotomy, at least in the instance of yellowfin tuna. Sightings and troll catches of small yellowfin tunas (<36.3 kg) were usually associated with emergent land or shoals (Murphy and Ikehara, 1955). As will be discussed later in the section on surface tunas, the longline when fished in such insular areas captures significantly more small fish (as small as 2.3 kg) than when fished in the open sea (>96.5 km from land). When moving away from land, the reduction in numbers of small fish in the longline catch is proportional to the reduction in school sightings which suggests that small yellowfin tuna are associated with land.

There is another difference between deep-swimming and surface tuna. Generally, surface tuna gather in compact schools, which occasionally contain thousands of individuals, whereas Murphy and Elliott (1954) provided evidence from the serial distribution of yellowfin tuna catches along the longline that deep-swimming yellowfin tuna gather in small schools. Little in their data, however, suggests that these groups
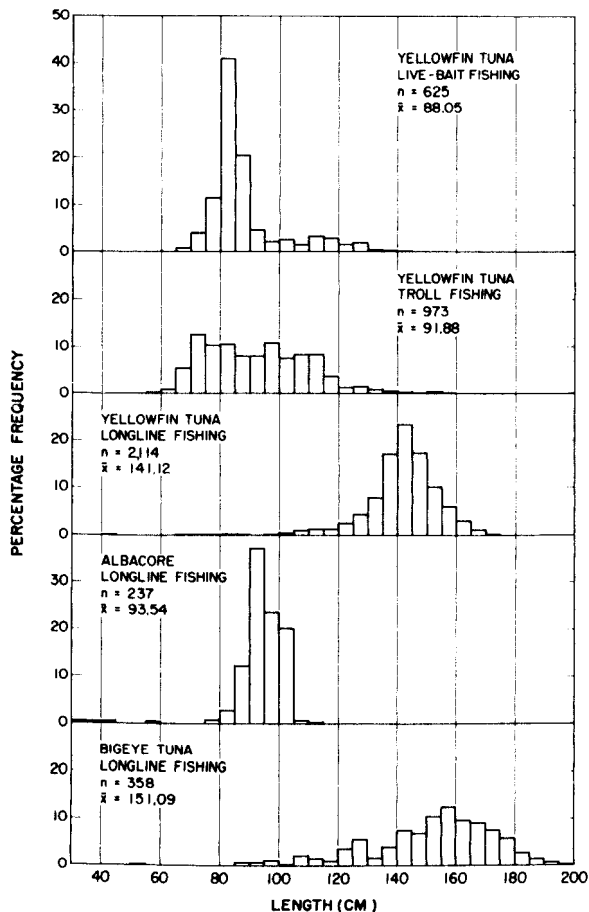

FIGURE 4.—Length frequencies (fork lengths) of the principal tuna species taken, by type of gear.

TABLE 1.—Yellowfin tuna, bigeye tuna, and albacore catches by relative hook depth (longline gear), 1950-53.

Tuna	Shallow	Intermediate	Deep	Total
Yellowfin	673	921	981	2,575
Bigeye	76	137	211	424
Albacore	10	68	122	200

are anything more than loose aggregations of a few large individuals. Thus both the degree of aggregation and the principal depth range differ with size of fish, at least insofar as yellowfin tuna are concerned. For these reasons it is convenient, and probably realistic, to treat the two categories separately.

DEEP-SWIMMING TUNAS

This section presents all the data on the distribution of deep-swimming tunas but emphasizes the yellowfin tuna and how the environment influences their distribution. Scientists have advanced certain hypotheses to explain the variations in the abundance of yellowfin tuna in the central Pacific (see, for example, Cromwell, 1953). These hypotheses, however, involve only portions of the total mass of data, and usually only a limited aspect of the variations in abundance, e.g., longitudinal variation.

The most elegant way to examine hypotheses about fish and the environment is to show step by step how precise interactions of energy flow and behavior (in a broad sense) result in a particular distribution of fish. This approach is not possible with the present data. Instead we have adopted the more generalized approach of advancing a hypothesis about one aspect of the data, i.e., the average distribution of yellowfin tuna with respect to the average distribution of environmental properties. Then we examine this hypothesis with respect to details of variation in abundance such as the north-south distribution and east-west distribution at particular times and places, and time variation at particular

places. Our assumption is that if the same basic hypothesis stands up under this kind of cross-examination, its merit is essentially proved, even though a great deal remains to be learned about the exact way the ecosystem functions. This approach results in some repetition of arguments, especially as it has been possible to explain nearly all aspects of variation in abundance with the same hypothesis—namely, that variations in the dominant species, the yellowfin tuna, are influenced by variations in the wind-driven ocean circulation that affect the food supply of that species.

AVERAGE AREAL DISTRIBUTION

In this section we provide a brief description of the circulation of the major surface currents and the general distribution and relative abundance of the deep-swimming tunas and skipjack tuna in the central equatorial Pacific Ocean.

Oceanography

The dominant features of the eastern tropical Pacific are the three great currents (Figure 5): the westerly flowing North Equatorial Current
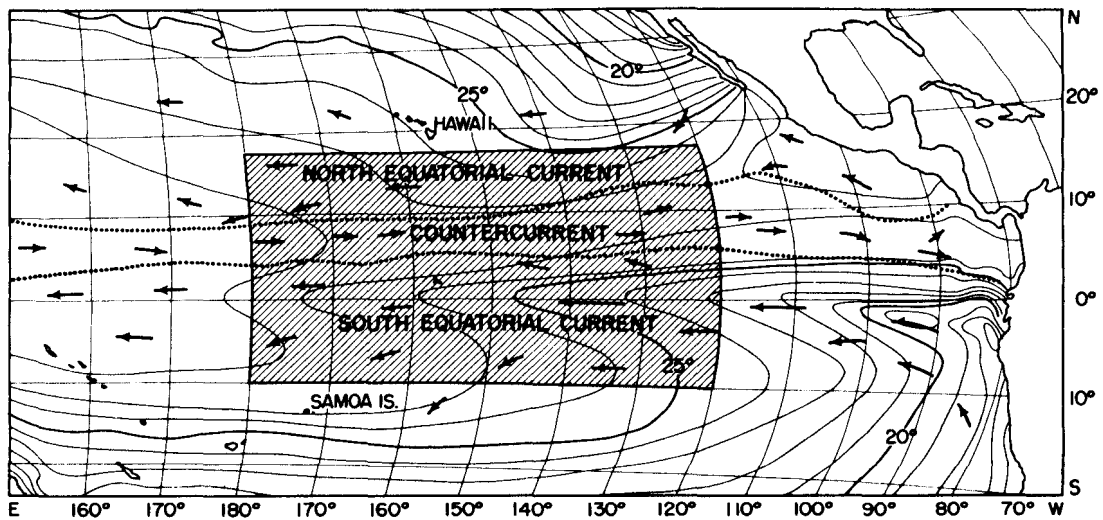

FIGURE 5.—Schematic representation of the major surface currents and surface isotherms in the central and eastern tropical Pacific. The area most intensively surveyed is shaded. Arrows denote approximate current direction. (Adapted from Schott, 1935.)

north of lat 10°N, the westerly flowing South Equatorial Current south of lat 5°N, and the easterly flowing equatorial Countercurrent lying between the two. Surface temperatures are generally high, mostly above 25°C.

Overlying the area are two major wind systems. The northeast trades blow over the North Equatorial Current and the southeast trades over the South Equatorial Current. Between them is a doldrum belt generally coinciding in latitude with the Countercurrent. The two equatorial currents are largely wind-driven, whereas the Countercurrent is simply the return flow caused by the piling up of the wind-driven water in the western portion of the Pacific. The speed of these currents at the surface is usually 1.85 to 3.70 km/hr (1-2 knots).

The configuration of the isotherms in Figure 5 shows that along any meridian the surface waters are cooler at the equator than in the adjacent waters to the north and south. This equatorial cooling is a result of wind-induced upwelling (Cromwell, 1953) and the divergence of water at the surface through the effect of the Coriolis Force. The Coriolis Force deflects the westerly moving water poleward, and this water is replaced by water rising from below (upwelling).

The equatorial upwelling, which brings deeper and enriched water upward into the euphotic zone, and the displacement of this water from the equator to a convergence south of the Countercurrent are the most important factors affecting the distribution of organisms in this region.

Tunas

The areal distribution of the large deep-swimming tunas can best be visualized from contour maps (Figures 6, 7, and 8). This series of diagrams was prepared from the catches of the Laboratory's longline fishing cruises (Figure 1) and the catches of several Japanese vessels (Murphy and Shomura, 1955; Shomura and Murphy, 1955). The presentation suppresses the random and temporal variability, yet it does convey the major features of the tuna distributions. It should be noted that the units used in contouring were those suggested by the catches.
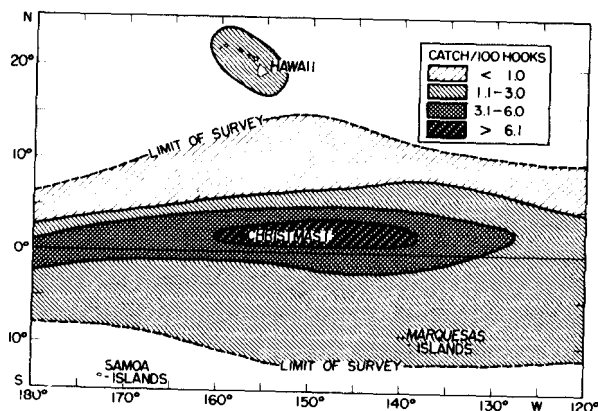

FIGURE 6.—The distribution of deep-swimming yellowfin tuna in the equatorial central Pacific. The isograms are in units of number of fish caught per 100 hooks.
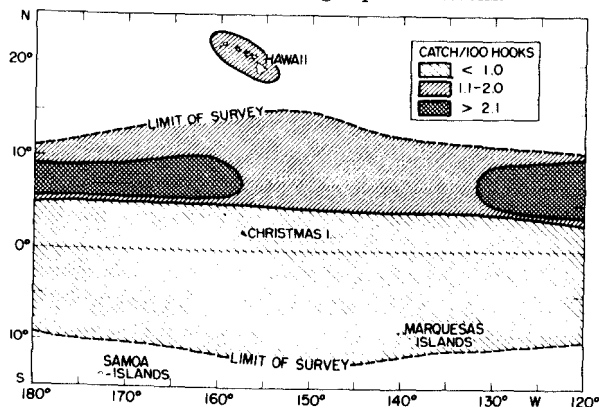

FIGURE 7.—The distribution of deep-swimming bigeye tuna in the equatorial central Pacific. The isograms are in units of number of fish caught per 100 hooks.
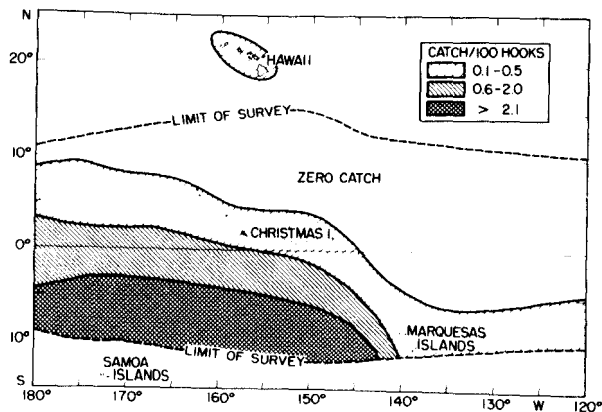

FIGURE 8.—The distribution of deep-swimming albacore in the equatorial central Pacific. The isograms are in units of number of fish caught per 100 hooks.
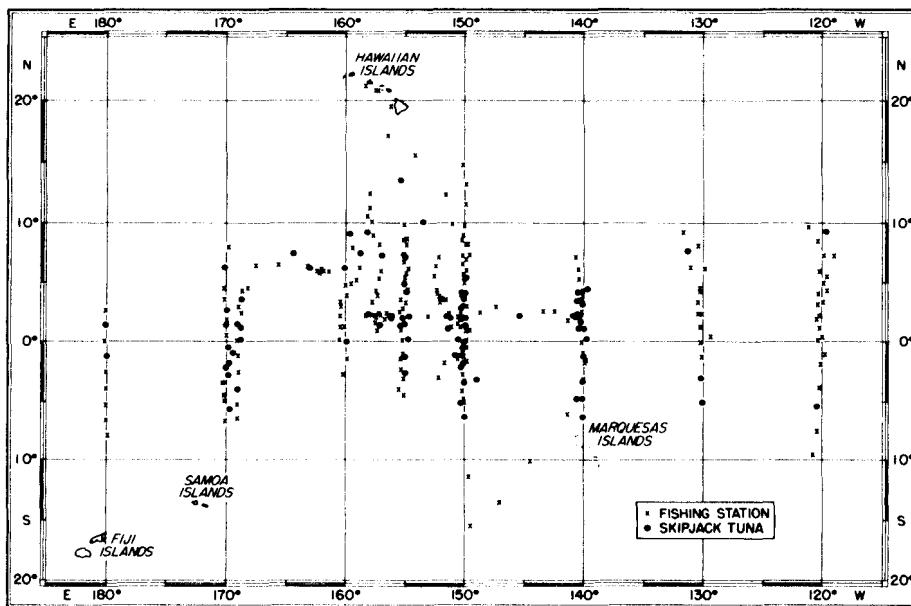
FIGURE 9.—The distribution of skipjack tuna in the equatorial central Pacific Ocean as shown by longline catches. A dot represents capture of one or more skipjack tuna.

Yellowfin tuna were found over the entire survey area (Figure 6), but the peak abundance occurred near the equator in the zone enriched by the equatorial upwelling. Between this zone and lat 10°N, the numbers decreased rapidly. Abundance south of the equator also declined but not as precipitously as to the north. Even near the equator this species was scarce at the eastern end of the survey area; it was most abundant in the center (between long 140° and 160°W) and somewhat less abundant to the west of long 160°W.

Bigeye tuna were not as abundant as yellowfin tuna, but their distribution, like that of the yellowfin tuna, was far more uniform over the area covered (Figure 7). On the basis of the small catches, two tongues of relatively high abundance were at the two ends of the survey area (Figure 7). These tongues, lying between lat 5° and 10°N, roughly coincide with the zone of the Countercurrent.

The distribution of albacore resembled neither that of the yellowfin nor the bigeye tunas. They were most numerous in the southwestern portion of the survey area (Figure 8) and their abundance declined to the northeast. Additionally, a broad zone to the north appeared to be completely devoid of the species. The reasons for this distribution are not at all clear.

In addition to the yellowfin tuna, bigeye tuna, and albacore that fit our definition of deep-swimming tunas, the longline captured a few skipjack tuna (Figure 9). The skipjack tuna is a smaller species (rarely over 18 kg) than the longline is designed to capture. Nevertheless, the gear is not absolutely selective because it has taken skipjack tuna as small as 2 kg.

The sporadic catches of skipjack tuna by longline are too scanty to estimate relative abundance and are therefore indicated in Figure 9 only as locality records. The skipjack tuna were present over a vast area of the central Pacific. Studies of the distribution of tuna larvae (Matsumoto, 1958) suggest that skipjack tuna are more abundant than yellowfin tuna in the central Pacific, the implication being that the equatorial central Pacific has a large underutilized stock of skipjack tuna.

SIZE OF DEEP-SWIMMING YELLOWFIN AND BIGEYE TUNAS

Though several species of tuna were taken by longline in the central Pacific, only the samples of yellowfin and bigeye tuna were substantial enough to warrant analysis of length differences by area. Iversen (1955, 1956) indicated that there were no significant changes in the size of yellowfin and bigeye tunas that could be related to time. Because of the wide temporal and spatial gaps in sampling, we confine ourselves to a descriptive summary of size differences with area. Most of the samples were taken between lat 5°N and 5°S and, as might be expected, no pronounced size differences were associated with latitude (only stations 96.5 km or more from land were considered in this analysis); only size

differences associated with longitude are left for consideration.

To describe length differences more fully, we include data from the western Pacific (Murphy and Otsu, 1954) as material from the primary study area. We pointed out in an earlier paper (Murphy and Shomura, 1955) that the lengths of deep-swimming yellowfin and bigeye tunas differ across the equatorial Pacific. Since essentially the same gear has been used to sample the tuna in all areas, these changes must reflect some biological attributes of the populations.

Length frequencies for several longitudes shown in Figure 10 suggest a trend to smaller yellowfin tuna in the western Pacific. The essentials of the material in Figure 10, more succinctly shown in Figure 11, suggest a rather regular cline along the equator with respect to
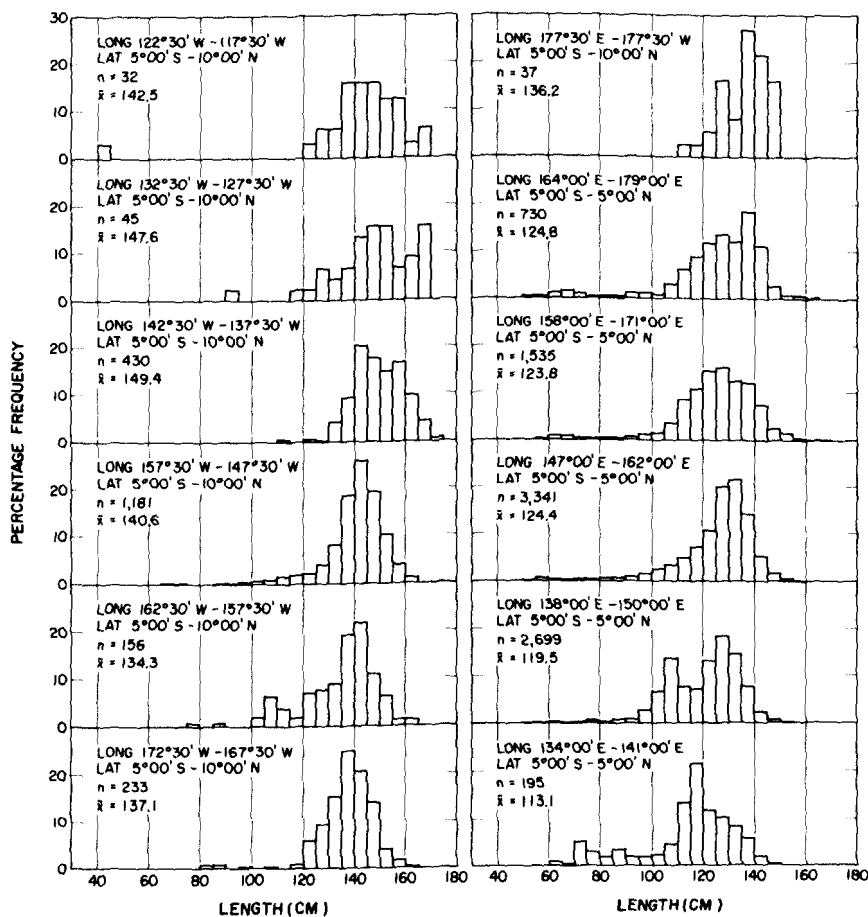

FIGURE 10.—Length frequencies of longline-caught yellowfin tuna by longitude of capture between lat 10°N and 5°S.
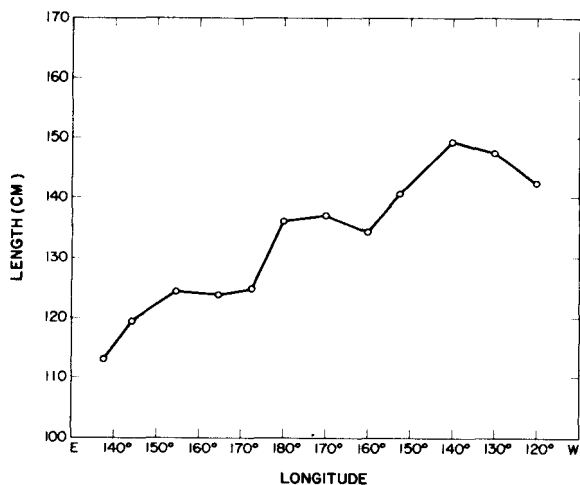
FIGURE 11.—Mean lengths of longline-caught yellowfin tuna.

average length. This same phenomenon is also evident for the bigeye tuna (Figures 12 and 13), which lends greater credibility to the view that the cline is not an artifact of the sampling system but due to a biological process.

This shift in length is reflected in other attributes of the populations. As indicated in Figure 14, males outnumbered females among the larger yellowfin tuna. Furthermore, the length at which males clearly dominate increases from west to east, as the average size of the fish sampled increases. Males also dominate the larger sizes of bigeye tuna (Otsu, 1954; Shomura and Murphy, 1955) but our data for this species are not adequate to examine the possibility that the length at which males dominate changes from west to east.

In addition to these clines, Royce (1953, 1964), in a study of yellowfin tuna morphometrics, dem-
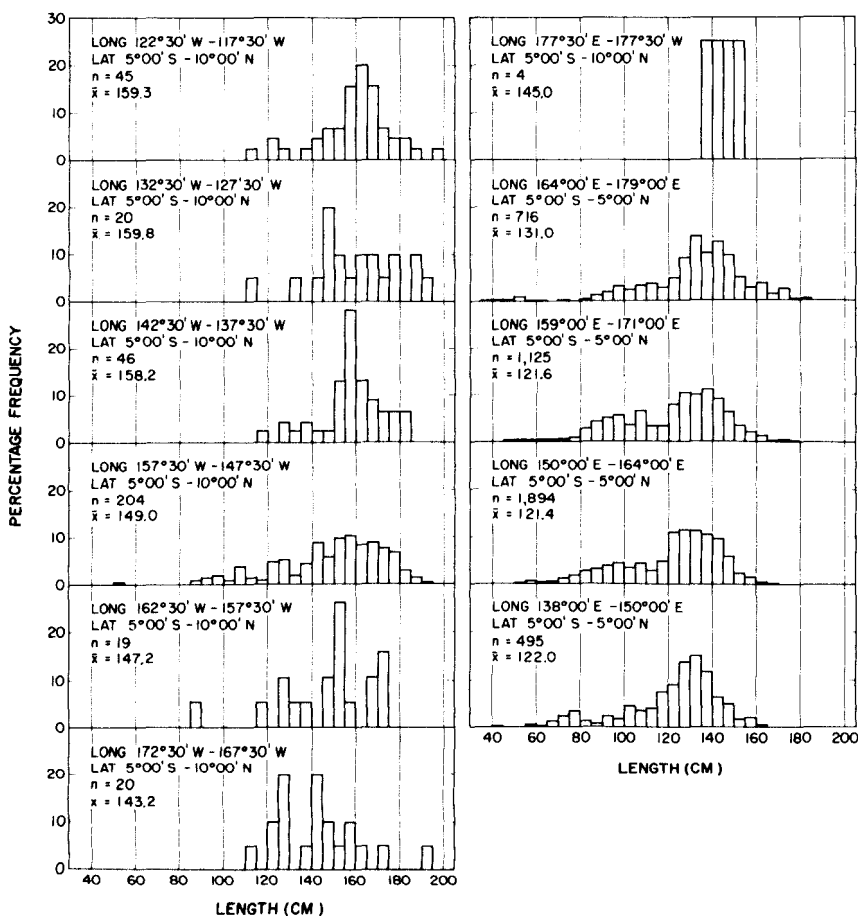

FIGURE 12.—Length frequencies of longline-caught bigeye tuna, by longitude of capture, between lat 10°N and 5°S.

onstrated east-west clines in the body proportions of yellowfin tuna taken in equatorial waters. For example, fin lengths decreased and head lengths increased to the east. Thus, along the equator we find more or less uniform clines in the yellowfin tuna of such biological characters as size, size at appearance of sex-ratio variations, and morphological characters. Limited evidence also suggests that the same phenomena are present in the bigeye tuna.

Inquiry into the basic causes for the east-west clines is somewhat speculative at the present time. Royce (1953, 1964) considered the morphometric evidence and concluded that the equatorial yellowfin tuna are made up of semi-independent stocks. Iversen (1956) focused his attention primarily on east-west size differences and suggested that the differences are maintained by easterly migration as the fish grow larger. An additional factor entering Iversen's hypothesis is that the number of small yellowfin tuna around the Line Islands, the only islands in the immediate vicinity of the equatorial central yellowfin tuna population, does not appear to be large enough to account for the sizable numbers of large deep-swimming yellowfin tuna in this general area, inferentially suggesting that recruitment must involve migration from somewhere else—the west, according to Iversen.

Conceivably recruitment could occur by movement of yellowfin tuna in a north-south direction, for there are large numbers of small islands in French Oceania, some 1,112 km (600 miles) to the south of the equatorial area. Small yellowfin tuna are known to occur near the surface around those islands (Royce, 1954), and the populations there, if extensive, could supply the necessary recruits to the large population of deep-swimming yellowfin tuna. This postulated movement, however, would be contrary to the conclusion reached by Royce (1964, p. 427) that ". . . most yellowfin tuna probably remain within a few hundred miles of where they occur as post larvae."

The length gradient of deep-swimming fish, with the attendant dearth of large fish in the west and small fish in the east, remains a strong argument favoring extensive west-east migration. If it is argued that there is no migration
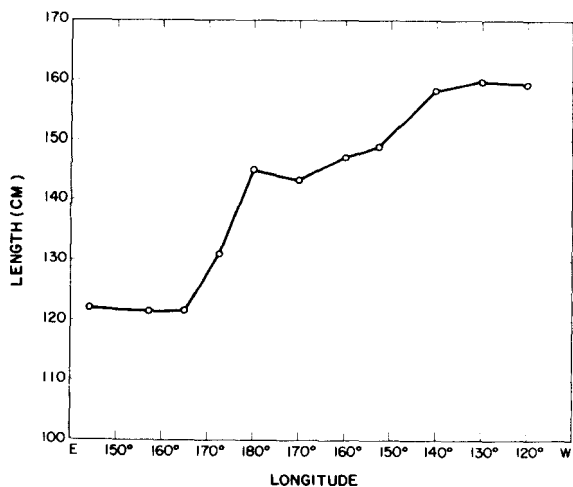
FIGURE 13.—Mean lengths of longline-caught bigeye tuna.

FIGURE 14.—Length distribution by sex of longline-caught yellowfin tuna (data from catches made in 1953).

and that the gradient exists simply because yellowfin tuna grow more slowly in the west, where the basic productivity is lower (Murphy and Otsu, 1954), there remains to be explained the relative scarcity of medium-sized fish in the eastern catches of deep-swimming tunas. This difficulty could be overcome by proposing that the

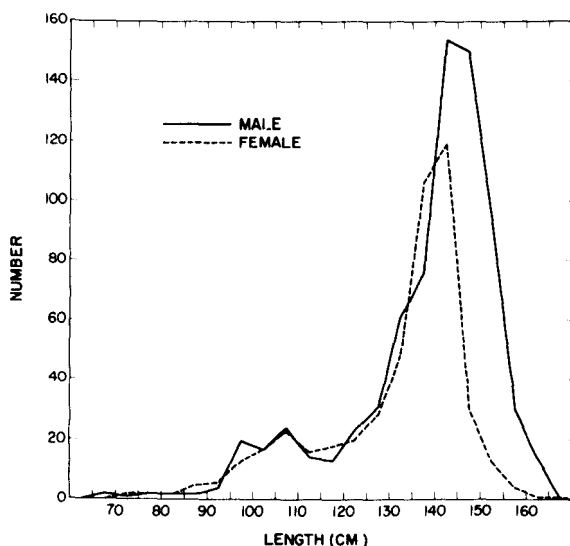adoption of the deep-swimming habit is age-specific rather than size-specific and that the smaller fish are scarce in eastern longline catches because they are not old enough to adopt the deep-swimming habit. This proposal is not as farfetched as it might seem, for albacore appear to adopt the deep-swimming habit at a size (about 13.6 kg) at which yellowfin tuna still school at the surface. Furthermore, the fact that the size at which males dominate the catches increases, as the average size of the individuals in the deep-swimming population increases (Figure 14) argues against migration and suggests that at least some physiological changes are age-specific. Behavior changes might easily be among these age-specific attributes.

In summary, there are east-west clines in morphological and other biological characters of the catches. These clines can be explained by migration, if one chooses to ignore the evidence of morphometry and the changes of size at the onset of male dominance. If the clines are attributed to genotypic or phenotypic changes in relatively sedentary stocks, all available evidence can be accepted, but additional assumptions such as slower growth rate in the west and age-specific behavior changes must be introduced.

MERIDIONAL DISTRIBUTION

In a preceding section we examined the ocean and the fish populations in plane view and concentrated on the descriptive aspects. Most of the prominent features of the environment and the fish populations are zonally aligned, and the relations among the several fields can be most effectively visualized when their properties are examined in a meridional section. In presenting the details of the oceanography, the tuna distribution, and the tuna-oceanography interrelation-
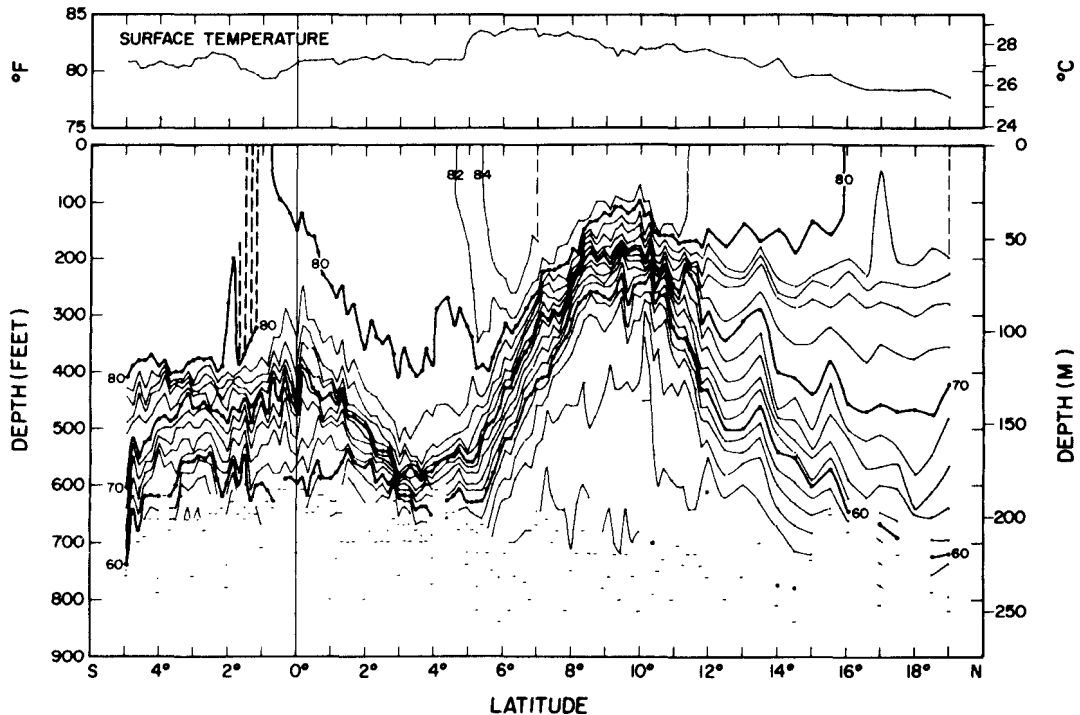

FIGURE 15.—Meridional temperature section based on bathythermograms, *Hugh M. Smith* cruise 11 along long 150°W (Austin, 1954b).
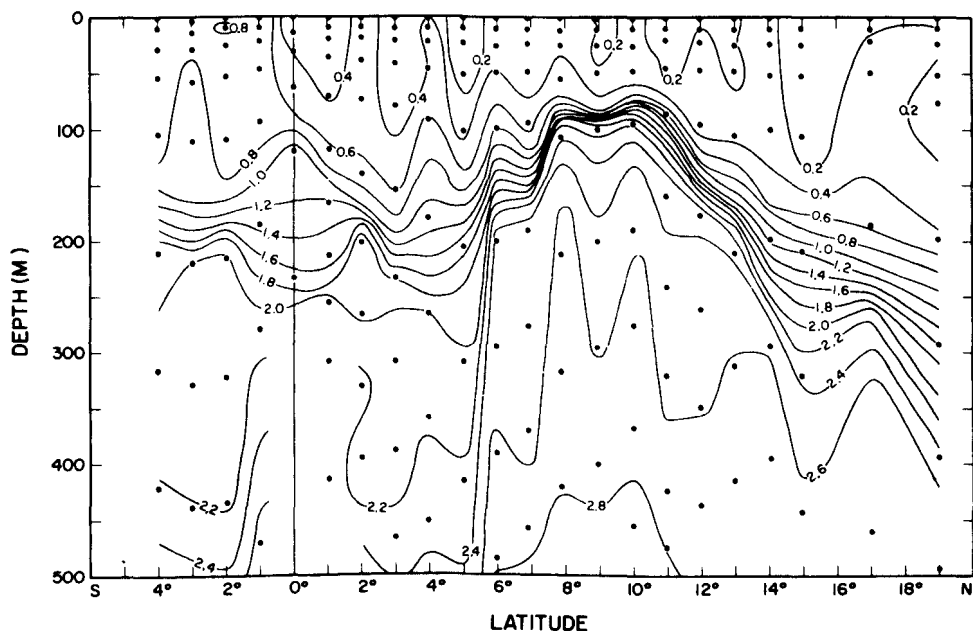
FIGURE 16.—Distribution of inorganic phosphate along long 150°W, September 26 through October 4, 1951, *Hugh M. Smith* cruise 11. PO_4 in micrograms per liter, isopleth intervals 0.2 μg atom per liter (Austin, 1954b).

Oceanography

ship, we have elected to use long 150°W, because more information is available from that meridian than from any other and it lies in the center of the region in which yellowfin tuna are most abundant (Figure 6).

Oceanography

A meridional temperature section along long 150°W (Figure 15) clearly shows the several features described in plane view (Figure 5). North of lat 10°N the isotherms sloping to the right indicate the westerly flowing North Equatorial Current. Between lat 10° and 5°N the isotherms slope to the left, indicating the easterly Countercurrent. South of the Countercurrent lies the westerly flowing South Equatorial Current.

The cool water at the equator is the result of divergence which disturbs the stability of the thermocline and thereby increases the rate of upward diffusion (upwelling). Under these con-

ditions the surface waters are always cooler than adjacent waters. Nutrient salts, such as phosphate (Figure 16), are also affected, and their distribution suggests that nutrients are diffusing into the euphotic zone near the equator faster than they are being utilized. According to Cromwell (1953), these enriched waters moving northward and southward within the framework of the westerly flow are warmed and the nutrients are utilized by organisms.

Between the upwelling at and near the equator and the southern boundary of the Countercurrent at about lat 5°N (Figure 15), there is convergence and sinking of the northward flowing waters (Cromwell, 1953). The downward sloping arrows in Figure 17 show schematically the convergence with its attendant sinking. Among other features shown in the figure are the easterly flowing Countercurrent (flow is toward the observer), the westerly North Equatorial Current to the north, and the westerly South Equatorial Current to the south. The figure also
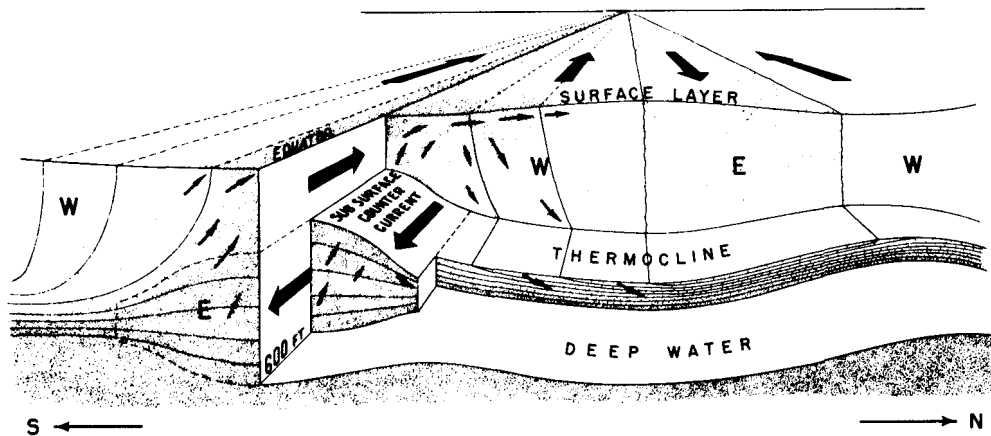
FIGURE 17.—Schematic representation of a meridional section of the equatorial central Pacific (Sette and staff of P.O.F.I., 1954, p. 3).

shows a feature new to this discussion, the Equatorial Undercurrent described by Cromwell, Montgomery, and Stroup (1954). This latter current is usually found in the upper portion of the thermocline and rarely flows as a surface current.

Tunas

Our aim is to compare the meridional distribution of fish with certain properties in the environment. Ideally, we should compare the weight of fish life at a given trophic level with such elements as plankton abundance and nutrient level. This comparison is difficult with the material at hand, but, as shown in Appendix A, the catches of yellowfin tuna, the dominant species, appear to reflect the abundance of the larger predators.

Tuna-Oceanography

In the discussion of the areal distribution of tunas we pointed out that the peak abundance of yellowfin tuna was near the equator. We now propose to examine the hypothesis that this striking concentration of yellowfin tuna is the result of the following sequence of events: (1) upwelling at the equator, (2) northward displacement of the water, (3) relatively rapid de-velopment of zooplankton, (4) a slower development of tuna forage, and (5) congregation of tuna in the region best supplied with forage.

It can be inferred from the distribution of yellowfin tuna and water temperature in Figures 6 and 15 that there is a general coincidence between the location of upwelling and the zone in which yellowfin tuna are most abundant. Figure 18 clearly shows this relation as well as the distribution of other variables such as plankton and current direction.

In the top panel (A), the temperature structure shows the cool surface waters at the equator that can be attributed to upwelling. That this is accompanied by enrichment was shown in Figure 16 in the distribution of inorganic phosphate. The sharp downward slope of the isotherms between lat 5° and 9°N is the region of the Countercurrent.

The second panel (B) shows the drift of the longline while in the water. This drift, which is essentially the movement of the gear between 0600 and 1600 hr, shows the direction of the several major water movements discussed earlier. North of lat 9°N, the drift is to the west, indicating the North Equatorial Current. Between lat 5° and 9°N, the drift is to the east, suggesting the Countercurrent. Except for the station nearest the equator, the drift is westerly south of lat 5°N, indicating the South Equatorial Current. The easterly drift at the equator is

probably caused by the easterly flowing Equatorial Undercurrent (Figure 17). It should also be noted that each side of the equator has a poleward component to the longline drift. These observations confirm empirically the conclusion by Cromwell (1953), based on theoretical considerations, that divergence at the equator leads to upwelling and that this enriched water moves poleward.

In the third panel (C), zooplankton is shown to be most abundant at the center of upwelling, falling off more precipitously to the north than to the south. The zooplankton reaches a maximum at or near the equator, where the upwelling is centered (panel A). The model proposed by Cromwell (1953) requires a net transport of water away from the equator, and because the zooplankton sampled is at least one trophic level removed from chemical nutrients, we might expect its peak abundance to be significantly displaced from the site of upwelling. The magnitude of the displacement would be a function of the rapidity with which the zooplankton reaches a peak, the speed of the north-south transport, and possibly the rate of grazing.

Since no displacement was observed in a series of stations spaced at 96.5-km intervals, the possible conditions include: (1) the zooplankton develops very rapidly, (2) the north-south transport is slow, (3) grazing is highest just north and south of the equator, or (4) a combination of the three factors. Nothing is known of the development rate of equatorial zooplankton (chiefly copepods), but some marine cladocerans have been reported (Wickstead, 1963) to reach a peak in 36 to 40 days at temperatures higher than 28°C. Assuming this rate of development for the equatorial zooplankton, a poleward displacement of water as rapid as 6.4 km a day would be readily detected in plankton hauls spaced 96.5 km apart. The lack of a displacement suggests that grazing may be an important factor controlling the spatial distribution of the standing stock of zooplankton in equatorial waters.

In addition to the lack of horizontal displacement of the peak of zooplankton from the equator (Figure 18), the plankton volumes south of the equator were slightly larger than those to the
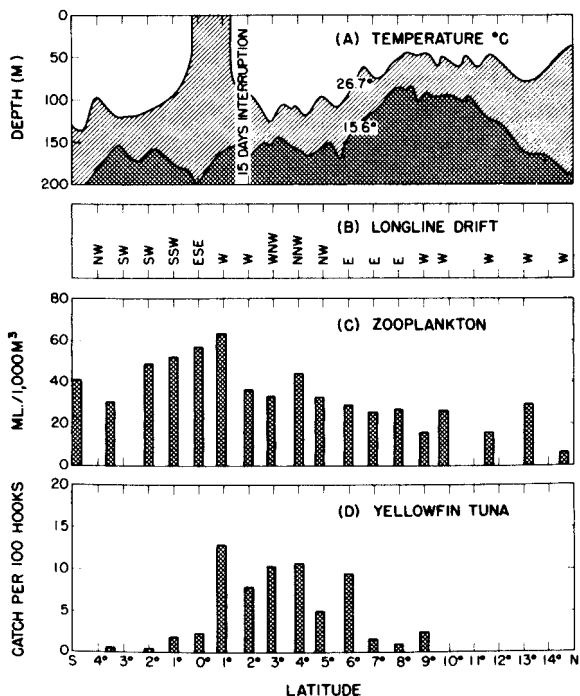

FIGURE 18.—Diagrams of several fields resulting from a section along long 150°W in September 1951. A. Temperature section from bathythermograms. B. Direction of longline drift at each fishing station. C. Volumes of zooplankton at each fishing station. D. Catch rate of yellowfin tuna at each fishing station. (Adapted from Sette, 1955.)

north. This situation, however, is not the usual one because King and Hida (1957) reported that the average standing crop of plankton is greater between lat 1.5°N and the southern boundary of the Countercurrent (about lat 5°N) than between lat 1.5° and 5°S. This general situation is thought to be the result of the dominance in this region of the central Pacific southeast trades which, according to Cromwell (1953), transport most of the enriched water northward. In the present instance, the longline drifts (Figure 18, panel B) give evidence that the momentary major transport was to the south of the equator. Thus, the observed asymmetry of the plankton is consistent with the momentary circulation.

The yellowfin tuna catches (Figure 18, panel D) show even less symmetry about the equator

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than the plankton. This asymmetry seems anomalous until it is considered in the light of the general northward transport of the enriched water and the probable time required for tuna forage to appear after the enrichment at the equator.

Tunas do not consume the smaller zooplankters that make up the bulk of the catches of the 1-m nets of $30 \times \times \times$ gage mesh used to sample zooplankton. Rather, tunas forage on the higher trophic levels, from euphausiids to all but the largest nekton (Reintjes and King, 1953). If the food supply is the chief determinant of tuna abundance, the tunas, which are capable of rapid and extensive migration, will concentrate where they can most readily obtain food. In the absence of poleward motion we would presume that tuna forage as well as tunas would concentrate or develop at the equator, where the enrichment and the zooplankton are centered. There is poleward motion, however, and the successive trophic levels above the zooplankton would be expected to have their greatest population density at some distance from the equator.

SPACE AND TIME VARIATION

In this section we focus attention on the variation in the distribution of yellowfin tuna and the variation in distribution of properties in the environment and attempt to show their relation. The zone between the equator and the Countercurrent receives primary attention simply because more information is on hand from this area than from others.

Space and time variation in the tuna distribution have been discussed in earlier publications. Murphy and Shomura (1953b) pointed out that when and where southeast winds prevailed the yellowfin tuna seemed to be concentrated north of the equator; when northeast winds prevailed the yellowfin tuna were concentrated south of the equator; and during periods of variable winds they straddled the equator. These observations were amplified and further discussed by Sette (1955, 1958), who suggested that the average distribution of the catch rates might well be a function of geographical vari-

ation in the strength of the trades, if a suitable but unknown lag period is assumed between maxima of upwelling and the occurrence of tuna forage.

The waters of the equatorial current system are in a state of constant flux, with upwelling, poleward motion, sinking, and westerly motion integrated into a whole that represents a continuously changing environment. In this environment we have made "instantaneous" observations at selected points and times, and as expected the data obtained are dissimilar in respect to space and time. In theory, at least, a true concept of the relative magnitudes of the several components of the water motion should make it possible to unify these results into a coherent whole. It appears that vertical motions (upwelling) and sinking (convergence) are counterbalancing within the geographical limits (north-south) of the area under consideration, but the relative strengths of the westward and northward motions, which cannot be counterbalancing, have not been adequately defined.

Sette (1958), in interpreting the then available information, assumed that the western component of flow near the equator was of overriding importance in comparison with the poleward flow associated with divergence and upwelling. This assumption is consistent with the mean surface flows indicated in climatological-type summaries of ship's drift observations (e.g., Figure 5) but is not consistent with certain empirical determinations derived from the drifts of longlines and drogues. These determinations suggest that the average poleward component of motion to the north of the equator on long 120°W would bear little relation to events at lat 5°N on long 140°W and even less to events at lat 5°N on long 150°W. In other words, water parcels upwelled at the equator on long 120°W are probably lost from the system by the time they are transported westward to long 130°W, because their northward motion will have carried them to the Countercurrent (near lat 5°N). Here, they must sink because the Countercurrent is warmer and less saline than the waters to the south.

Most of the evidence for these arguments lies in measurements of the drifts of sets of longline

gear. The longline, which is suspended from the surface to the thermocline, gives a useful measure of the net movement of the mixed layer. Between the surface and the thermocline are about 512 linear meters of 0.635-cm diameter cotton line having about 10.2 sq m of surface for each basket of gear. The buoys that support the line are acted on by the wind, but they present only about 0.56 sq m of surface to each basket of gear. Typical sets consist of 40 to 60 such units, which are in the water about 10 hr. Since the gear is set at dawn, the morning fixes based on celestial navigation provide a good starting point. Because the last unit (first one set) is retrieved at about 1600 hr, it is necessary to rely on sun lines, dead reckoning, and the evening stars for the final position determination.

This procedure is routine during longline fishing surveys, but most determinations of drifts of the gear are somewhat unreliable for various reasons. There are, however, 14 measurements from the area between long 140° and 155°W and between the equator and lat 5°N that appear reliable within the limits of celestial navigation. These given a mean northward motion of 0.67 km/hr (0.36 knot) and a mean westward motion of 1.06 km/hr (0.57 knot), or a ratio of 1 to 1.6. Wind effect on the longline sets is unknown, but the relative amount of exposure to the two forces and the relative viscosities of the water and air suggest it is negligible. It can also be argued that the sample of 14 measurements is inadequate, and this cannot be denied. The 14 measurements were, however, well scattered in time and space and vary so markedly from pilot-chart summaries that we feel a revision of the existing concept is in order.

In addition to the longline drifts, special measurements of the motion of the surface water north of the equator were made in August 1952 by using drogues (Cromwell, Montgomery, and Stroup, 1954). A surface drogue placed in the water at lat 0°01′N, long 149°31.5′W, moved to lat 2°48.5′N, long 151°42′W in 10 days. The mean westward component was 0.85 km/hr (0.46 knot) and the northward component 1.18 km/hr (0.64 knot), values that are relatively consistent with the longline drifts.
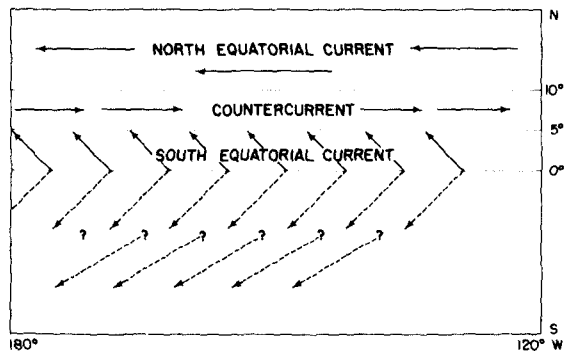
Such high rates of northward flow seem to

FIGURE 19.—Schematic view of the equatorial current system incorporating recent empirical determinations of flow north of the equator. Flow south of the equator is indicated as questionable.

imply an exceedingly rapid rate of upwelling, which should possibly be characterized by an even more marked cooling at the equator than is indicated by the measurements at hand. In this regard, however, several factors must be considered. Although we do not know the depth from which water is being upwelled, it is most likely to be coming from near the top of the thermocline, where the temperatures are not strikingly low (Figure 15). A further complication is the possible return flow along the top of the thermocline towards the equator suggested by Fofonoff and Montgomery (1955). This mechanism could return water that has converged north of the equator to the undercurrent, where it might be enriched and re-upwelled. Thus, even rapid north-south circulation and upwelling at the equator do not necessarily call for intense cooling at the equator.

These arguments show that the circulation between the equator and the Countercurrent is exceedingly complex and as yet imperfectly known. There is, however, enough evidence to suggest that the region between long 120°W and 180° is not a single east-west system with respect to identity or homogeneity of origin of its water. The available evidence indicates that it should be regarded as a series of adjacent homologous northwesterly flowing circulation cells (Figure 19). As will be demonstrated, the distribution of properties, e.g., nutrients, plankton, and fish,

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is more readily reconcilable with this concept than with the classical flow pattern depicted in Figure 5.

Geographical Variation

We have advanced the concept that the flow pattern in the northern latitudes of the equatorial waters consists of a series of homologous northwesterly flowing cells. A study of the distribution of physical and biological properties, e.g., winds, water temperature, nutrients, plankton, and fish, indicates that they are more readily reconcilable with the homologous cell concept than with the classical flow pattern depicted in Figure 5.

Winds.—The wind system is the source of energy for the equatorial circulation, and it is logical to approach the problem of geographical variation of tuna by first examining the variations in the winds. The average distribution of winds (Figure 20) clearly shows a peak of wind stress near long 130°W, and in this area the equator is dominated by the southeast trades. Farther west the two trade systems are about equally distributed and the average force declines. In the far west the northeast trades dominate and the average force is low.

Water temperature.—If the wind is the causal force behind the upwelling and poleward displacement of enriched (cooled) water, there should be a demonstrable relation between variation in the mean wind and variation in the mean water temperature. Table 2 depicts the mean monthly temperature of the surface waters north of the equator. It clearly shows the general trend to warmer water in the west in the zone between the equator and lat 5°N, which is the expected result of the wind gradient (Figure 21).

More significant is the variation in the size of the water temperature gradient from east to west. For instance, during March there is practically no slope but during October there is a steep slope (Table 2). The size of these grad-
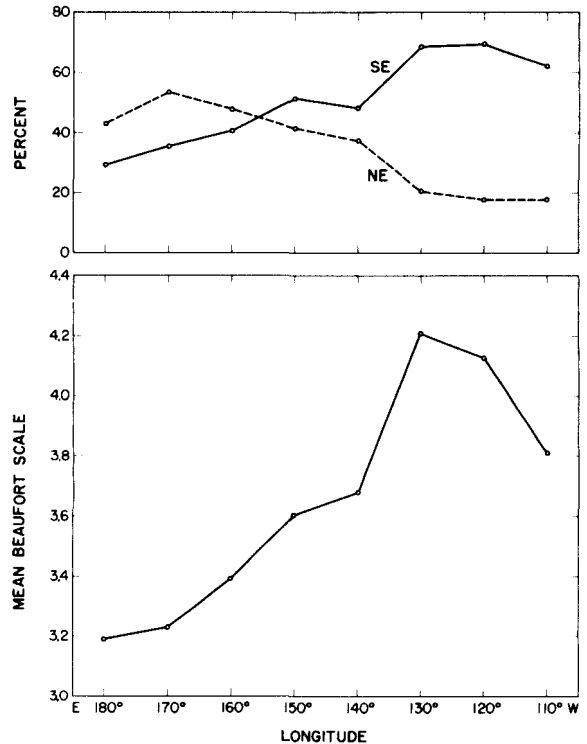

FIGURE 20.—Average direction and force of winds over the equator. The values were derived from U.S. pilot charts for 1953. In arriving at a value for a given longitude we averaged the winds in the four 5° squares focusing on the intersection of the meridian and the equator. East winds were apportioned equally between northeast and southeast.

ients, when plotted against a measure of the gradient of southeasterly winds (Figure 21), suggests a causal relationship. When the wind gradient is large the gradient in water temperature is steep, and vice versa. We can now proceed with confidence on the assumption that variations in the winds are responsible for variations in water temperature through altering the rates of upwelling and the northward displacement of cool water.

Nutrients.—It is now in order to examine the distribution of nutrient salts in the euphotic zone along the equator to see whether the concentration varies with the amount of upwelling as evidenced by winds and water temperature.

TABLE 2.—Mean surface temperatures by longitudes and months for lat 0° to 5°N (basic data from U.S. Weather Bureau, 1938).

| Month	Longitude west						
	110°	120°	130°	140°	150°	160°	170°
January	24.9	25.7	25.0	25.7	26.3	26.7	27.2
February	25.6	25.6	25.7	26.2	26.1	26.2	27.0
March	26.6	26.2	25.9	26.7	26.8	26.7	26.7
April	26.8	27.1	26.4	26.6	26.9	26.9	27.2
May	27.1	26.9	26.4	26.8	27.1	27.1	28.0
June	26.1	25.9	26.8	27.7	27.6	27.5	27.9
July	25.1	25.6	25.9	26.6	26.9	27.3	27.5
August	24.6	25.1	25.6	26.0	26.7	27.1	27.7
September	24.6	24.6	24.9	26.0	26.7	27.2	27.8
October	24.4	24.6	25.3	25.9	26.9	27.3	27.7
November	24.9	25.1	24.9	26.0	26.7	27.3	27.3
December	24.9	25.1	25.1	25 2	26.1	26.4	27.3
Mean	25.4	25.6	25.7	26.3	26.7	27.0	27.4
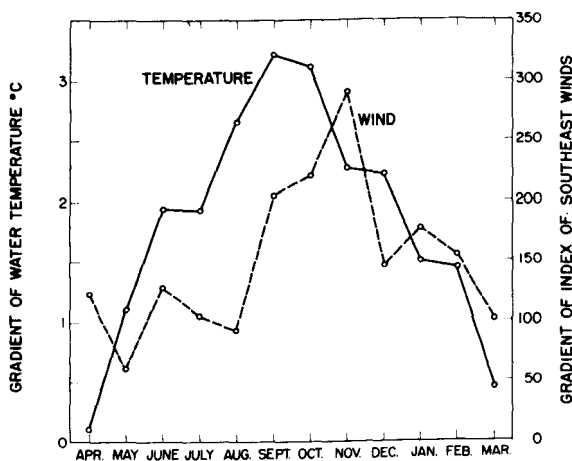
FIGURE 21.—Gradients of mean surface water temperature, equator to lat 5°N, and stress of southeast winds across the equator between long 120° and 170°W. We prepared the index of southeast wind stress by multiplying the percentage occurrence by the average force. The basic data are from the four wind roses that focus on the intersection of the equator and the appropriate longitude in the U.S. pilot charts for 1953. Half of the due east winds were arbitrarily assigned to the southeast quadrant.

Because of the lack of measurements of other salts, we will consider only inorganic phosphate. Even a discussion limited to this property must be considered poorly documented, however, because of the few measurements and the inherently erratic nature of phosphate determinations.

In considering the distribution of phosphate, we have constructed several temperature-phosphate curves from along the equator (Figure 22). We elected to use the temperature-phosphate curve because it seemed to yield the best available index of enrichment. Although low temperatures appear to be a good index of upwelling and relative enrichment when a single meridional section is being considered, it does not necessarily follow that relative coolness among meridians along the equator is a good index of enrichment, for there are marked east-west gradients in such factors as the depth of the thermocline (Austin, 1958). Temperature-phosphate curves should permit evaluation of the differences associated with these gradients and should indicate the "enrichment potential" along the equator.

The surface temperature relations among the temperature-phosphate curves in Figure 22 are consistent with the general east-west distribution of temperature, i.e., cooler water to the east suggests that they represent typical rather than atypical conditions. Phosphate, however, does not follow temperature when the several longitudes are considered together. Inorganic phosphate is lowest along long 117°W, where the surface water is coldest, and highest along long 140°W, where water temperature is intermediate. These differences in the basic temperature-phosphate relation appear to persist to rather low temperatures and therefore to considerable depths.

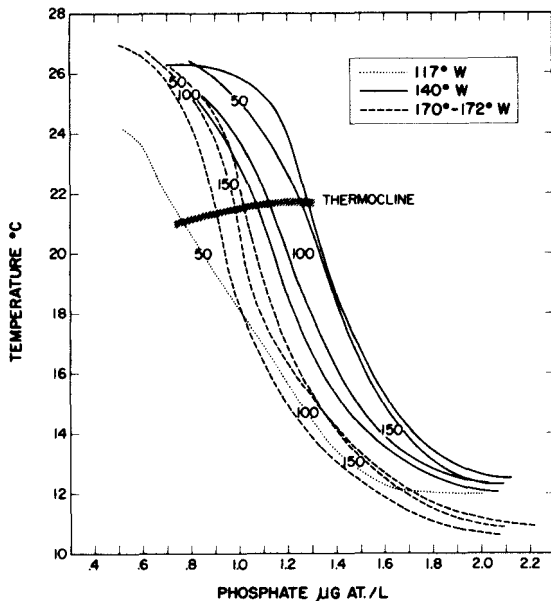We will not attempt to explain the differences

FIGURE 22.—Temperature-phosphate curves from the equator at several longitudes. The thermocline approximately corresponds with the 21°C isotherm. The approximate depth in meters for each group of curves is shown. Where one longitude is represented by several curves, the stations are separated in time from several weeks to several months.

geographical distribution of wind stress (Figure 20), it appears that on the average the greatest enrichment might be in the center of the system (near long 140°W), for in this region wind stress is high and the thermocline is abundantly supplied with nutrients. To the west, enrichment could very well fall off, since the wind stress declines, and to the east, enrichment might decrease because the thermocline is impoverished.

The discussion above is admittedly based on scanty and perhaps unreliable data. The general conclusion—that we should expect the most enrichment near the center of the area under consideration—is, however, compatible with the biological data to be considered next. Even more important, the phosphate-temperature curves indicate an east-west heterogeneity in the distribution of physical and chemical properties. This heterogeneity is consistent with the model of flow pattern (Figure 19) evolved from longline drift data.

Biological properties.—The biological properties along a latitudinal axis (Figure 23B, C) do not follow the temperature gradient (Figure 23A and Table 2) but rather tend to be distributed in conformance with the general enrichment pattern described in the previous section on nutrients. Both plankton and yellowfin tuna tend to be highest in the center of the region, where the measurements suggest enrichment is greatest.

The plankton distribution (Figure 23B) is somewhat unreliable to the east of long 150°W because the samples are few and unequally distributed in time (King, 1954; King and Hida, 1957). Nevertheless, all evidence points to a peak of plankton coinciding with or slightly west of the peak in enrichment.

The distribution of yellowfin tuna (Figure 23C) is more orderly than that of zooplankton, possibly because of a more orderly temporal and spatial stratification of the samples. The peak abundance of tuna is close to the longitude of maximum enrichment and the longitude of maximum standing crop of zooplankton.

Though there is general agreement between the standing crop of zooplankton and tuna, there are several discrepancies. For instance, the

in the distribution of phosphate. Accepting the differences among longitudes (Figure 22) as valid, it is clear that, though inequality in wind stress might be directly related to the amount of upwelling and consequently of cooling of the euphotic zone (as appears to be the case), these inequalities in wind stress will not necessarily be directly related to variations in the amount of enrichment. A given wind stress will probably produce the most enrichment along long 140°W, whether the energy is chiefly dissipated in the region of the thermocline or is dissipated uniformly with depth. The difference, however, will be most striking if the principal effect of the wind is expended in disturbing the thermocline. For instance, water diffused up from the thermocline along long 140°W will contain nearly twice the amount of nutrient salts as water diffused up from the thermocline at long 117°W.

Considering the variations in the vertical distribution of nutrient salts (Figure 22) and the

high in zooplankton volume is only about 50% greater than the low, whereas for yellowfin tuna this difference is about 300%. These facts could indicate the inadequacy of some of the implicit assumptions, such as the standing crop of zooplankton is a measure of the standing crop of tuna forage, and the latter is a measure of the abundance of tuna; the longline catches are a measure of the abundance of yellowfin tuna; the abundance of yellowfin tuna is representative of its trophic level; and the system is equally efficient at all levels. Nevertheless, the general correspondence of the peak of zooplankton and yellowfin tuna appears more than casual (King and Hida, 1957).

FIGURE 24.—Mean distribution of deep-swimming tuna. (The zero figures in the panels represent fishing effort expended, but no catches made; all stations 96.5 km or more miles from land.)
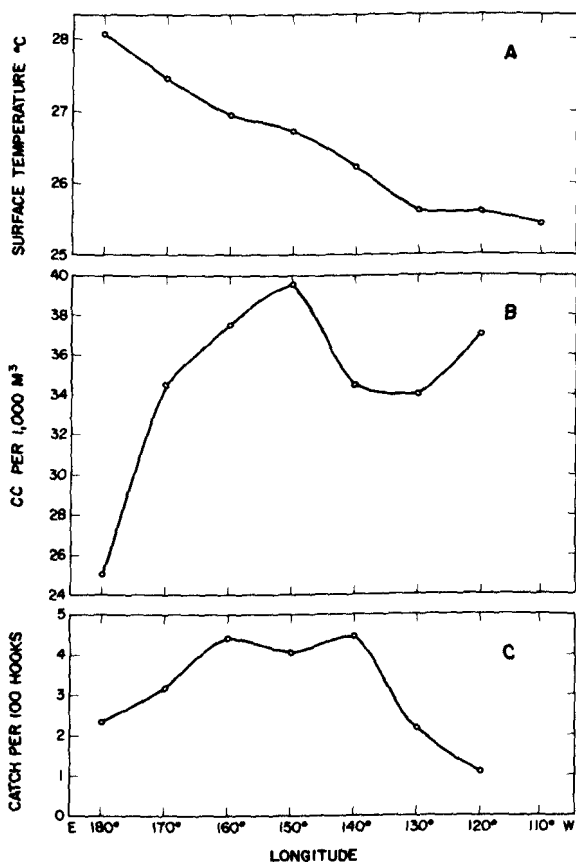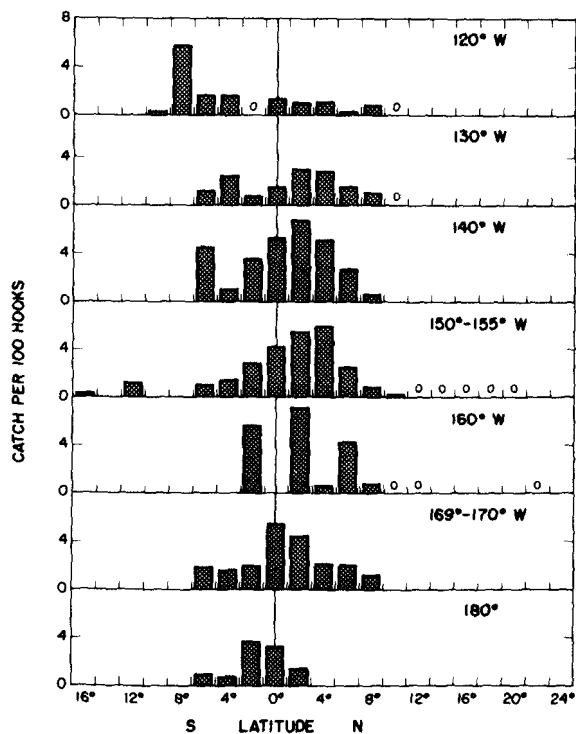

FIGURE 23.—A. Mean surface temperature from the equator to lat 5°N (U.S. Weather Bureau, 1938). B. Mean zooplankton from lat 5°N to lat 5°S (King and Hida, 1957). C. Mean yellowfin tuna catch from lat 5°N to lat 5°S.
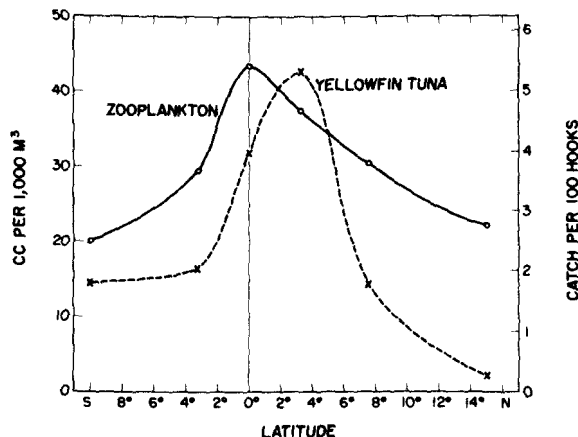

FIGURE 25.—Relative north-south displacement of zooplankton and yellowfin tuna. (Adapted from King and Hida, 1957.)

Associated with the longitudinal variations in average catch rates, the distribution of yellowfin tuna on a meridional plane appears to differ with latitude (Figure 24). In the extreme east (long 120°W), where enrichment is low, abundance of yellowfin tuna is also low and there is little evidence of increased abundance associated with the equator. Farther west (long 130°W) the abundance of yellowfin tuna is higher, and the expected peaking under prevailing southeast trades appears north of the equator. In the center (about long 150°W), where enrichment is thought to be highest and southeast trades predominate, abundance is high and centered well north of the equator. In the west, where enrichment is low and northeast trades are predominant, abundance of these tuna falls off and their distribution center is at or slightly south of the equator.

Discussion.—The available physical measurements, e.g., drogue movements and longline drifts, suggest that the northward movement from the equator is of considerable importance relative to the westward motion, and this conclusion is at variance with the results, based on ship's logs, depicted on either pilot charts or other summaries, such as our Figure 5.

As discussed in earlier sections, northward displacement of tuna with respect to plankton (Figure 25) is attributed to the time lag in the development of tuna forage, for during this period the waters are moving in a northerly direction. This northward displacement appears perfectly logical, but if so, and if the westerly flow is greater than the northerly flow, as we have generally assumed, the peak of tuna abundance should be displaced well to the west of the zooplankton peak.

The available data (Figure 23) give little or no evidence of westerly displacement of the tuna peak relative to the zooplankton peak. This observation, coupled with empirical measurements showing that the northerly component of flow is vigorous and that the phosphate distribution is heterogeneous, makes it difficult to accept the earlier concept of an overriding western element of flow. The model, elaborated in the previous sections, that is consonant with all the evidence

regards this portion of the South Equatorial Current from the equator to lat 5°N and long 120°W to 180° as comprising a series of homologous, parallel, northwesterly transport systems (Figure 19).

Temporal Variation

Variations in enrichment and distance from the source of enrichment were advanced as explanations for north-south and east-west variations in the abundance of yellowfin tuna in the region north of the equator. Most of the north-south distributions were readily reconcilable with temperature, phosphate, and plankton fields. The east-west distributions can also be explained in the same general terms, but the arguments are somewhat weaker, because the sampling program gave first priority to elucidating the distribution along the north-south axis. As a final step we propose to show that even the temporal variations in yellowfin tuna can be explained within the same framework as the spatial variation.

Murphy and Shomura (1953b) pointed out that during seasons or in areas dominated by the southeast trades yellowfin tuna tend to be concentrated north of the equator and that during periods of variable or northeast winds they tend to straddle the equator (Figure 26). This finding is consistent with the hypothesis, because either light, variable, or northeast winds should reduce the northward motion of water from the equator.

Averages such as those in Figure 26 may be misleading simply because the sampling has not been well stratified. Furthermore, although there are climatological seasons along the equator, they may frequently be altered or obscured by short-term changes to the extent that during a given year the "seasons" may not materialize. Because of the few meteorological observations in the area under consideration, it is difficult to evaluate the years in which we fished in terms of the normal. For these reasons, we evaluate the temporal changes in fish catch along a meridian in terms of the environment prevailing at the time of the catches, thus overcoming the lack
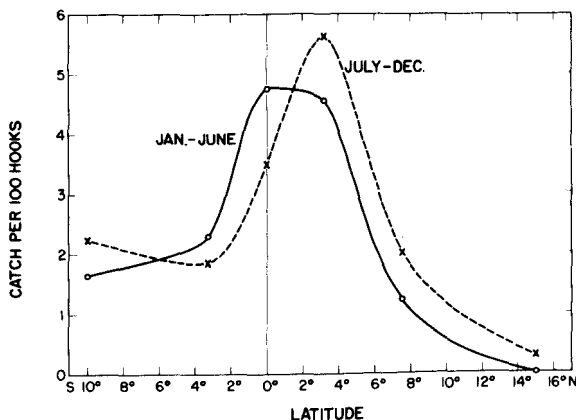
FIGURE 26.—Variation in yellowfin tuna catch with the current system for the two 6-month periods, January-June, a period with northeasterly or light and variable winds, and July-December, a period of prevailing southeasterly winds (in the equatorial central Pacific). (Adapted from King and Hida, 1957.)

of continuity of measurements of the fish and the environment.

To effect this type of analysis we must use some property in the environment that is consistently measured at each fishing station. Atmospheric data, such as winds and water temperature, are available. Winds are not suitable, because they are not conservative and because theory holds that there is a considerable lag between wind action and the response of the fish. Water temperature is more promising, since it is relatively conservative and is also a property of the immediate environment of the fish.[6]

In effect the study becomes limited to an analysis of variation along separate meridians or groups of adjacent meridians, because the water on widely spaced meridians is in all likelihood different with respect to origin and properties, such as the temperature-phosphate ratios. Furthermore, we have restricted the analyses to the zone north of the equator (lat 1°-5°N), where sampling was most intensive and where the theory of circulation is most advanced (Cromwell, 1953). The immediate vicinity of the equator is avoided on the basis of possible complications arising when this site of upwelling is considered and the unknown influence of the easterly flowing undercurrent.

Defining the geographical unit to be used in the time variation analysis as a single longitude or immediately adjacent longitudes between lat 1° and 5°N permits the development of a hypothesis. Wind action causes upwelling at the equator and a northward movement of upwelled water. This water, which might be termed "new," is cold, high in phosphate, high in plankton, and low in yellowfin tuna abundance. The meridional sections indicate that after it moves north, away from the possibility of further enrichment, it warms; phosphate declines, presumably from use; zooplankton declines, presumably from grazing; and yellowfin tuna abundance increases, presumably because the tunas congregate to feed on the forage organisms responsible for the decline in zooplankton. Water that has reached this final stage can be termed "mature."

This same reasoning can be applied to temporal variation in water temperature in places removed from the site of upwelling, i.e., the zone between lat 1° and 5°N. In this zone, the presence of cooler water must mean that the wind-driven northward movement was or is more vigorous and that the water there has been more recently enriched and has been in the euphotic zone for a shorter period of time. Consequently, it should contain more phosphate, more plankton, and fewer yellowfin tuna. Warmer water must have been longer in the euphotic zone, perhaps the result of a slowing of the wind circulation, and should contain less phosphate, less plankton, and more yellowfin tuna.

Phosphate.—If the hypothesis outlined above is correct, the concentration of phosphate in the ocean water north of the equator should be less in warmer water than in colder water, without regard to the time of sampling or place of sampling, providing consideration is restricted to the zone between upwelling and the Countercurrent
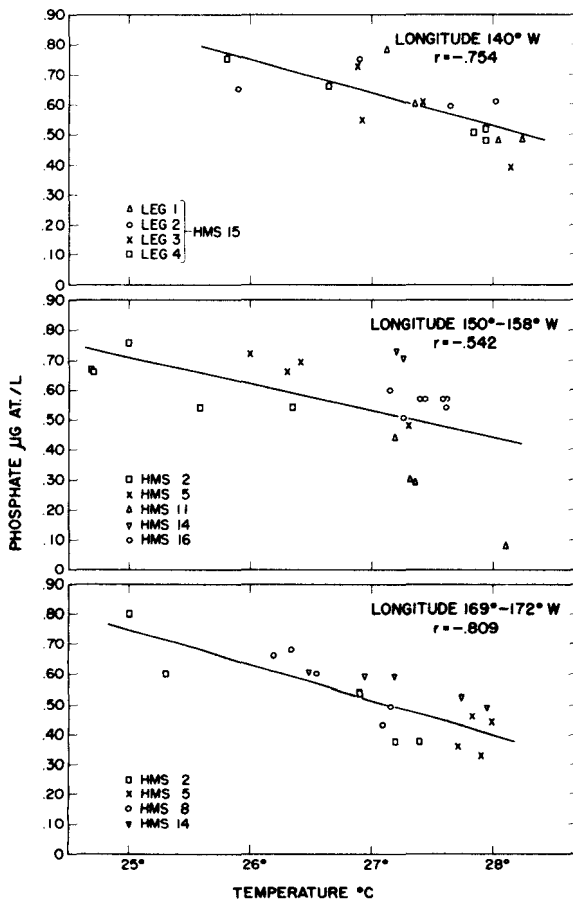
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[6] It might be argued that surface temperature does not represent any substantial body of water. Fortunately, in the zone north of the equator the surface temperature is generally representative of the entire mixed layer, providing the effect of diurnal heating is suppressed. This has been done by using temperatures measured at about 9 m below the surface.

FIGURE 27.—Relations between temperatures and inorganic phosphate between lat 1° and 5°N.

TABLE 3.—Relation of temperature to phosphate in the zone of lat 1° to 5°N[1].

Longitude	Number of sections	Number of paired observations	Correlation coefficient (r)	Probability
140°W	4	17	—0.754	<0.01
150°-158°W	5	22	—0.542	<0.01
169°-172°W	4	19	—0.809	<0.01
180°	1	5	—0.833	>0.05
All observations	14	63	—0.377	<0.01

[1] Data from Cromwell (1954), Austin (1954a, b), and Stroup (1954). Each temperature and phosphate measurement is from the Nansen bottle immediately below the surface bottle, generally at about 10 m.

curve skewed to the right, for time should elapse between enrichment and peaking of the copepods that form the bulk of the catches. We already know, however, that the peak of zooplankton is coincident or nearly so with the center of upwelling, and since we have restricted ourselves to the zone north of the upwelling (lat 1°-5°N), we should expect to find only the descending limb of the curve.

The plots in Figure 28 indicate a significant negative relation between temperature and zooplankton, though the relation is not as striking as that between temperature and phosphate. Some of the variability may be attributable to sampling errors and some to systematic errors, such as day-night variation. As in the instance or the phosphate, the values of the correlation coefficients are higher (except for long 140°W) for the individual sections than for the data as a whole (—0.472, —0.718, —0.679 versus —0.567 for all data).

Yellowfin tuna.—We have shown that maturity of the water, as indicated by the temperature of the mixed layer, appears significantly related to the amount of dissolved nutrients (phosphate) and the amount of zooplankton. It remains to project this reasoning up the trophic levels to yellowfin tuna. Probably one or more trophic levels must intervene between the zooplankton sampled and tuna, for King and Demond (1953) showed the zooplankton to be mainly copepods, and Reintjes and King (1953) showed that, although yellowfin tuna consume a variety of organisms, the bulk of their diet is composed of squid and fish.

and also providing single or closely adjacent longitudes are considered.

Unfortunately, there is not enough material available for a rigorous examination of surface temperature-phosphate ratios. The available data (Figure 27) between lat 1° and 5°N behave in a manner consistent with the hypothesis. Along each longitude is the expected negative regression with respect to temperature. The heterogeneity among longitudes is indicated by the reduced value of *r* (Table 3) when all data are considered together.

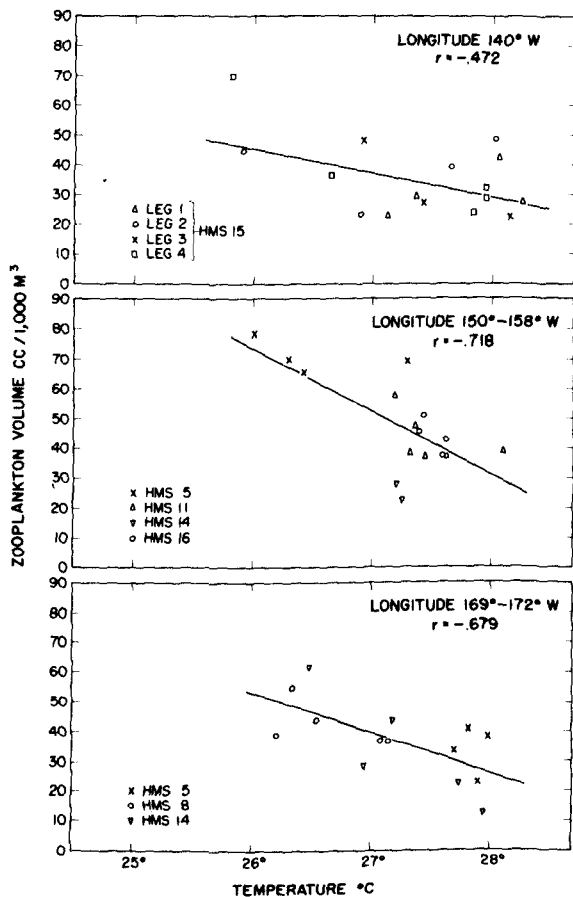*Zooplankton.*—The relation between temperature and zooplankton should theoretically be a

FIGURE 28.—Relation between temperature and zooplankton abundance between lat 1° and 5°N.

In attempting to specify the expected relation between yellowfin tuna and water maturity (temperature), it is helpful to start with the tuna and work back through the trophic levels. The tuna are highly motile and are capable of concentrating where food is most abundant. That is, they are not restricted to development in situ in a mass of water. To a lesser extent some of their food organisms (the larger squid and fishes) are undoubtedly able to concentrate in favorable areas that they discover either by following gradients or by random movements. It seems extremely unlikely, on the other hand, that the members of the next lower trophic level (or-

ganisms that feed on the small zooplankton) are capable of long migrations.

If this intermediate link is incapable of migration, it must develop in situ; it must be, at least indirectly, responsible for grazing down the "net zooplankton" which we measure, and because of the time needed for growth, it must reach a climax at some time after the zooplankton. Thus, we expect the forage for tuna to keep improving for some time after the zooplankton has reached its maximum development.

Since the water is warming during this period, there should be a positive relation between temperature and yellowfin tuna abundance until the water reaches senescence, at which point further increases in temperature should be accompanied by a decline in yellowfin tuna abundance. It appears, however, that actual senescence is never attained, at least in the portion of the system under study (long 120°-170°W). Instead, water probably is withdrawn from the system through convergence and possibly by the Countercurrent before reaching senescence, or even possibly before reaching maturity.

When fish catches are plotted against temperature (Figure 29), a striking relation is shown between maturity of the water (as measured by temperature) and abundance of yellowfin tuna. The measure of abundance of the tuna requires some explanation. As shown by Murphy and Elliott (1954), the catch at a single longline station is subject to very wide sampling errors—so wide in fact that any relations between catch and variables in the environment are likely to be poorly defined. For this reason the several catches in the zone of lat 1° to 5°N, during a single crossing, are considered as a unit. This treatment, in addition to suppressing sampling error, also has the advantage of directing attention to a zonal situation rather than to a point in the ocean, thereby eliminating the possible effect of other regressions along a meridional section. The temperature index parallels the tuna index in that it is also the average surface temperature over the lat 1° to 5°N zone.

Returning to the temperature-yellowfin tuna regressions, the steep slopes on long 120° and 130°W suggest a positive relation between maturity and catch. At long 148° to 155°W the
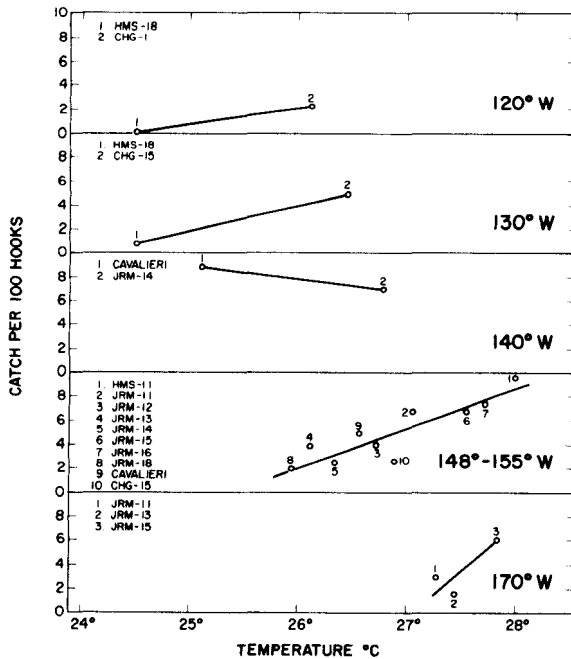
FIGURE 29.—Relations between yellowfin tuna catch and surface temperature at several longitudes for the zone lying between lat 1° and 5°N.

FIGURE 30.—Temperatures and fish catches between long 148° and 155°W plotted against time, 1951-54.

relation is striking and highly significant, and finally on long 170°W the positive relation is again suggested. Thus, with the exception of long 140°W, all of the fish catch data agree with the hypothesis that time variations can be explained in terms of the maturity of the water and that variations in the biota can be estimated by water temperature in this region.

The single exception (long 140°W) appears atypical in other respects. Good catches of tuna were obtained in relatively cool water, but the fishing evidently coincided with a time of rapid change; a few days after the good fishing the water cooled further and the fishing became poor. Thus, the good fishing occurred during a change from environmental conditions associated with good fishing to those associated with poor fishing. During such transitions we might expect irregularities in the relation between water maturity and catch.

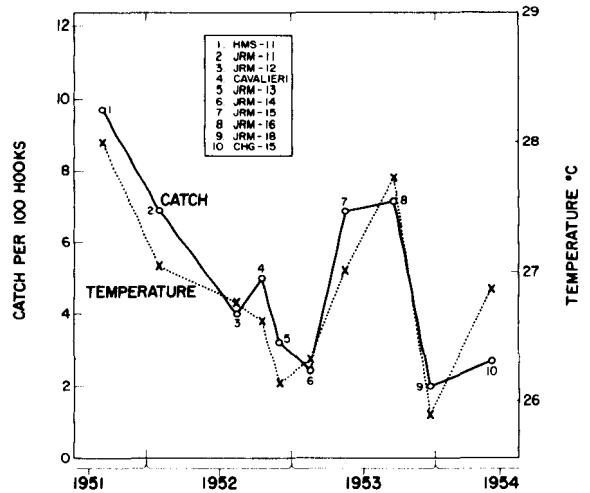The fish catches and temperatures at long 148° to 155°W plotted against time from 1951 to 1954

(Figure 30) reveal the basic relation shown in Figure 29. Generally cooler water and poorer fishing are indicated, however, in 1951-54. Superimposed on this trend is a suggestion of rising temperatures during the first half of each year and falling temperatures during the second half. These bear some resemblance to the average trends given in Table 2, but, insofar as these data are adequate, a long-term trend to cooler water appears to have almost completely suppressed the seasonal trend during 1952, thus pointing up the difficulties attending "seasonal analysis" in the equatorial area.

Temperature profiles.—It is instructive to examine the shape of the several meridional surface temperature profiles at long 148° to 155°W, because the average temperature that was compared with yellowfin tuna abundance tends to obscure certain important features. The several profiles in Figure 31 suggest that a variety of situations exists.

Two of the profiles (panel A) show relatively cool water from the equator to at least lat 4°N. This "flat" feature at low temperatures suggests very active upwelling and a northward displacement of immature water; therefore, it is not surprising that these two transects are associ-

ated with the lowest catch rates shown in Figures 29 and 30.

A second group of three profiles (panel B) has in common cool water at the equator and a steep gradient rising from south to north. This steepness of the gradients also suggests active upwelling and northward movement, and the average low water temperature implies the presence of immature water. Like the two profiles shown in panel A, these three are also associated with poor catch rates.

The profiles in the last group (panel C) show relatively little gradient, at least from lat 1.5° to 5°N. Such "flat" profiles at high temperatures should arise if upwelling and northward movement of water has slowed down, possibly in response to a shift from southeast to northeast winds or simply a marked decline in wind force. The four high catch rates shown in Figures 29 and 30 were obtained during these four periods.

The nature of the sequence of events leading to a relatively high abundance of yellowfin tuna can be inferred from the temperature profiles. First a body of enriched water should be created, and this body of water should be permitted to mature relatively undisturbed; that is, the north-south system should be slowed down. The distribution of the winds (Figure 20) suggests that such a sequence of events is most apt to occur in the central portion of the area (long 140°-160°W). In the east, southeast trades of high velocity persist during most of the year, possibly creating a south-to-north circulation with attendant convergence of such vigor that the water rarely matures in terms of tuna forage production. In the center, the southeast trades still have the substantial velocity needed to induce upwelling, but their frequency is only about 50%, suggesting there is frequently an opportunity for the water to mature. In the far west, neither
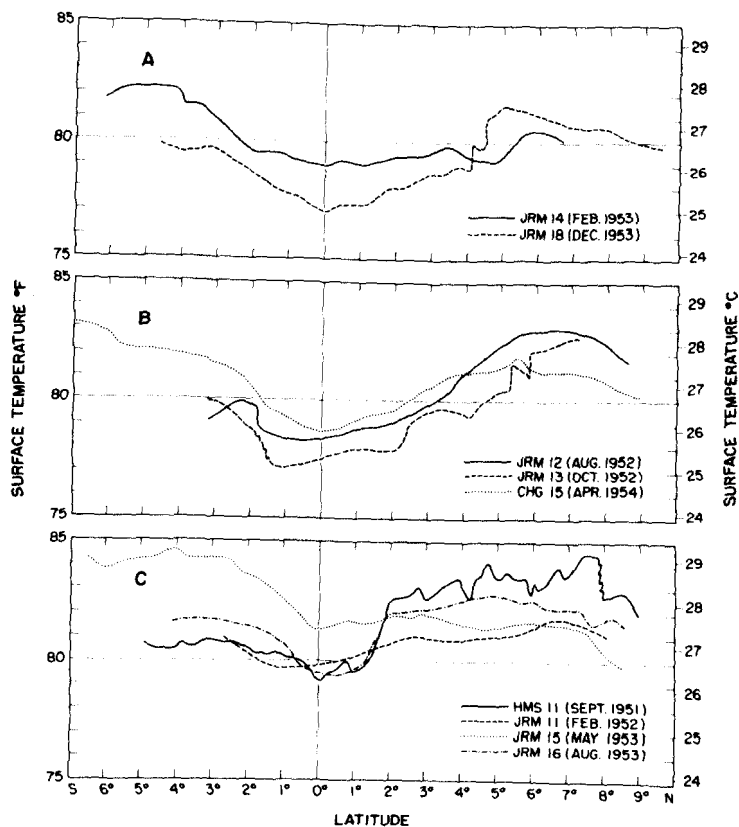

FIGURE 31.—Surface temperature profiles on longline fishing cruises along long 148° to 155°W. A. Low temperatures between lat 1° and 5°N. B. Low temperatures and a steep north-south gradient between lat 1° and 5°N. High temperatures between lat 1.5° and 5°N.

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the velocity nor the frequency of the southeast trades appear high enough to create substantial bodies of enriched water north of the equator.

We now have two processes that might account for poor yellowfin tuna fishing in the east and west and good fishing in the center. The one, involving the wind pattern just described, rests on the assumption that if enriched water is to result in a dense population of yellowfin tuna, it must remain relatively undisturbed in the euphotic zone long enough for a forage population to develop. The other, discussed in the section on nutrients, is based on the vertical distribution of phosphate at various longitudes along the equator. Phosphate distribution, when viewed against the wind distribution, suggests that the absolute amount of enrichment might be greatest in the center of the area, and it is in this area that the enriched water appears to have a reasonable chance to mature before convergence. The two processes are independent but interact in a way consistent with the occurrence of the best yellowfin tuna fishing in time and space.

In addition to variation in the catch rates at a given longitude, there have been changes in the meridian of the best catches. For the year 1953 there are enough records to illustrate this phenomenon (Figure 32). Such shifts are in harmony with the present theories of the factors controlling yellowfin tuna abundance. The yellowfin tuna are highly motile, and we expect them to be most abundant where conditions best suit them. For instance, if upwelling is too vigorous over the area from long 120° to 150°W and less vigorous farther west, conditions should be better in the west. This situation may well explain the pattern in May-June of 1953 (Figure 32). On the other hand, in August 1953 yellowfin tuna seemed to be most abundant near long 155°W; this distribution would be expected if strong upwelling and northward displacement at some time in the past was followed by a period of relative quiet.

These deductions are difficult to test critically, i.e., it is difficult to make a critical comparison between fish catch and some factor in the environment such as temperature because of the heterogeneity of the water when considering the equator as a whole. However, there is a suggestion of an association in our data: During February-April 1953 (Figure 32) the catch was better on long 140°W than on long 150°W, and at the same time the mixed layer was about 0.5°C lower on long 150°W than on long 140°W. This is a reversal of the average trend (Figure 23) and could only have resulted from the water at long 150°W being more recently affected by upwelling and northward displacement than that at long 140°W. In perfect agreement with our hypothesis, this relatively newer water at long 150°W had a smaller population of tuna.

In summary, it has been possible to develop a functional hypothesis consonant with the mechanics of the equatorial system that can logically account for all, or nearly all, of the major observed variations in the abundance of the large deep-swimming yellowfin tuna. The theory successfully embraces variations in catch rate in respect to time and in respect to space. Since the root of the system lies in the winds, it should be possible eventually to anticipate the variations in the yellowfin tuna population by examining variations in the wind regime.

SURFACE TUNAS

The principal methods we have used to sample surface tunas are surface scouting and trolling. Live-bait fishing has also been used occasionally. These are the same methods used to locate tunas by the several live-bait and purse-seine fisheries in the Pacific.

Each of these survey methods has inherent weaknesses that cannot be estimated quantitatively. Perhaps the greatest difficulty in surface sighting lies in the state of the sea. The central Pacific is nearly always choppy, practically precluding detection of schools at the surface unless they are breaking water or are accompanied by feeding birds, e.g., in our experience 85% of all schools were first sighted through the accompanying "working birds." In effect, we do not see tuna unless their presence is marked by birds; this relation casts doubt on the census method. The problem, however, may not be as serious as it seems, for the association between birds
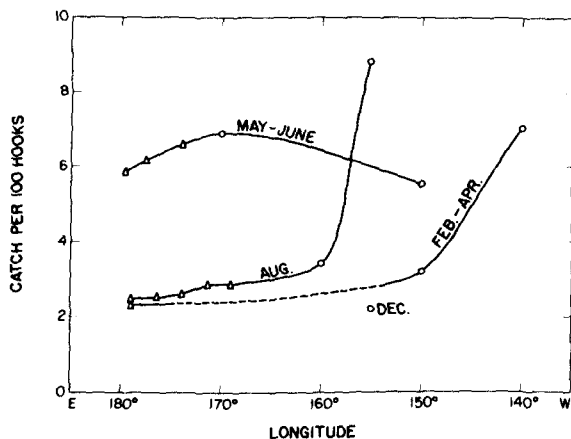
FIGURE 32.—Catch rates of yellowfin tuna by longitude and by time of year (1953).

and fish may have a firm biological basis in that feeding tunas, by driving small fish and squid to the surface, appear to be an important factor in making food available to birds.

The observed behavior of working bird flocks substantiates this contention. A bird flock may be first seen when it is feeding over a school, the birds excitedly circling close to the sea surface and frequently plummeting into the sea to capture prey. Subsequently, the school may sound and the birds discontinue feeding, scatter somewhat, and rise to a higher elevation as though scouting for the school. As soon as the school appears again at the surface, the birds quickly assemble over it and resume feeding. This relationship suggests that the abundance of pelagic predators such as tuna may directly affect the abundance of birds by controlling the amount of food available to them. Insofar as this is true, bird abundance should form an index of fish abundance.

On the other hand, it is difficult to discount completely the possibility of introducing error through the use of birds as an indicator of fish, for the frequency of sightings of both birds and fish is everywhere parallel (Murphy and Ikehara, 1955), and it seems unlikely a priori that the populations of both need always be parallel. For instance, birds and fish are seen more frequently around islands than far at sea. Oceanic

birds nest on land, thus tending to make islands focal points for their populations; but, is the vicinity of land also a focal point for tuna schools? Perhaps so, for nesting birds have an even greater demand for food than wandering birds, and thus the magnitude of their concentrations around islands must be based on the food supply too and, to the extent that they obtain their food over schooling tunas, on the abundance of schools of surface tunas.

Aside from the problem of just what surface sightings mean in relation to tuna abundance, the validity of conclusions based on relatively scanty sampling of so vast an area as the central Pacific (Figure 3) can be questioned. The only available test, a comparison of sightings from the Laboratory's vessels with the seasonal changes in Hawaiian commercial landings (Figure 33), shows that in general a seasonal prediction based on our relatively scanty observations would have been borne out by the commercial catch. Thus, it appears that rather limited scanning of the sea can yield results compatible with those from a very large amount of effort (the commercial fishery).
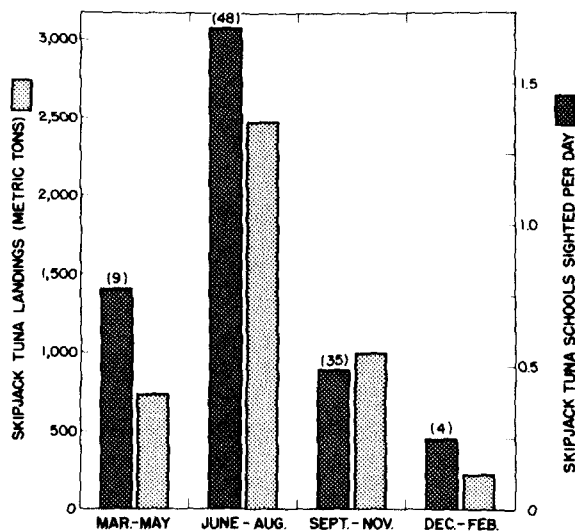

FIGURE 33.—Comparison between average Hawaiian skipjack tuna landings (1950-52) and surface sightings of skipjack tuna schools (number of schools sighted noted above bar diagrams) from research vessels in the Hawaiian Islands area (data from Murphy and Ikehara, 1955).
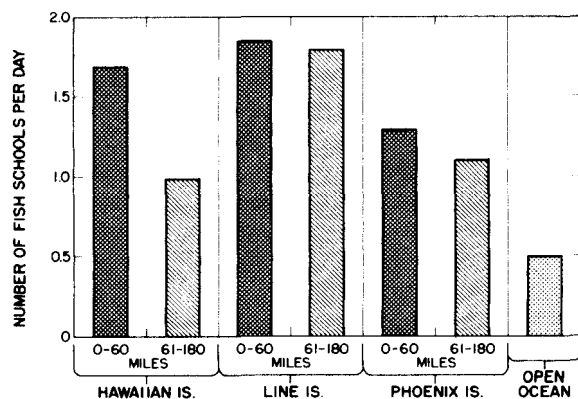
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FIGURE 34.—Frequency of sighting fish schools in various zones (distance from land) and areas of the central Pacific (data from Murphy and Ikehara, 1955).

Systematic trolling is a well-known and established method of quantitatively surveying the availability of surface fish. The only serious flaw in our data has been the difference in availability to troll lures of the principal surface species, skipjack and yellowfin tunas (Murphy and Ikehara, 1955). For instance, near the Hawaiian Islands half as many yellowfin tuna were taken by trolling as skipjack tuna, whereas other measures, e.g., the commercial catch (June, 1951), suggest that there are only about one-tenth as many yellowfin tuna as skipjack tuna.

DISTRIBUTION OF SURFACE TUNAS RELATIVE TO LAND

The general abundance of surface schools depicted in Figure 34 shows that schools are seen several times more frequently near islands than in the open ocean. This can be interpreted as merely indicating the abundance of birds, but, as is shown later, it is also possible to regard the islands as creating in their vicinity special conditions that are conducive to the occurrence of surface-schooling tunas.

In addition to differences in abundance between island waters and the open ocean, species composition appears to shift, in that yellowfin tuna schools tend to favor the vicinity of islands (Figure 35). About 47% of all schools sighted
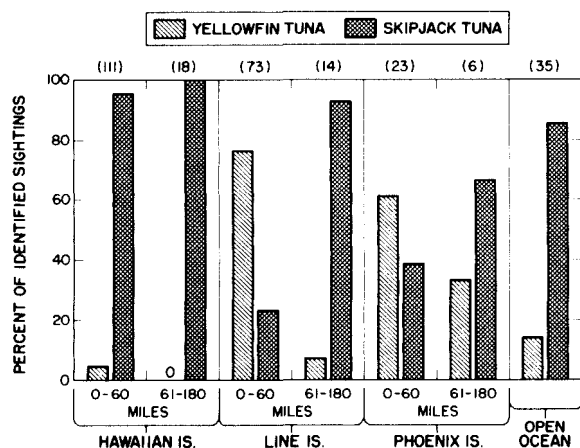

FIGURE 35.—Relative occurrence of yellowfin and skipjack tuna schools at various distances from land. Number above bar diagram represents total number of schools sighted.
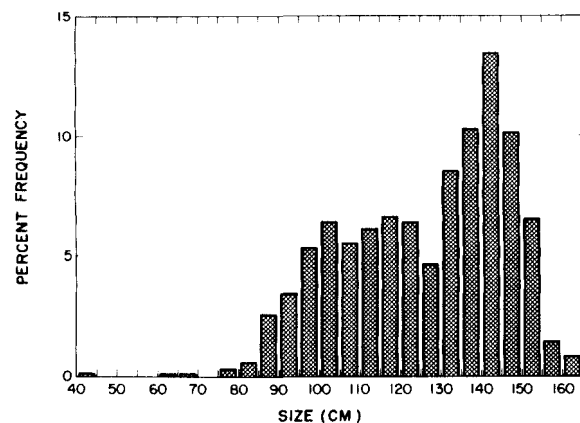

FIGURE 36.—Length frequency of longline-caught yellowfin tuna at all insular fishing stations (within 96.5 km of land).

were identified as either yellowfin tuna or skipjack tuna, a small percentage were identified as other species, e.g., the common dolphin, and the rest were unidentified (Murphy and Ikehara, 1955). The relative percentages of the two important species plotted in Figure 35 show very clearly that (1) skipjack tuna are dominant in the Hawaiian Islands area and in all offshore areas, and (2) in each instance relatively more

yellowfin tuna schools are found near land than offshore. In fact, in the Line and Phoenix groups yellowfin tuna appear to have replaced skipjack tuna near land. Thus the presence of land seems to create favorable circumstances for the occurrence of tuna schools in general and yellowfin tuna schools in particular.

This distribution of yellowfin tuna in relation to land is also borne out by longline catches of yellowfin tuna near land and offshore. Figure 36 shows that when longline gear is fished near islands it catches more of the smaller yellowfin tuna that compose surface schools than it does when fished offshore (compare Figure 36 with Figure 4). This increased abundance of small yellowfin tuna near islands is also shown in Figure 37, which indicates that about half of the increase in longline catch rates near shore stems from the addition of small fish to the catch. Furthermore, the increase in small fish in the longline catches is roughly proportional to the increase in the rate of surface sighting of this species near land. A final indication that small yellowfin tuna are more abundant near land is that surface trolling took 10 times as many yellowfin tuna per unit of effort within 96.5 km of land as beyond that limit (Murphy and Ikehara, 1955). Since all three sampling methods—longlining, sighting, and trolling—clearly show small surface yellowfin tuna to be more abundant near land, we conclude with little or no reservation that the occurrence of young yellowfin tuna in the central Pacific is intimately related to the presence of land.

OCEANIC DISTRIBUTION

Despite the low average abundance of tuna schools in the open ocean (Figure 34) certain areas or zones appear to support populations with a density comparable to that of the island areas. Over most of the central Pacific our sampling is not adequate to focus attention on particular areas except in the central portion of the study area (long 140°-170°W). Here, there are enough days' observations to make meaningful zonal comparisons (Figure 38A). It is apparent that the number of schools sighted in some
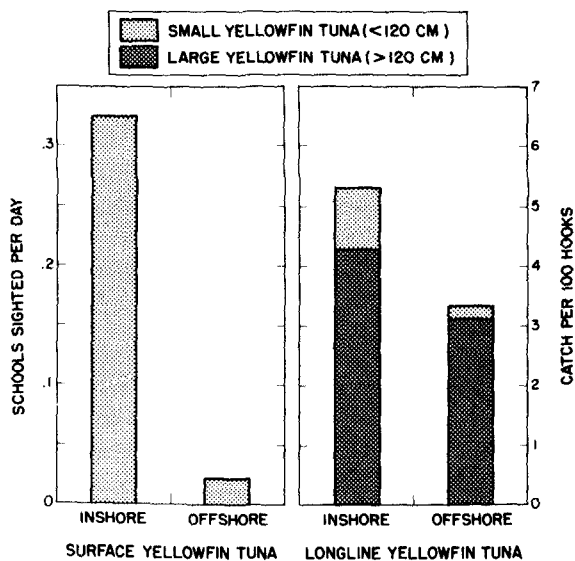

FIGURE 37.—Relative occurrence of schooling yellowfin tuna in surface sightings and longline catches for inshore and offshore areas.
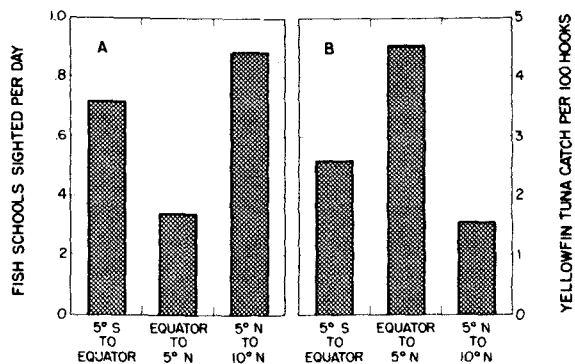

FIGURE 38.—Latitudinal distribution of surface tuna schools and deep-swimming yellowfin tuna. A. Sightings of surface tuna schools in the open ocean (Murphy and Ikehara, 1955). B. Yellowfin tuna catches from fishing stations more than 96.5 km from land and between long 140° and 170°W.

of these zones is nearly the same as for the Hawaiian Islands area, e.g., 0.9 school seen per day in the Countercurrent (Figure 38A, lat 5°-10°N) and 1.7 near the Hawaiian Islands (Figure 34). Considering how far removed these zones are from land, we might conjecture that considerably more schools would have been sighted if

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more birds had been available. Such pelagic populations as these must represent a vast untapped resource, judging from the 5,000 tons or so taken annually in a limited area around the Hawaiian Islands (June, 1951).

The distribution of oceanic schools is at variance with the distribution of deep-swimming yellowfin tuna (Figure 38B), the most striking differences being the high density of schools in the Countercurrent (lat 5°-10°N) and south of the equator. In fact, the distribution of surface schools is almost the inverse of the distribution of deep-swimming tunas. This apparent inverse relation poses a serious problem, for a priori we would expect surface schools to respond to the equatorial enrichment in the same manner as the deep-swimming tunas.

The problem can be approached by considering the environmental factors that make it possible for an area to support large numbers of surface schools. The obvious one that comes to mind is the standing crop of forage, as indicated by zooplankton. We have already indicated, however, that zooplankton tends to peak at the equator (Figure 25), and thus food supply as indicated by the standing crop of zooplankton does not account for the north-south distribution of surface fish. In a possibly parallel situation, King and Hida (1954) found little or no more zooplankton around the Hawaiian Islands than in the North Pacific Current and were unable to account for the population of skipjack tuna around Hawaii on the basis of the standing crop of zooplankton.

A suggestion of an important environmental factor controlling the abundance of skipjack tuna was given by Robins (1952), who found a positive association between skipjack tuna troll catches and temperature discontinuities or "fronts." The circulation associated with fronts involves horizontal convergence and sinking, according to Cromwell (1956). This type of movement could act to concentrate organisms, particularly those that float or can actively resist sinking. Fronts might act as modifiers of the average standing crop by altering its distribution in space so that fishes can more effectively forage.

The effect of fronts on the distribution of for-

age might account for the abundance of schools near islands. An island mass in a moving ocean current must set up patterns of "frontlike" circulation cells and eddies, as has been shown for the Hawaiian Islands (McGary, 1955). These features, although perhaps not increasing the basic supply of food, should concentrate some of it so that fish can feed more efficiently.

In an effort to determine whether this same mechanism could be offered as an explanation of the irregular distribution of surface schools in the equatorial region (Figure 38), we determined the frequency of temperature irregularities at the sea surface, confining ourselves to the best-sampled zones, i.e., lat 5°S to 10°N, long 140° to 170°W. The frequency of occurrence of temperature irregularities or "fronts" was estimated from thermograph traces made while the ships were crossing the equatorial system in a north-south direction. An irregularity was simply defined as a temperature change that was completed during 15 min or less when the ships traveled at a speed of about 8 knots, i.e., long, even temperature clines were not considered. If the temperature rose (or fell) quickly to a new level, this was counted as one "front." If it both rose and fell during any interval, it was counted as two "fronts," providing the rise and the fall each took no more than 15 min.

An inquiry can logically be made into the relation of wind velocity to the number of such fronts, for on calm, hot days there may be many irregularities caused by convection currents set up by diurnal heating. A plot of wind force against the number of fronts in unit time, however (Figure 39), suggests that we are dealing with phenomena that are independent of the immediate wind stress and heating.

When we compare the rate of crossing fronts with the rate of sighting surface schools, we find a remarkable correspondence (Figure 40), enabling us to advance the same explanation for differences in abundance of surface schools among different areas of the open ocean and between the vicinity of islands and the open ocean. The responsible feature of the environment, the "front," meets the test of biological and physical logic, for temperature fronts are symptomatic of horizontal movement of water toward the dis-

continuity and sinking at the discontinuity, a mechanism that should concentrate certain types of tuna forage or food for tuna forage.

We are still confronted with the basic difference in the distribution of surface and deep-swimming tunas (Figure 38), though we have logically advanced two hypotheses that seem adequate to explain each distribution pattern when the problems are considered independently, i.e., basic enrichment and northward drift of upwelled water in the instance of the deep-swimming tunas, and "fronts" in the instance of surface schools. An entering wedge is offered by the difference in social behavior between the deep-swimming and surface schools.

Sette (1950), in discussing mackerel, proposed that schooling was advantageous to any predator feeding on prey that was aggregated. In fact, the very existence of schools of carnivores would seem to require schools or aggregations of prey, for if prey were distributed at random, it could be most effectively harvested by pursuit and capture of individuals by individual predators. In other words, where we find scattered prey we should expect scattered predators. In the present instance, where we have a mechanism ("fronts") for concentrating prey, we find surface schools, and where the mechanism is not present we do not find the schools. The deep-swimming tunas, on the other hand, are not aggregated into large, compact schools (Murphy and Elliott, 1954) and so might be expected to use more or less scattered forage organisms more efficiently, and the distribution of such tunas might be expected to conform more closely to the mean distribution of forage, rather than the distribution of concentrating mechanisms.

SUMMARY

1. Surveys of tuna populations and environmental conditions were made in the equatorial central Pacific in 1950-53.

2. Tunas were sampled by longline, trolling, live-bait fishing, and sighting from the bridge of a research vessel.
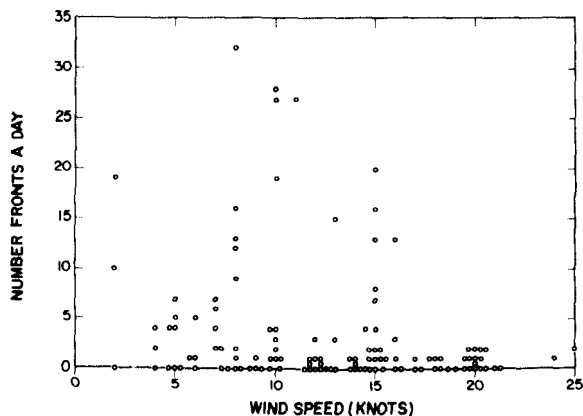
3. The longline was used more than the other

FIGURE 39.—Daily frequency of fronts as a function of daily noon wind speed (lat 5°S-10°N, long 148°-170°W).
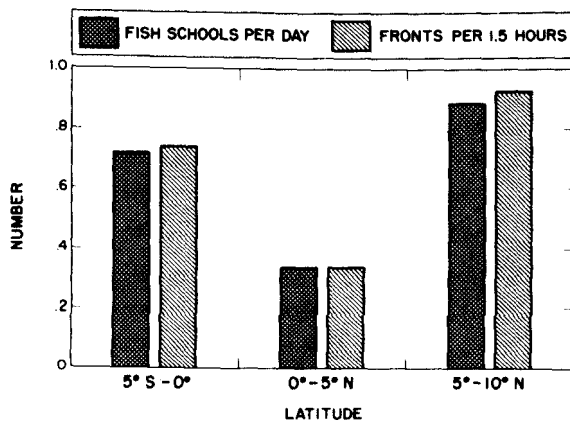

FIGURE 40.—Rate of crossing temperature discontinuities and rate of sighting fish schools near the equator (vessel speed about 8 knots, vessel course always north or south). Longitudinal limits 140° to 170°W.

methods of fishing, because it was the most consistently productive sampling method, particularly on the high seas.

4. Tunas, especially yellowfin tuna, may be divided into two groups, small surface-swimming tunas and large deep-swimming tunas.

5. On the basis of longline catches, deep-swimming yellowfin in the central Pacific were most abundant near the equator.

6. Deep-swimming bigeye tuna were nowhere as abundant as yellowfin tuna. Two tongues of

relatively high bigeye tuna catches occurred in the equatorial Countercurrent.

7. Deep-swimming albacore were most abundant in the southwestern area, e.g., around lat 5°S, long 170°W.

8. Skipjack tuna were found over the entire area.

9. Deep-swimming yellowfin and bigeye tunas were larger in the east (e.g., 120°W) than in the west (e.g., 130°E). The reason for this difference is obscure.

10. Analyses of tuna catches and properties of the environment in a meridional plane revealed the following: There is upwelling and enrichment at the equator; the upwelled water is displaced northward; zooplankton peaks are at the center of upwelling, apparently because of a time lag in the development of tuna forage.

11. The water flow near the equator differs from the classical concept in that empirical measurements suggest the northward motion is of the same magnitude as the westward motion. Thus the South Equatorial Current just north of the equator should be regarded as a series of parallel, homologous, northwesterly flow systems.

12. Variation in surface temperatures at the equator is a function of surface winds, through alteration of the rate of upwelling.

13. Interaction of geographical variation in the vertical distribution of nutrient salts and the geographical distribution of wind stress cause the greatest enrichment through equatorial upwelling to occur in the central area (near long 140°W).

14. In the area surveyed, between long 120°W and 180°, both zooplankton and yellowfin tuna were most abundant near the center of the area (near long 150°W).

15. When northeast trades prevail, yellowfin tuna seem most abundant south of the equator; during southeast trades, north of the equator; and during variable winds, the peak abundance straddles the equator.

16. Between the equator and the Countercurrent the presence of colder water is associated with more phosphate, more zooplankton, and fewer yellowfin tuna. Warmer water is associated with less phosphate, less zooplankton, and more yellowfin tuna. We believe that these differences are a reflection of the time lapse since enrichment and that variations at a geographical locality are in response to variations in wind flow that affect the rate of upwelling.

17. There are suggestions of annual seasonal variations in the abundance of yellowfin tuna near the equator, but these may be masked by longer term secular trends.

18. Changes in abundance at a point on the ocean may result from east-west shifts in the yellowfin tuna population as well as north-south shifts, or simply general dispersion from or concentration at that point. All of these variations may be logically attributed to variations in the enrichment at the equator, brought about by variations in the winds.

19. Surface tunas are seen more often close to land, possibly because more birds are present there.

20. In the equatorial central Pacific, yellowfin tuna tend to predominate in surface schools close to land and skipjack tuna far from land.

21. Near the equator, the abundance of surface schools does not seem to coincide with the peaks in abundance of the deep-swimming tunas. Food concentrating mechanisms appear to be more important than basic food supply in affecting the local abundance of surface-swimming schools.

ACKNOWLEDGMENTS

Sette, several other persons devoted thought and time to the formulation of the program. Chiefly, these are Donald L. McKernan, Thomas S. Austin, and the late Townsend Cromwell.

O. E. Kerns and Frank Williams reviewed the manuscript.

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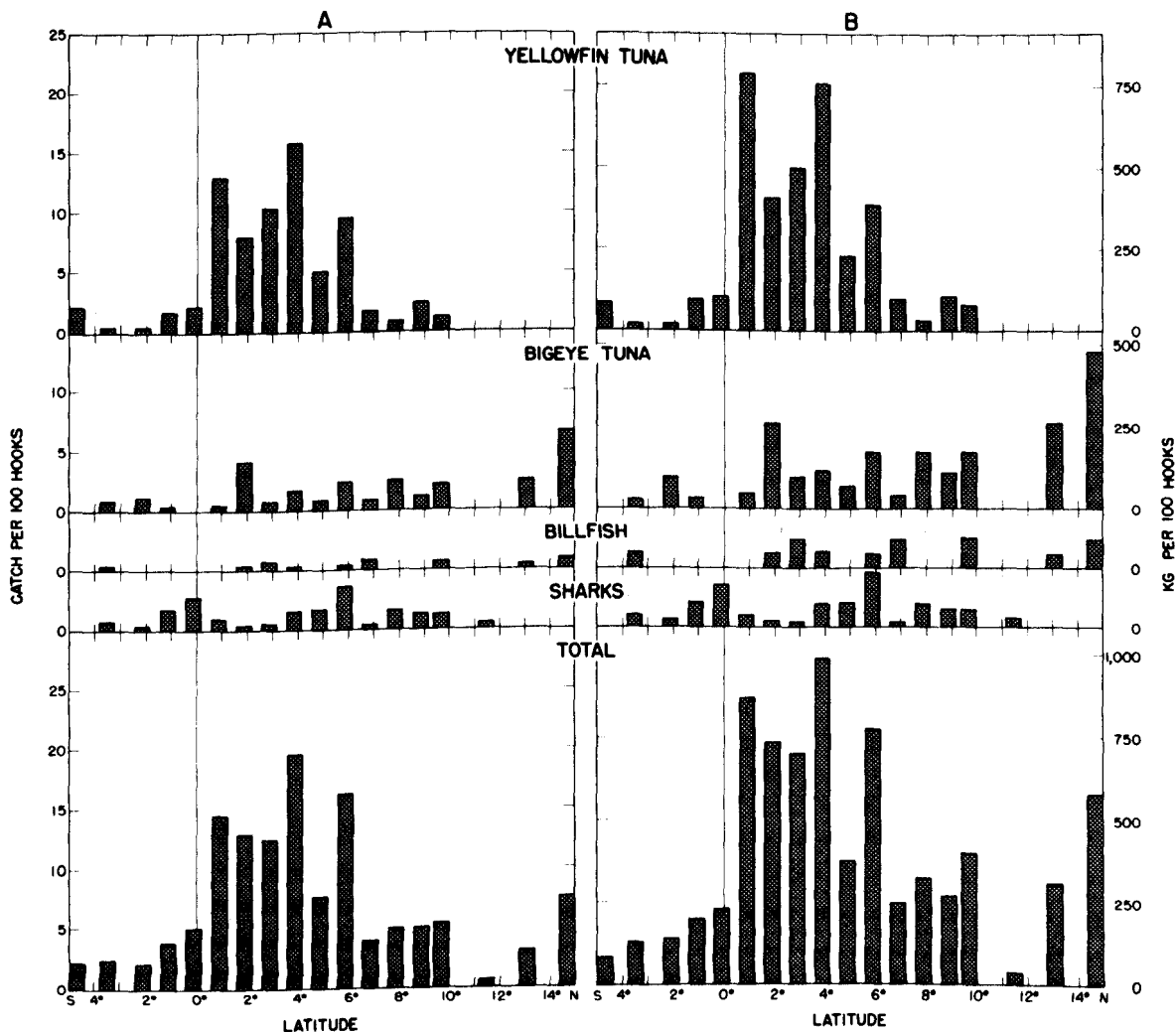
APPENDIX A

VALIDITY OF YELLOWFIN TUNA AS AN INDEX OF THE TUNA-SHARK TROPHIC LEVEL

Throughout this paper we have compared the distribution of tuna with the distribution of certain biological and physical properties of the environment. We have examined these environmental properties in relation to the number of yellowfin and other tuna captured per 100 hooks.

This procedure could lead to misinterpretation, if the size of the individuals taken varies significantly or if the relative abundance of species within a trophic level changes with respect to time or space.

Ideally, we wish to ascertain the relative

APPENDIX FIGURE 1.—Latitudinal distribution of longline-caught fish on long 150°W during August-September 1951, a period of good fishing success. A. Number of fish per 100 hooks. B. Weight (in kilograms) per 100 hooks.

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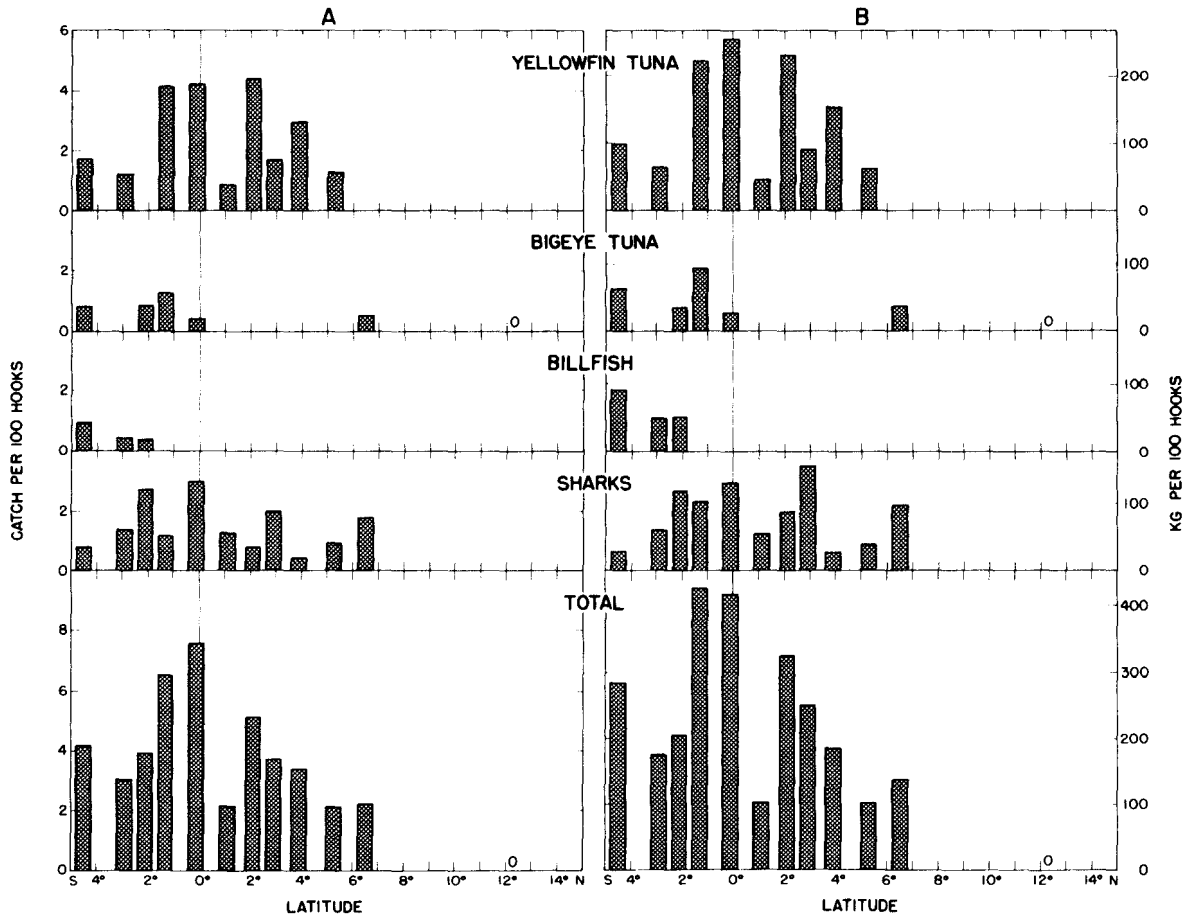
APPENDIX FIGURE 2.—Latitudinal distribution of longline-caught fish on long 150°W during January-February 1953, a period of poor fishing success. A. Number of fish per 100 hooks. B. Weight (in kilograms) per 100 hooks.

weight of fish life at a given trophic level and compare that weight with other properties of the biosphere, e.g., standing crop of zooplankton. Uniform sampling of a given trophic level, especially if it comprises several species, is difficult. In the longline, however, we have a tool that appears to sample a reasonably restricted trophic level. All of the principal species taken are definitely carnivorous, as shown by their attraction to fish baits, so this characteristic defines and restricts the "trophic level." In the present instance the trophic level is composed principally of tunas, sharks, and billfishes.

Additional information that aids in defining the trophic level stems from studies of the food habits of the fishes. King and Ikehara (1956) have shown that the yellowfin and bigeye tunas in the central Pacific essentially share a common diet of small to medium-sized invertebrates and fishes. Recent studies suggest that the same statement applies to the skipjack tuna and albacore. Most pelagic sharks taken on the longline in the central Pacific also seem to share the tuna forage (Strasburg, 1958). Large billfishes, however, appear to represent a somewhat higher trophic level. The smaller items in their diet approximately coincide with the large items in the diet of the tunas and sharks. Thus, there are good grounds for considering tunas and sharks as representatives of a restricted trophic

level, but the inclusion of billfishes is open to question.

On the subject of numbers of fish versus weight, Appendix Figures 1 and 2 depict the results of two section lines along long 150°W, one representing good and the other poor fishing. The members of each pair of panels give the same impressions. In the first series abundance is very high between lat 1° and 6°N and considerably lower to the north and south. In the second series the total abundance is much lower, but the catches definitely peak between lat 2°S and 4°N. The inclusion or omission of the billfishes, thought to represent a slightly higher trophic level than the tunas and sharks, has little effect on the major trends.

We may draw two important conclusions from the plots of number and weight. Because the trends are nearly the same, the average size of each of the component species must change little, if at all, with latitude. Even more important, it is apparent that latitudinal variations in catch are largely a function of variations in yellowfin tuna abundance, particularly between lat 5°S and 5°N, the general area in which this study has been focused. Because the yellowfin tuna is the most important species in this region, we lose little biologically and gain much in ease of understanding by restricting comparisons of the fish population and the environment to yellowfin tuna.

One flaw in these arguments for considering yellowfin tuna only is our failure to take into account the skipjack tuna, for it almost certainly belongs to the same trophic level as the yellowfin tuna. Although small yellowfin tuna are almost absent from longline catches in the oceanic areas under consideration, skipjack tuna are strongly represented. In fact the available evidence suggests they are abundant to the north of the concentration of yellowfin tuna (lat 5°-10°N). We can offer no satisfactory solution, for it is not yet possible to combine quantitatively measures of abundance of deep-swimming fishes with those of surface fishes. In our opinion, however, if it were possible to add skipjack tuna to the weight diagrams of Appendix Figure 2, there would be little change in the relative distribution of the tuna-shark trophic level near the equator.